Scientific editors

Didier Paugy Christian Lévêque Olga Otero

The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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RMCA/Isabelle Gérard
IRD/Catherine Guedj

Translation and correction
RMCA/Emily Divinagracia

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Cécile Paugy
Pierre Opic

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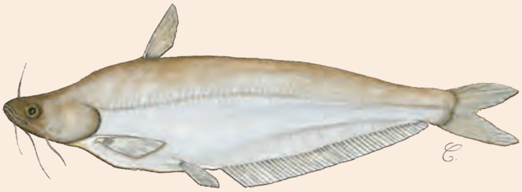
Christian Lévêque

Olga Otero



Since 1992, the International Convention on Biodiversity has emphasized the need for conservation of species and natural environments. Much discussion has involved the biological diversity of tropical forests and terrestrial ecosystems, as well as the consequences, often negative, of human activity on the long-term evolution of these environments. Although freshwaters did not always receive enough attention, their present state is often worrying.

Yet continental aquatic biodiversity displays interesting characteristics:

- a relatively high rate of endemicity, particularly in lakes and rivers that were isolated for millions of years such as the East African great lakes, Lakes Baïkal, Biwa, and Titicaca, as well as the forest basins of the Amazon and the Congo, to name a few;
- high genetic variability between populations of species with an enormous geographic distribution, but occupying hydrographic systems that have been isolated for more or less long periods;
- a disproportionately large number of vertebrates in relation to the surface area occupied by continental waters (0.01% of the planet's waters, for an area of around 1 or 2% of land mass).

Out of some 30,000 known fish species, an estimated 12,800 are freshwater species. The inland waters of the African continent host no fewer than 3,000 fish species and many families of ancient origin.

If we take into account all the other vertebrates (amphibians, reptiles, birds, and mammals) that depend heavily on continental waters to complete their life cycle, then at least a third of these vertebrates are present in the hydrosystems or largely depend upon them.

The very concept of biodiversity presumes that we take an interest in the different levels of biological organization within a hierarchical system: genes, species, communities, and ecosystems. The backdrop of biodiversity has both spatial (stations, ecosystems, regions) and temporal (from the present to millions of years past) aspects. In other words, the diversity we see now is the legacy of the long evolutionary history of species, in an also-evolving climatic and geomorphological context. Research on palaeo-environments and the phylogeny of species help us reconstruct the dynamics of species evolution and distribution, which in turn allow us to interpret and explain the composition of local and regional fauna today.

But biodiversity also encompasses the knowledge of the genetic diversity of species, especially for fragmented populations that are isolated from each other – the case of many widely-distributed species for whom watersheds are, in fact, equivalent to islands. This field, which emerged only in the 1980s with the development of molecular biology tools, is an area of research that has already yielded much new information and become of paramount importance in recent years.

The diversity of biological traits is also a matter of interest. To some, these are adaptive responses to environmental conditions, though within the bounds of the constraints posed by phylogenetic characteristics. Biodiversity's role in ecosystem function is also explored. Do all species play a useful role in ecosystem function? What consequences are derived from the disappearance or, conversely, the introduction of certain species? What are the roles and significance of key species and rare species? All these questions on biological diversity are, in themselves, fascinating research topics.

In Africa, fishes were long preserved from anthropogenic impacts but are now endangered by human activities:

- water planning and management (dams, dikes, channels, etc.);
- industrial, urban, or non-point source pollution;
- overexploitation of existing stocks;
- introduction of exotic species.

The conservation of aquatic biodiversity requires emergency measures practically everywhere in the world, including Africa where, for instance, the fauna of the East African lakes is seriously endangered.

Fishes are in fact an excellent biological model for tackling questions raised by the myriad aspects of biodiversity:

- this biological heritage, of global value, is the fruit of a long evolutionary history; Africa in particular has a large number of endemic species and numerous so-called "archaic" families;
- a wide range of biological and ecological models are available thanks to the variety of life history, space occupation, and resource use strategies, and physiological and morphological adaptations;
- the group is seriously threatened by human activity, either through fishing and the introduction of foreign species, or through physical (landscape planning) or chemical (pollution) changes that affect aquatic environments;
- specific issues regarding fish protection are raised in the context of conservation biology;
- fishes are an economic resource of utmost importance, be it though fishing or aquaculture (and the sole source of protein in some developing countries), or the activities surrounding it in the fields of sport fishing or aquariology.
- fishes are an element of cultural diversity, and may be the subject of myth and tradition.

Wise management of continental waters is a real economic issue for African countries. This book is a synthesis of multiple research activities on African aquatic ecosystems. It compiles the existing information on African fishes, which displays a broad diversity of biological models. It provides a synthesis of biological and ecological data needed to cope with conservation.

Six main themes are developed in this book:

- diversity of aquatic environments (p. 12 to p. 49);
- origins and ecology (p. 51 to p. 188);
- biology and evolution (p. 189 to p. 257);
- population richness and community structure (p. 259 to p. 440);
- impacts of human activities on fish species and populations (p. 441 to p. 478);
- fishing and fish farming end the book (p. 479 to p. 545).

With regard to fish biology, ecology, and populations of African continental waters, this book is the obvious sequel and companion to two other books that reviewed the state of taxonomic and faunistic knowledge, and that were published in 2003 (The fresh and brackish water fishes of West Africa) and 2007 (The fresh and brackish water fishes of Lower Guinea, West-Central Africa) as an initial contribution to the topic of ichthyofaunal diversity in the continental waters of Africa.

The Scientific Editors

We dedicate this book to Rosemary Lowe-McConnell (1921-2014) who was a pioneer in the study of tropical fish and made a highly significant contribution to our understanding of the taxonomy, evolution and ecology to tropical fishes, particularly in Africa. Ro's research (Ro is her nickname for friends) on tilapia, an important food source for many communities in the developing world, provided a valuable basis for further studies of fish farming in tropical waters. Tilapia is now a major food fish, stocked in lakes and dams, and cultivated in ponds worldwide (see later in this book).

Ro began her African scientific research in 1945 in Malawi (Lake Nyassa/Malawi). Later she went in Jinja, Uganda, at the East African Fisheries Research Organization, now the National Fisheries Resources Research Institute. Her main purpose was to study the biology of tilapia in the lakes of east Africa. Life in Africa had its challenges, but was fun, too, as described in Ro's very readable book The tilapia trail. The life history of a fish biologist *(2006).*

Ro never actually retired and her work in the field never did end. She participated in many international conferences on ichthyology, limnology, and ecology, and produced more than 60 academic publications and published several books bringing together studies on the ecology of freshwater fishes from the tropics.

Acknowledgements

It goes without saying that this book would not have been possible without the extraordinary participation of the 16 contributing authors.

Special thanks are also due to a number of individuals whose additional efforts have been pivotal in bringing this book to fruition. In particular we would like to thank Emily Divinagracia (Publications Service, Royal Museum for Central Africa) for her outstanding translation and correction work on all the chapters.

Our special thanks also go to Isabelle Gérard (Publications Service, Royal Museum for Central Africa), and Catherine Guedj and Thomas Mourier (IRD Éditions) for keeping us on course to publication.

The diversity of aquatic environments

Jacques Lemoalle

The long-term survival of a fish species in an aquatic system depends on whether that system provides conditions that favour, among other requirements, the species' growth and reproduction. These conditions are grouped into two categories:

- the physico-chemical (or abiotic) environment deriving from the geological context and the climatic conditions as well as the aquatic landscape as perceived by the fish;
- the trophic (biotic) environment defined by the interactions between species, notably the predator-prey relationships during the successive stages of the fish development.

These habitat characteristics must be considered in both their spatial and temporal dynamics: the survival of a cohort or population depends on the synchronization between the needs of an eco-phase and the characteristics of its environment (Lévêque, 1995a).

The physico-chemical quality of both lotic and lentic aquatic systems is indirectly but rather precisely regulated by their geographic location. This takes place through complex interactions of different environmental variables (figure 1.1). The abiotic conditions (seasonality and spatial distribution of turbulence, oxygen, temperature, salinity and transparency, habitat structure) that have a direct influence on fish communities depend on two constraints: the local climatic conditions and the geology of the basin. In general, an aquatic system is a component of a landscape, which itself depends on the same two constraints. It is within these interactions between terrestrial landscapes and the aquatic environment that we will discuss, in brief, the variety of African environments, first by dividing Africa into two large regions, and then reviewing the main characteristics of the aquatic systems encountered in each region.

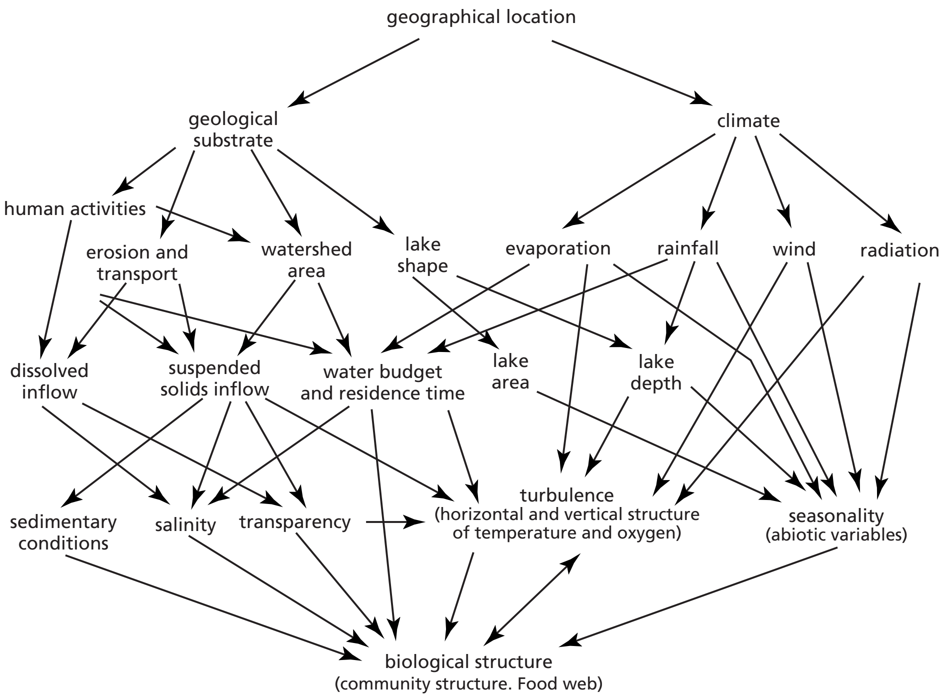


FIGURE 1.1

An example of a network of environmental abiotic characteristics that determine the quality of a lacustrine system. The proximal variables (bottom line of the figure) have a more direct action on the composition of communities.

The role of physico-chemical variables: temperature and salinity

The water temperature of rivers and shallow lakes are normally close to the mean air temperature, in contrast with deeper lakes where temperature is unevenly distributed over depth in the water column. The diurnal and seasonal solar irradiance cycle variations result in delayed cycles of temperature in the water column and alternation of stratification and mixing.

The main factors that determine the temperature of water are latitude and altitude, with a local influence from atmospheric circulation. The latter explains why climate is often more variable than expected in equatorial regions of Africa where seasonality is expected to be minimal. The temperatures observed in different shallow African aquatic environments show that seasonality increases with latitude (figure 1.2). In the entire inter-tropical Africa, the average temperatures are high, most often above 20°C, thereby favouring the rate of chemical and biological reactions at different trophic levels, such as bacterial decomposition, photosynthesis or metabolic reactions (Lemoalle, 1981).

The effect of altitude on the temperature of a series of shallow tropical lakes (figure 1.3) also applies to rivers: it is a major factor of species distribution in inter-tropical regions.

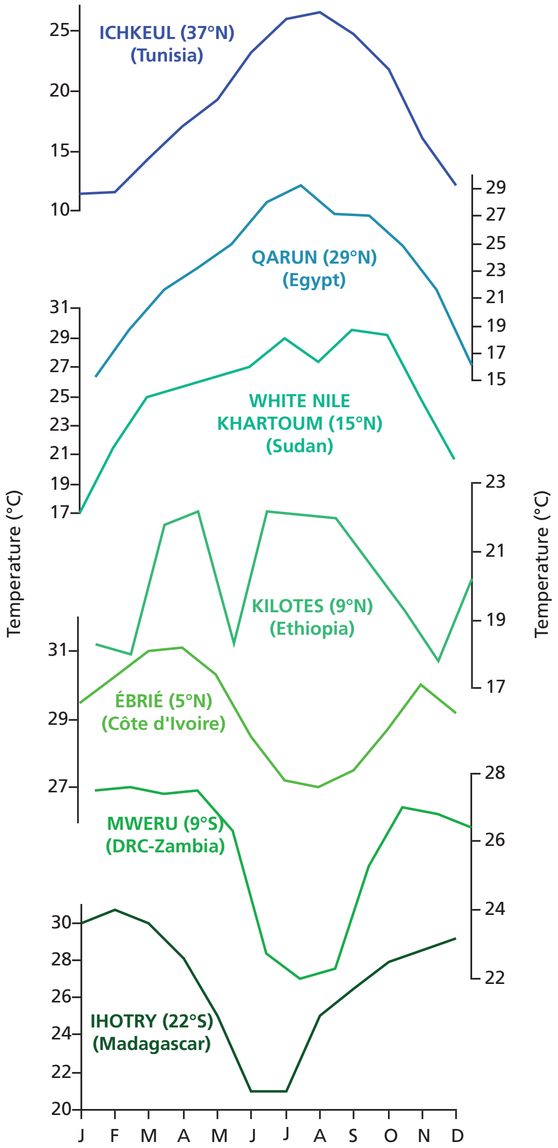


FIGURE 1.2.
Annual variations of surface water temperature of some shallow African lakes (from Talling, 1992).

From a physicochemical point of view, shallow lakes offer a great variety of conditions owing to the relative importance of evaporation in comparison to the water depth. The water salinity ranges from that of rain water (with a conductivity of about 10 µS.cm^{-1}) in very dilute environments or on bedrock, to far above that of sea water as observed for the lake of Latir (175 g L^{-1} or 100,000 µS.cm^{-1}) in Chad located in a highly evaporative environment. Salt water lakes in Africa include Lakes Magadi, Nakuru, Natron in Kenya, the

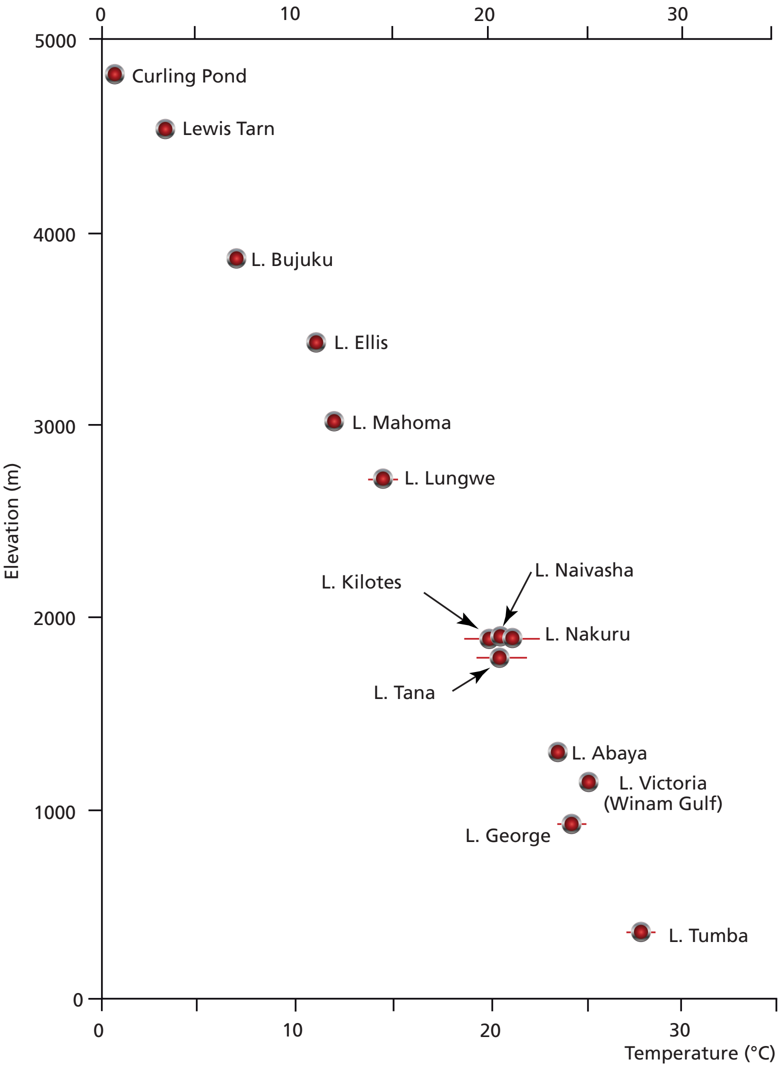


FIGURE 1.3.
Decrease of bottom water temperature according to altitude in some shallow African lakes (from Talling, 1992).

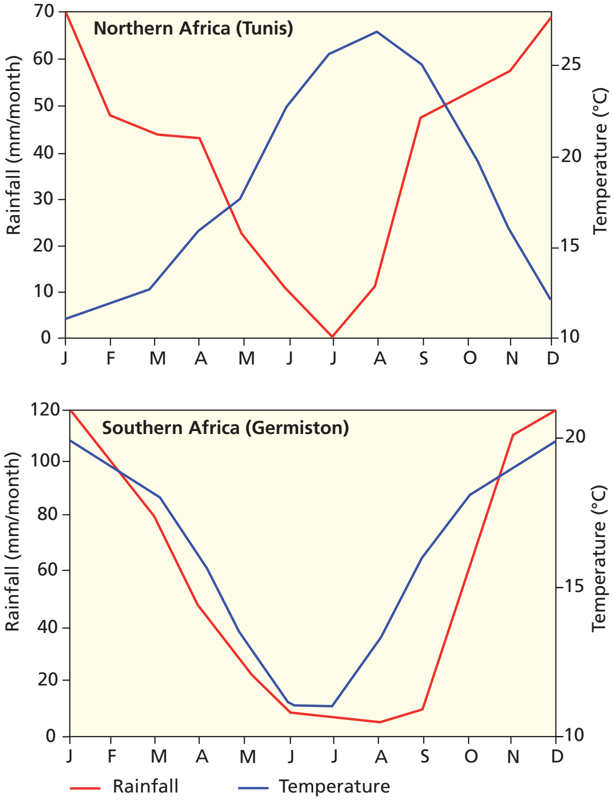
Kanem lakes in Chad and Pink Lake in Senegal (Burgis & Symoens, 1987). Regardless of the quantitative aspect, the chemical composition of water is also variable, with different relative proportions in anions and major cations (figure 1.5 and table 1.I). In tropical zones, specific soil formation processes result in the production of laterite. During this process, high concentrations of ions are released, notably sodium, bicarbonate and silicate which are characteristic of tropical waters.

Whereas high salinity can be shown to be a limiting factor for the diversity of the fish community, a selective effect of the relative ionic composition does not appear to influence fish communities in diluted waters.

Rain or temperature?

FIGURE 1.4.

Mean opposite rainfall and water temperature cycles in Northern and Southern Africa. In Northern Africa (Tunis) the rains occur during the cold season (boreal winter) whereas in Southern Africa (Germiston), they occur during the warm season (southern summer). From Griffiths, 1972).



The triggering factor of some phases of the biological cycle of many organisms is often related with climatic variables.

Sometimes the factor is clearly identified, such as a flood resulting from local rain.

In other cases, it may result from a season change, with no possibility to determine which individual factor is involved as many climatic factors change synchronously.

In Northern Africa, the rainy season starts in autumn when the temperature starts decreasing.

Which factor – temperature or rain – triggers the reproductive migrations of some fish populations?

It may be useful here to compare Northern Africa with Southern Africa where the warm season occurs respectively in the dry season in the north and in the wet season in the south (figure 1.4).

TABLE 1.I

Physicochemical characteristics of some African lakes and rivers
Na, K, Ca, Mg, HCO3, Cl, SO4 expressed in mg/L; conductivity expressed in µS.cm-1
Pmoy: mean depth in meters
* : HCO3 + CO3; ** : meq/L
References: B & S., 1987: Burgis & Symoens, 1987; H & H, 1992: Hughes & Hughes, 1992; VB & B, 1990: Van den Bossche & Bernacsek, 1990; W, 1972: Welcomme, 1972a.

	Na	K	Ca	Mg	HCO_3	Cl	SO_4	Conductivity	Sources
Lake Bangweulu	1.7	0.5	1.8	0.1	9.8	0.8	2.3	14	W, 1972
at depth: 4.14 m	5.1	2.2	3.1	2	17.1	2		52	VB & B, 1990
Lake Baringo	95	13	11.5	2	341.6*		19	416	VB & B, 1990
at depth: 5.6 m	126	15	22	3.15	347.7*		40		
Lake Chilwa	189	10.5	10.8	6.3		182		800	VB & B, 1990
at depth: 2 m	780	23.1	13.4	8.6		515		2 500	
Lake Edward	110	9	12.4	47.3	600*	36	31	900	VB & B, 1990
at depth: 34 m								925	
Lake Ihema	3.9	1	2.46	3.9	42.7*	7.8		103	VB & B, 1990
at depth: 4.8 m	5.9	1.9	6.92	5.4		8.8		110	
Lake Kivu	129	85	5	84	915*	31	15	1240	VB & B, 1990
at depth: 480 m	130	100	21.2	100	1000.4*	35	30	1294	H & H, 1992
Lake Magadi	38 000	537	<10	<30	7 980*	22 600	900	160 000	VB & B, 1990
at depth: <1 m									
Lake Malawi	21	6.4	15.1	4.7	144	4.3	5	220	VB & B, 1990
at depth: 426 m			20.2	6.9			5.5		
Lake Albert	91	65	9.8	31.5	445.3*	31	25	675	B & S, 1987
at depth: 25 m	97	66		32.1	475.8*		32	730	
Lake Mweru	4.06	1.25	7.1	4.3	46.2	3.5	2	49	VB & B, 1990
at depth: 3-10 m	5.6	2.05	13.1	6	48.8*	19.1	3.1	125	B & S, 1987
Lake Naivasha	41	21.6	15.2	6.9	190.9*	14.4	2	318	VB & B, 1990
at depth: 11 m	45	22.6	21.9	7.7	209.2	16		400	
Lake Nakuru	3 300	237		0.9		1 020	62	9 500	VB & B, 1990
at depth: 2 m								165 000	
Lake Natron		3 000			158 600*	65 000	3 100		VB & B, 1990
at depth: < 1 m									
Lake Rukwa	149.4	19.4	1	1	7.09**	25.8	2.9	354	VB & B, 1990
at depth: < 5 m	1 140	85	12.2	4.6	53.5**	383	130	5 120	
Lake Tanganyika	57	35	9.3	43.3	409.3*	26.5	5	520	VB & B, 1990
at depth: 700 m								610	
Lake Turkana	770	21	5	3	1 323.7*	429	56	2 860	VB & B, 1990
at depth: 29.7 m	810	23	5.7	4	1 494.5*	475	64	3 300	
Lake Victoria	10.4	3.7	5	2.3	54.9*	3.9	0.8	91	VB & B, 1990
a depth: 40 m	13.5	4.2	7	3.5	67.1*			98	
Bandama River	3.2	2.3	4.6	2	36	0	1.7	90	VB & B, 1990
	6	4	5.5	2.5	45.7	0.8	10.1	200	
Corubal River	96.8	3.2	21.4	5	24.4	193.7	56.2		VB & B, 1990
Niger (Inner Delta)	2.99	1.96	4.01			1.07		31	VB & B, 1990
Senegal River	2.5	2.4	10	1		3	11	72	VB & B, 1990
Black Volta River	3.9	0.25		11.86		17.5		41	VB & B, 1990
								124	
Congo River	1.7	1.1	2.4	1.25	11.2	2.85	2.95		VB & B, 1990
Zambezi River	1.7	0.88	4.93	1.47				50	VB & B, 1990
	3.26			3.86				96	

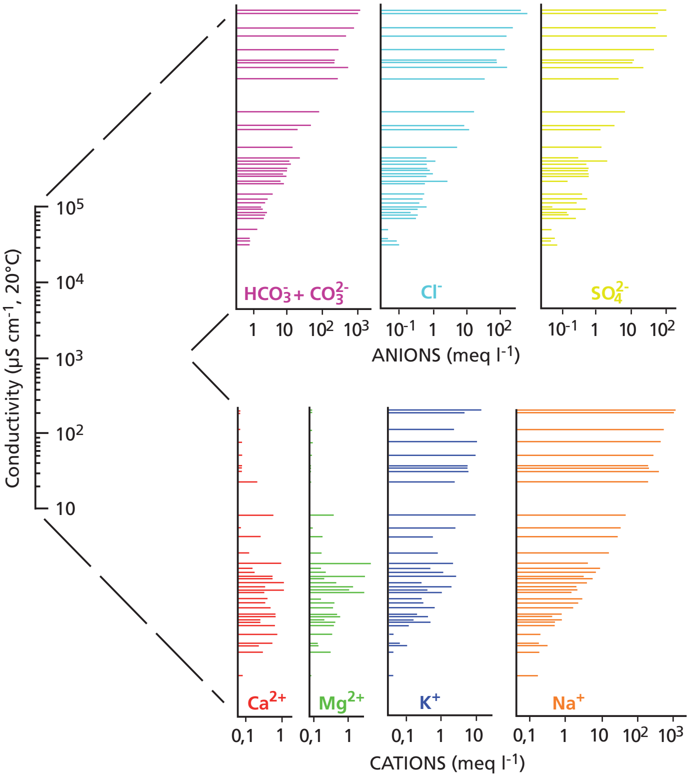


FIGURE 1.5.
Concentrations of major anions and cations as a function of conductivity for a series of African lakes in East and Central Africa (from Talling & Talling, 1965)

The lakes and rivers of Africa

Africa is an ancient shield with a consolidated continental base dating at least 600 million years. This base is composed of gneiss, shale and slab and is grooved in a criss-cross manner resulting in basins with raised edges (moles) levelled by erosion. With the exception of the Atlas to the north and the Cape Mountains to the south, this general relief does not seem to have been modified by the folding which is responsible for the creation of other mountains in the world.

Five large basins occupy the centre of the continent (figure 1.6). The flow of most of the rivers towards the ocean occurs via gorges and cataracts which have a major influence on the distribution of aquatic species in the Congo, Zambezi, Nile or Niger basins (Lévêque, 1997a). Some basins have no outlet to the sea (endorheic basins). A good illustration is the Chad basin which during the Pleistocene enclosed an inland sea larger than any of the present lakes. Another example is the Kalahari and Okavango which, although drained by the Zambezi River, lose a major portion of their water in the Okavango and Makarikari marshes. Finally, to the north of the continent, almost all the tributaries south of the Atlas drain into chotts and seasonal saline pools in regions of semi-arid climate.

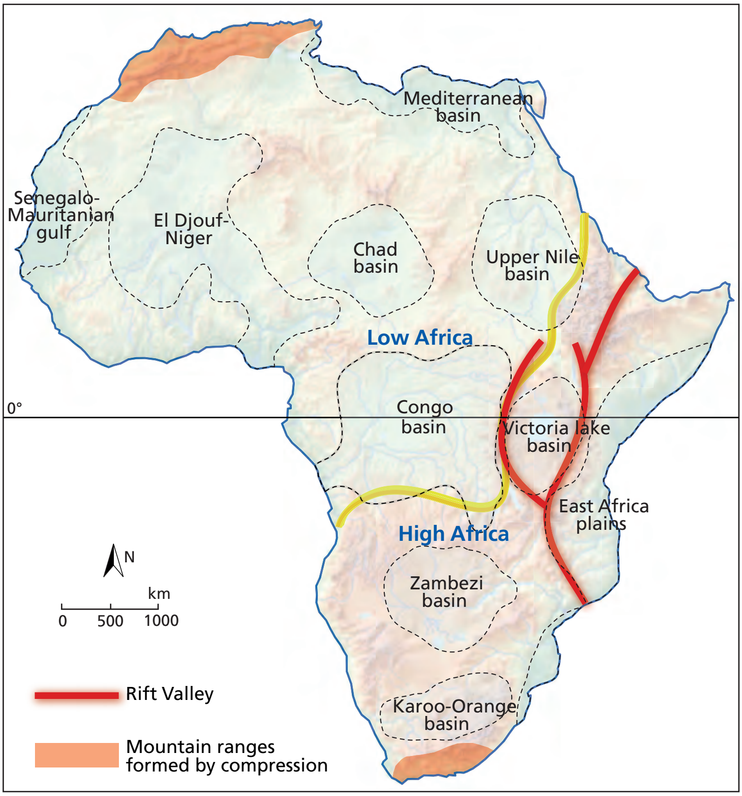


FIGURE 1.6.
General topography of Africa showing the principal hydrographic basins, the altitude zones above 1,000 m, and the approximate division between lower and higher Africa (redrawn from Beadle, 1981).

The ancient repartition of the main basins of pre-Miocene age was altered in the eastern part of the continent by the uprising of a wide band of 500 to 800 km width, oriented north-south from Eritrea to Zambezi. The trough, approximately 1,000 m deep, is due to plate tectonics and was formed about 20 million years ago. It is the origin of the creation of the vast depressions of the Rift Valley oriented in NE/SW direction and in which most of the Great African Lakes were formed. Lake Victoria, which covers an area of 65,000 km², occupies a depression located at the centre of the two branches of the Rift Valley. The volcanic activity associated with these different rifts resulted in the creation of hundreds of crater lakes, mainly along the Western Rift.

The African continent is thus divided schematically into two large regions:

- to the East, the highland Africa, with an altitude generally above 1,000 m, where the Rift Valley and the great lakes are located;

- to the West, an Africa characterized by large sedimentary basins, with average altitudes less than 500 m, encircled by eroded plateaus which isolate these basins from each other and from the sea (figure 1.6).

It is in this geomorphologic context that the current aquatic environments and their biological communities have developed progressively.

The main types of aquatic environments

Lotic systems

The African hydrographic system is well developed despite the presence of vast barren zones (figure 1.7 and table 1.II). Some water courses originating from rainy upper basins flow through arid regions, such as sections of the Senegal, Niger, and especially the Nile River, which seems contradictory given the dryness of their surrounding landscapes.

A distinction may be made between the large and the smaller river basins. The hydrological regime of the large rivers of Africa (Congo, Nile, Niger, Volta, Senegal, Chari, Zambezi), results from a diversity of rainfall regimes on different parts of the basin, with different landscapes and biotopes. The smaller coastal basins, hydrologically isolated from one another, are situated in small homogenous climatic zones. They are more directly in phase with the local climate, and therefore likely to experience sharper variations in their discharge.

In most water courses a progressive change occurs in altitude, slope, flow rate and section (width and depth) of the river, from the source to the estuary.

FIGURE 1.7.
Distribution of river systems in Africa.

TABLE 1.II
Physical characteristics of the principal rivers of Africa
(* volume: $km^3 s^{-1}$)

Rivers	Length (km)	Basin area (km^2)	Annual mean flood ($m^3.s^{-1}$)
Congo	4 700	3 457 000	40 487
Nile	6 695	3 349 000	2 640
Zambezi	2 574	1 300 000	7 070
Niger	4 200	1 125 000	6 100
Orange	2 300	650 000	
Chari	950	600 000	1 100
Senegal	1 640	441 000	687
Volta	1 270	398 371	1 260
Limpopo	1 680	358 000	5,33*
Ogowe	920	205 000	4 758
Rufiji	300	177 000	1 133
Ruvuma	640	165 760	
Kafue	945	154 200	10,3*
Sanaga	890	135 000	2 060
Malagarasi	470	131 572	
Cuanza	960	121 470	58
Okavango	2 560	115 000	254
Bandama	1 050	97 000	392
Save/Sabi	715	88 395	5*
Great Ruaha	750	84 000	103
Cunene	975	83 000	6,77*
Comoé	1 160	78 000	206
Gambia	1 120	77 000	170
Cross	485	75 000	569
Sassandra	840	75 000	513
Logone	550	73 700	1 500
Kouilou	605	60 000	700
Ouémé	700	50 000	220
Wami	490	46 361	2*
Incomati	714	46 246	2,3*
Tana	800	42 217	151
Ntem	460	31 000	348
Pongolo	565	29 800	2,8*
Pagani	395	29 526	0,85*
Cavally	700	28 850	384
Ruzi (Buzi)	360	28 800	1,45*
Nyong	690	27 800	443
Corubal	600	23 200	
Pra	445	22 710	238
Mono	360	22 000	104
Ruvu	270	18 389	2*
Moa	425	17 900	
Tano	625	16 000	129
Sewa	385	14 200	
Kaba	280	12 900	
Rokel	280	10 600	
Bia	300	9 500	83
Oshun	267	9 014	
Geba	255	8 000	
Awash	815	7 700	40
Jong	249	7 500	
Bengo	300	7 370	47

These conditions determine a variety of successive biotopes, from small rocky mountain streams to wider silted meandering rivers. Each corresponds to equally differentiated communities.

Most of the main river basins have been the subject of monographic studies: the Nile (Rzoska, 1976; Said, 1993; Dumont, 2009) and Jonglei Canal (Howell *et al.,* 1988), Niger (Grove, 1985), Bandama (Lévêque *et al.*, 1983), Volta (Petr, 1986; Lemoalle & de Condappa, 2009) and Zambezi (Davies, 1986).

Floodplains and marshes

The most remarkable influence of the seasonality of rains and water flow regimes concerns the floodplains, ox-bow lakes and temporary pools. These systems are similar to shallow lakes and are located in plains and landscapes of low relief.

The term '*temporary pools*' groups together shallow water bodies that are not necessarily linked to a hydrographic system. Their water input is via local runoff and by direct rainfall on their surface (the term '*rain-pool*' would be more explicit). In savannahs, they are completely dry during part of the year but are flooded annually. Their number and total area within the savannah is however often underestimated. In arid zones, their flooding is more irregular. Their principal characteristic, however, regards their aquatic vegetation and fauna. These organisms are adapted to a pronounced metabolic resting period (aestivation) during some stages of their life or may be actively or passively migratory (transported by other organisms). As regards fish, the genus *Protopterus* demonstrates two complementary modes of adaptation to these environments which also provide habitat to *Nothobranchius* (Cyprinodontidae) which accomplishes its entire biological cycle within a few months.

Alluvial floodplains are often composed of depressions, including ox-bow lakes which are permanent water systems seasonally linked to the river and which form an active, biological and chemical transition zone between the terrestrial and aquatic environments. Several classifications of these interface environments have been proposed, according to their size and the chronology of their link with the main river, some being fed via intermediary pools or depressions connected to the river (Junk, 1982). In floodplains, the ratio of the area covered by permanent water to the total surface liable to flooding is also an important ecological variable. The Sudd (Nile basin) and Okavango (Botswana) have a permanent/seasonal ratio of 1:1.7. These are primarily vast marshes with variable water levels during the year; the recruitment of their fish communities does not rely heavily on the fluvial stocks. A ratio of 1:6 has been estimated for the Niger floodplains (Niger Inner Delta, in Mali) or the Senegal River before the Manantali and Diama dams were constructed. Much higher ratios (1:20 to 1:100) apply for the Chari and Logone floodplains (Chad and Cameroon) and in particular to the Grand Yaéré in North Cameroon (figure 1.8). In this case the fish community of the flooded zone is composed mainly of juvenile fish originating from the spawning of the river adults at the beginning of the flood.

In tropical regions, the inundation of floodplains is initiated directly by rainfall while the flooding from the river occurs later. These environments are primarily colonized by herbaceous plants. In equatorial regions however, rain exceeds evaporation most of the time and the river water level is less variable. The alluvial plains are therefore permanently covered by a flooded forest. A good example is the great flooded forest of the Congo basin (about 200,000 km^2). Coastal alluvial environments are characterized by a gradient from fresh to saline water in the inter-tidal zone which favours the establishment of mangroves, such as those on the coast of the Guinean Gulf. In both cases, fallen leaves from the trees form the principal organic source of the aquatic trophic web.

FIGURE 1.8.

Location of the main wetlands of Africa (modified from White, 1983 and Denny, 1993).

The permanent marshes (Sudd, Okavango, shallow annexes of Central African lakes, banks of Lakes Chad, Chilwa, Bangweulu or Kyoga) are covered with a dense vegetation of helophytes such as *Cyperus papyrus*, *Phragmites* spp., *Vossia cuspidata*, *Typha* spp. and sometimes *Echinochloa pyramidalis*. These macrophytes significantly modify the oxygenation and chemical composition of the water via the assimilation of nutrient and dissolved ions (Denny, 1985). Some plants such as the leguminous *Aeschynomene elaphroxylon,* which can reach 8 to 10 metres in height, are indicators of recent past arid periods because their seeds can germinate only in exposed sediments. Although the life span of one of these trees lasts no more than four to six years, a forest may last more than twenty years due to lateral re-growth (Howard-Williams 1975, 1979). The conductivity of water or sediment is also a factor in species selection: *C. papyrus* is limited to fresh water (400 µS.cm^{-1} being its highest limit in Lake Chad), while *Phragmites*, *Typha* and *Cyperus laevigatus* are tolerant to higher salinities (up to 20,000 µS.cm^{-1} in the Kanem small lakes) (Iltis & Lemoalle, 1983).

The herbaceous riverside floodplains are characterized by currents that favour the oxygenation of the water. In addition, the low density of the vegetation allows the penetration of light into the water where the stems support an epiphytic algae (with a net production of oxygen) and an epibiotic community which is eaten by the fish, mostly juveniles. Finally, the herbaceous biomass is mineralized only after the water has receded, which is favourable for the preservation of oxygen in the water and later promotes local soil fertility.

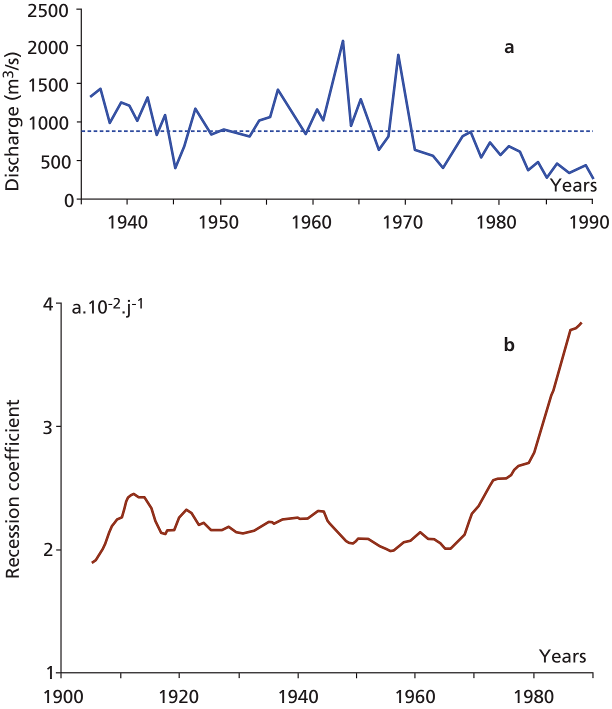
In marshes with dense permanent vegetation, a large segment of the primary production is aerial but the bulk of decomposition occurs in the water. Little light penetrates into the water and oxygen exchange at the water-atmosphere interface is limited, resulting in a lack of dissolved oxygen in the water. The fish must get their oxygen close to the water surface or in shallow areas. Some fish have however developed lungs that allow them to use oxygen directly from the air.

Whereas micro-epiphytes constitute the first link in the trophic foodweb in herbaceous floodplains, the base of the web in marshes originates from decomposing debris from the aerial parts of vegetation and their bacterial associated fauna (the detritic food chain). The former environment is temporary and harbours mostly an eco-phase of various riverine or lacustrine fish species while the latter provides habitats for adapted species during their whole life cycle with a predominance of juveniles on the more oxygenated edges.

The role of underground water

A main component of a river system is the related aquifer groundwater. Between the river and the underground layers, a permanent process of water transfer occurs. It has been estimated that the transfer of water between a river

FIGURE 1.9.
a: monthly discharge at low flows (Ubangi);
b: evolution of the recession coefficient of rivers in the Sahelo-Sudanian part of Africa) (from Olivry *et al.*, 1993).



flowing over a pervious substrate and the underground is as large as the river flow itself. During the river flood, the water table is fed by the surface network. Conversely, during low flow, the stored water is returned to the surficial river network and maintains the surface flow in the rivers. In general, groundwater systems are more permanent and less variable than surface systems because the transfers are slower and the hydrologic surface variations are damped.

In the recent context of rain deficit over inter-tropical Africa, the river flow of the Sahelo-Sudanian rivers has decreased significantly during the last forty years. The cumulated impact of weak rainfall has resulted, with a delay, in a continuous and significant decrease of the river discharge. Whereas the decrease in total discharge was only 7% in the 1970s, it reached 16% in the 80s although rainfall had partially recovered (Olivry *et al.*, 1993). This decrease is accompanied by frequent very low water levels and accelerated receding of the water (figure 1.9). The decline of underground storage has impacted the surface river flows with a lag of about a decade, before a possible future climatic improvement.

Shallow lakes

Unlike marshes, the largest part of the area of shallow lakes is not colonized by vegetation. However, when the lake lies in a flat landscape, its shores are often composed of a vegetation belt with the same species. In Africa, shallow lakes are numerous and very different in size, from those with dimensions of a pool to Lake Chad which in the 1960s covered about to 22,000 km² (table 1.III). Some lakes such as Chad and Chilwa are endorheic (with no surface outlet) and all the water input from the rain and tributaries is lost through evaporation and seepage to the underground water table.

Shallow lakes are polymictic, meaning that the water column is homogenous virtually every morning after the night cooling. Depending on the season and wind regime they may become stratified again during the day. The high frequency of the thermal cycle assures that the whole column of water is well oxygenated and that the regeneration of nutriments is continuous, promoting an abundant phytoplankton community. Most of these lakes are eutrophic (average chlorophyll concentrations above 25 mg/m^3) and are susceptible to climatic accidents. If it happens that the stratification may last several days due to the lack of wind or no cooling during the night, anoxic conditions may develop in the water mass and thus result in massive fish mortalities. The turbulence created by strong storms may also stir the organic sediments leading to similar anoxia.

Several large African lakes have been the subject of monographs: Lake Chad (Carmouze *et al.*, 1983), Lake Turkana in Kenya (Hopson, 1982), Lake Bangweulu in Zambia (Toews, 1975). Smaller lakes have also been studied: Lake George in Uganda (Burgis *et al.*, 1973; Ganf & Viner, 1973; Talling, 1992), Lake Chilwa in Malawi (Kalk *et al.*, 1979), Lake Guiers in Senegal (Cogels 1984), Lake Naivasha (Litterick *et al.*, 1979) and Lake Nakuru in Kenya (Vareschi, 1978, 1979). Detailed information on these environments is available in Serruya & Pollingher (1983) and Burgis & Symoens (1987).

TABLE 1.III

The main shallow lakes of inter-tropical Africa (source: Van Den Bossche & Bernacsek, 1990)

Lakes	Countries	Area (km^2)	Average depth (m)
Chilwa	Malawi, Mozambique	750-1 000	2
Guiers	Senegal	170-300	2.5
Naivasha	Kenya	115-150	11
Bam	Burkina Faso	12-20	0.8
Chad “normal”	Cameroon, Niger, Nigeria, Chad	18 000	3.9
Mweru	DRC, Zambia	4 650	3-10
Tana	Ethiopia	3 500	8
Rukwa	Tanzania	2 300	< 6
Mai-Ndombe	DRC	2 300	5
Kyoga	Uganda	1 822	2.3
Bangweulu	Zambia	1 721	4.1
Natron	Kenya	900	0.5
Tumba	DRC	765	2.4
Upemba	DRC	530	1.7
Malombe	Malawi	390	4
George	Uganda	250	2.4
Ngami	Botswana	200	1
Chiuta	Malawi, Mozambique	200	5
Baringo	Kenya	130	5.6
Awasa	Ethiopia	130	10.7
Magadi	Kenya	108	0.6
Ihema	Rwanda	86	4.8
Nakuru	Kenya	52	05-4.5
Lere	Chad	40.5	4.5
Nabugabo	Uganda	30	< 5
Dilolo	Angola	18.9	

FROM LAKE TO MARSH: THE CASE OF LAKE CHAD

During the 1950-1970 period, the surface area of Lake Chad was about 20,000 km^2 with a volume of 50 km^3, and thus a mean depth of 2.5 m. Owing to its water turbidity and wind induced turbulence, the riparian vegetation was restricted to a narrow band. Most of the lake area was covered with open water, and the fish diversity corresponded well with this lacustrine environment (Bénech & Quensière, 1989). As a result of the decrease in rainfall that started around 1970, a large part of the lake dried out between 1973 and 1975 (Lemoalle, 1991). The seeds present in the dried sediment could then sprout, and many plants developed (among which *Cyperus papyrus* and *Aeschynomeme elaphroxylon*) and continued to grow when the water came back. In the southern basin of the lake, with the same water level (280.5 m asl) the open water area which was about 6,000 km^2 before 1972 has decreased to around 1,700 km^2 afterwards. A wide marsh covered most of the inundated area, with impacts on the fishing techniques not only because of this new environment, but also because the fish species had changed from a lacustrine to a marsh community with different behaviours (Neiland & Verinumbe, 1991).

Deep lakes

The great lakes of East Africa are characterized by unusual dimensions in terms of volume (Tanganyika, 18,900 km^3), surface area (Victoria, 68,800 km^2; Tanganyika, 32,900 km^2; Malawi, 30,800 km^2) or depth (Tanganyika, 1,435 m max; Malawi, 758 m max.) (Table 1.IV). Pelagic processes are dominant

Lakes	Countries	Area (km²)	Average depth (m)	Maximum depth (m)
Victoria	Kenya, Tanzania, Uganda	68 800	40	84
Tanganyika	Burundi, Tanzania, DRC, Zambia	32 900	700	1 435
Malawi	Malawi, Mozambique, Tanzania	30 800	426	758
Turkana	Ethiopia, Kenya	7 570	29.7	73
Albert	Uganda, DRC	5 270	25	58
Kivu	Rwanda, DRC	2 370	240	489
Edward	Uganda, DRC	2 300	34	117

TABLE 1.IV
The main large inter-tropical deep lakes of Africa (source: Van Den Bossche & Bernacsek, 1990)

in the Rift Valley lakes owing to the reduced littoral zone and immense depth linked with the high local relief. A synthesis of their characteristics is available in Johnson & Odada (1996).

Deep lakes, large or moderate in size, are generally characterized by seasonal or permanent stratification. The water of the upper layers is warmer and less dense than in the deeper layers. The lake is thus constituted by two superimposed layers that hardly mix. Schematically, the upper layer is well illuminated and oxygenated whereas decomposition processes dominate in the deeper layer which is less oxygenated. This character can also be found in lakes with low surface area but sheltered from the wind such as crater lakes or small forest basins such as Lake Opi in Nigeria (Hare & Crankcase, 1984).

Hundreds of deep crater lakes are found in volcanic regions of Africa, notably in East Africa and Cameroon. These include Lake Bunyoni (Uganda), and lakes Nyos (with a maximum depth of 208 m and surface area of 1.58 km²) and Tizong (48 m and 0.08 km²) in Cameroon (Kling, 1988). These are usually small lakes with poor native fauna while others such as the Barombi Mbo in Cameroon accommodate several endemic fish species (Trewavas *et al.*, 1972). Lake Kivu, which was formed after a volcanic eruption blocking the course of a river, is permanently stratified with a deep anoxic zone saturated with methane.

In a stratified lake, the fish live mainly in the upper layer where they feed and breed. In such cases the shores are therefore important for species that are not strictly pelagic.

The accumulation of substances in most deep African lakes is slow and involves, though rarely, gases likely to accelerate the onset of de-stratification (a notable exception being Lake Kivu with methane). Climatic variations, cooling or wind may sometimes initiate mixing in the transition zone between the surface and deep layers thereby enriching surface waters with nutrients. It is however less frequent than in shallow polymictic lakes where this enrichment occurs daily.

Reservoirs

In recent decades, numerous dams have been constructed across rivers in Africa chiefly for hydroelectric power, irrigation and/or urban water supply. The largest and most well-known of these are Lake Nasser on the Nile (the Aswan

LAKE VICTORIA: AN EXAMPLE OF RAPID EVOLUTION

Measurements performed in the centre of Lake Victoria in 1990-91 have been compared with results from 1960-61 surveys (Hecky *et al.*, 1994). The deep, poorly oxygenated layer has increased: it started at a 40 m depth in 1990-91 compared with more than 50 m in 1960, and its oxygen concentration has decreased.

This change points to the eutrophication of the lake that results from several causes. A slight climate change with an increase in temperature may have contributed (Diaz & Graham, 1996).

But the main cause is related to human activities in the watershed, with increased inputs of nutrients to the lake, that induce a change in the phytoplankton and in the distribution of oxygen.

During the same time, the small endemic cichlids, either pelagic or demersal, have partly disappeared as a result of the introduction of new fish species, such as *Lates*, and also because of the new distribution of dissolved oxygen in the lake which has significantly reduced their biotope.

In a span of 30 years, the trophic web in the lake has been radically modified.

The process is likely to be accelerating and the further changes in the aquatic environment may lead to important modifications in the fish communities (see the chapter *Fish communities in East African rift lakes*).

NYOS, AN EXTREME EXAMPLE

On August 21, 1986, 1,700 inhabitants in a village close to Lake Nyos, in Cameroon, were poisoned in their sleep by a cloud of carbon dioxide emitted by the lake.

In this lake, as in other crater lakes of the region, CO_2 accumulates in the deep water layer. The gas originates partly from the decomposition of settling organic matter, and mostly from telluric activity.

Large quantities of gas may accumulate due to the high pressure existing at the bottom of the lake (208 m deep), up to 10 or 20 times more than in surface waters.

Similar to many deep African lakes, Lake Nyos, being protected from the wind by high crater sides and submitted to a very stable climate, is (almost) permanently stratified.

What triggered the overturn (destratification) of the lake in August 1986 has not been clearly identified. Some authors have put forward a stronger than usual atmospheric cooling (Kling, 1987; Kling *et al.*, 1989); others have assumed that a telluric microseism was the trigger. The resulting mechanism and its effects are however unambiguous: a first volume of deep water was uplifted, its dissolved CO_2 thus became oversaturated at a lower pressure (depth) and was converted into gas bubbles. The bubbles amplified the upward stream, as when a giant soda water bottle is opened.

Great Dam), Lake Volta on the Volta, Lake Kariba and Lake Cabora Bassa on the Zambezi (Balon & Notch, 1974), Lake Kainji on the Niger and Lake Kossou on the Bandama (figure 1.10 and table 1.V). These reservoirs have created new aquatic environments, promoting the development of autochthonous or introduced species adapted to lentic conditions, but in addition, have disrupted the cycle of species more dependent on the seasonal flow of the river.

Filling of large reservoirs with water often occurs without prior removal of the previously existing vegetation. Decomposition of this organic matter consumes oxygen and liberates nutrients into the water. This results into a phase of high phytoplankton production favourable for phytoplanktivorous fish, a situation that may last a while before stabilization to lower production levels. The consumption of oxygen is however more durable and its effects may continue for over twenty years (e.g. Lake Volta and Lake McIlwaine).

As regards fish, two environmental variables are important in a reservoir: the residence time of the water and the fluctuations of the water level during the year. Although rapid and substantial changes in water level may largely prevent the development of a littoral community important for the recruitment of juveniles (as occurs in Lake Nasser), it has been shown that these changes are often related with a higher fish catch (Kolding & van Zwieten, 2012) The stratification of the lake and the anoxia of deep zones are directly dependent on the horizontal flow of the water mass which in turn is evaluated by its residence time.

Dams	**Basins**	**Countries**	**Closing date**	**Area (km^2)**	**Maximum depth (m)**
Akosombo	Volta	Ghana	1964	8 270	74
Nasser/Nubia	Nile	Egypt, Sudan	05/1964	6 850	110-130
Kariba	Zambezi	Zambia, Zimbabwe	1958	5 364	120
Kafue Gorge	Kafue	Zambia	1972	1 600-4 340	2 *
Cahora Bassa	Zambezi	Mozambique	1975	2 665	156
Kossou	Bandama	Côte d’Ivoire	02/1971	1 600	60
Jebel Aulia	White Nile	Sudan	1937	600-1 500	12
Kainji	Niger	Nigeria	1968	1 270	60
Buyo	Sassandra	Côte d’Ivoire	1980	900	32
Lagdo	Benue	Cameroon	1982	700	11 *
Manantali	Senegal	Mali	1987	500	20
Mwadingusha	Lufira	DRC	1938	446	14
Sélingué	Niger	Mali	07/1980	409	20
Roseires	Blue Nile	Sudan	1966	290	68
Nzilo	Lualaba	DRC		280	8.3 *
Koka	Awash	Ethiopia	1960	255	14
Ayamé	Bia	Côte d’Ivoire	1959	197	20
Nyumba Ya Mungu	Pangani	Tanzania	12/1965	181	41
Nangbeto	Mono	Togo	1987	180	8
Sennar	Blue Nile	Sudan	1925	140-160	26
McIlwaine	Hunyani	Zimbabwe	1952	26.3	27.4

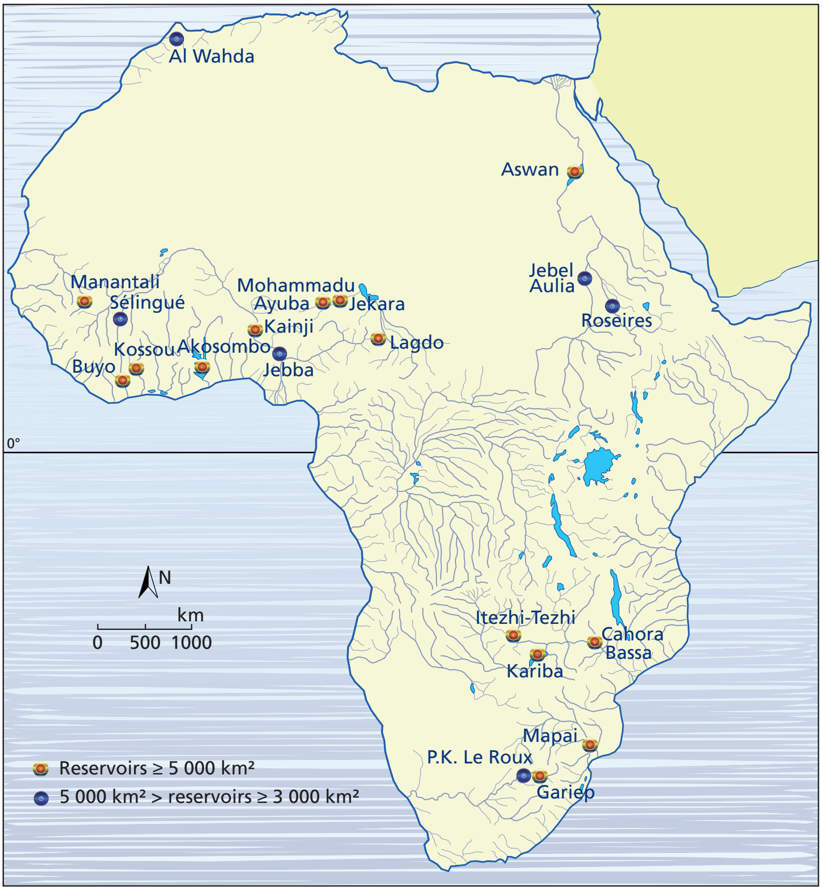
TABLE 1.V

The main reservoirs of inter-tropical Africa (source: Van Den Bossche & Bernacsek, 1990) (*: average depth)

Below reservoirs, the river regime is often modified with smaller floods and, in some cases, counter season floods, leading to narrower flood plains and changes of the environmental conditions necessary for fish reproduction.

Reservoirs constructed close to urban centres or highly populated regions experience very high nitrogen and phosphorus inputs which induce a proliferation of phytoplankton in the surficial layers and anoxia in deeper layers. When such reservoirs are intended for human supply in cities, eutrophication impinges on the treatment costs (filtration and the elimination of taste and toxins produced by some algae) as in Lake McIlwaine in Zimbabwe (Thornton, 1982). The introduction of phytoplanktivorous fish, such as *Hypophtalmichthys molitrix*, may be used to fight against the proliferation of the phytoplankton,

FIGURE 1.10.
The main manmade lakes in Africa.



as in Lake Sidi Mohamed Ben Abdallah, which supplies water to one third of the urban population of Morocco (Bouloud, 1982).

Thousands of small dams have also been constructed on seasonal rivers in Africa, notably in the sub-arid zones in order to store water supplies for livestock, agriculture and domestic use. Numerous trials of fish culture have been developed in these small reservoirs, as fishing is another means of optimizing their use (Baijot *et al.*, 1994).

Conclusions

The characteristics that may be used to describe an aquatic system are multiple and of several orders. These result in the large variety of environments observed in Africa and other continents. Within each aquatic system, a variety of biotopes coexist that may be best described by means of a comparative approach.

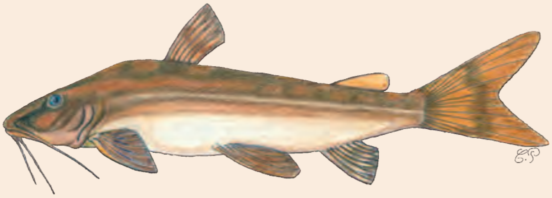
The diversity of the biotopes may rely on water quality and its relation to the metabolism of fish. Salinity and temperature are thus important and selective environmental variables. For example, Mormyridae do not occur in waters of conductivity above 500 µS.cm^{-1} while *Oreochromis* spp. do not tolerate temperatures below 10°C. Few species are likely to survive in water containing less than 2 mgL^{-1} of oxygen, which is the respiratory threshold for species strictly dependent on dissolved oxygen for their respiration (Bénech & Lek, 1981).

Trophic relationships may also be considered as the main characteristics of a biotope. Although most fish are opportunistic, it is necessary for their survival that each eco-phase is able to fulfil its nutritional requirements at the right time. This is the point at which the primary productivity (whether autochthonous or allochthonous, benthic or pelagic), the position of the species in the trophic web, competition for resources and predatory relationships play important roles.

Finally, an environment must be capable of supporting a complete biological cycle. Although the scale is different for migratory fish species, in all cases it is necessary that eggs and larval stages benefit from a suitable environment, as well as a protection from predation. The variety of environments and of biotopes in a given system is one of the conditions for the diversity of species.

Variability of climate and hydrological systems

CHRISTIAN LÉVÊQUE



The role of hydrology in the structuring of aquatic ecology has long been well-acknowledged (Statzner & Highler, 1986; Junk *et al.*, 1989; Lowe McConnell, 1987). Of equal importance is the understanding of the history of aquatic environments in order to accurately understand the present composition and structure of communities (Lévêque, 1997a). Ichthyologists therefore have granted much attention to the hydrological conditions of environments inhabited by fish. Hydrological variability resulting from the seasonal distribution of rains or inter-annual variations in precipitation has substantial consequences for the biology and dynamics of fish communities.

Rainfall is distributed very unevenly in Africa (figure 2.1). In parts of the west coast, for example, annual rainfall averages more than 1,250 centimetres. In contrast, more than half of Africa receives less than 50 centimetres) of rainfall yearly. The Sahara and the Namib Desert receive an average of less than 10-25 centimetres a year. In parts of the deserts, rain may not fall for six or seven years in a row. The annual rainfall is normally higher at the equator and diminishes towards the tropics, but nevertheless with local variations that can be linked to relief or to other geomorphologic factors.

The existence and the range of aquatic environments depend mainly on climatic conditions, particularly the link between gains and losses in water during seasonal cycles or in long-term changes at geological time scales. This results in a highly contrasted distribution of aquatic environments, with vast zones (40 to 50% of the continent) in which permanent hydrographical systems are extremely reduced or absent (figure 2.2; see also box "From Mega to Marshy Chad" and chapter *The diversity of aquatic environments*).

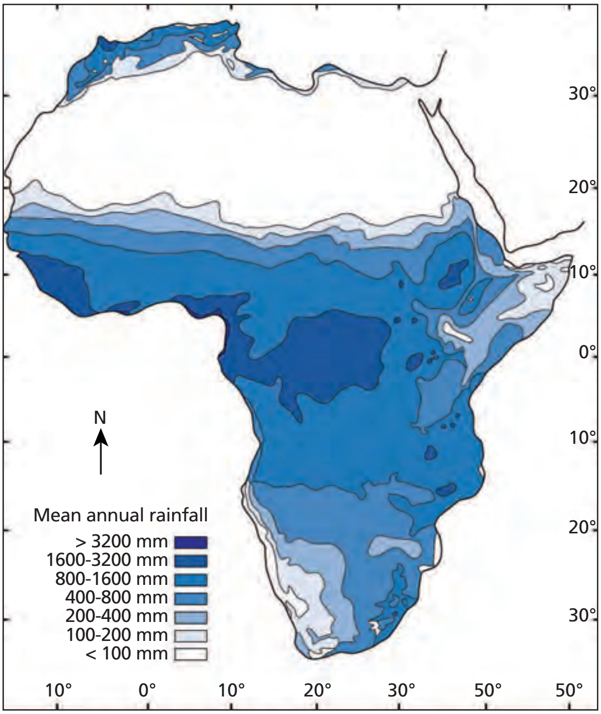


FIGURE 2.1.
Distribution of mean annual rainfall (from Balek, 1977).

FIGURE 2.2.
Comparison between the current geographical distribution of river and lacustrine systems (right) with that of the theoretical maxima that these systems attained during wetter periods (left) (from Dürr, 2003).

Seasonal climatic variations and river discharge

Climatic conditions depend on the circulation of air currents driven by the energy budget of the earth-atmosphere system. The equator is a zone of updraft in which air currents cool during their rise and then descend at the subtropical anticyclone level. These in turn re-converge around the equator forming trade winds. The meteorological equator, or convergence zone of the trade winds, does not coincide with the exact position of the geographical equator, and is situated about 5°N during the boreal winter and about 10°N during the boreal summer.

During the year, the distribution of rainfall at different latitudes is uneven. At the equator it rains throughout the year with two maxima, one in April, and the other in November. North and to the south of the equator, rain distribution patterns become more seasonal, leading towards a single rain season. In the tropics, the rain season becomes comparatively short, with a peak in July-August in the northern hemisphere, and January-February in the southern hemisphere. The relative humidity of the air diminishes while evaporation increases considerably with distance from the equator.

River discharge varies considerably following the seasonality of rainfall, and two major types of hydrological systems are recognized, reflecting strict rain patterns:

- Equatorial systems characterized by a sustained flow throughout the year and two flood periods (Congo and Ogowe, figure 2.3)

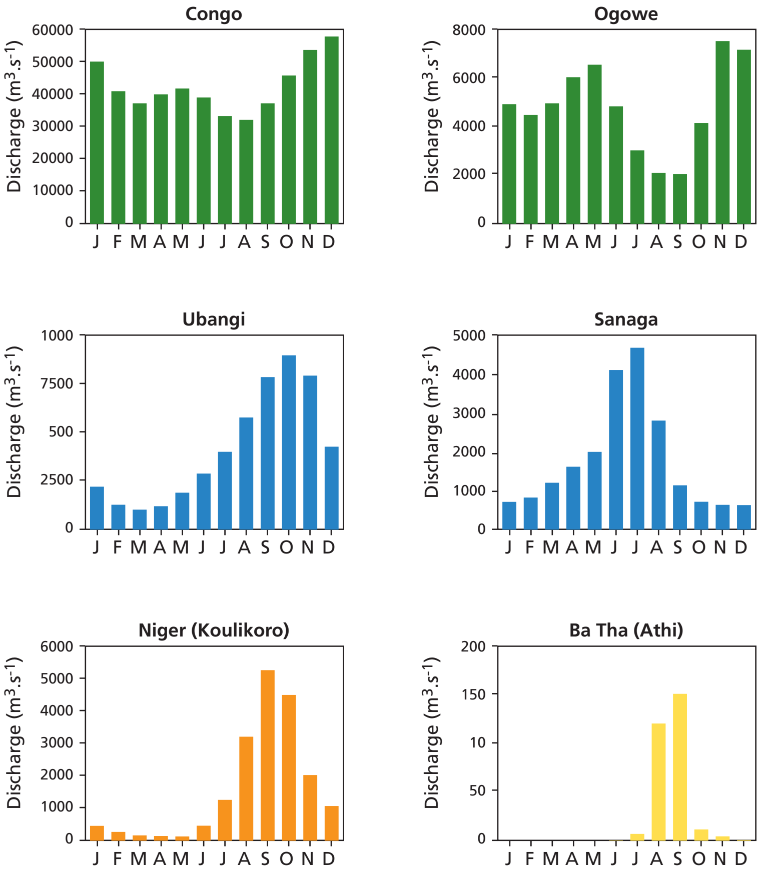


FIGURE 2.3.
Comparison of the hydrological systems of some African rivers (discharge in m^3 per second): *Sahelian type*: Ba Tha at Ati, Chad (data from Orstom) *Tropical type*: Niger at Koulikoro, Mali (data from Orstom) *Tropical transition type:* Sanaga at Edéa, Cameroon (according to Olivry, 1986) Ubangi at Bangui, RCA (data from Orstom) *Equatorial type:* Ogowe at Lambaréné, Gabon (data from Orstom) Congo at Brazzaville, Republic of the Congo *(data from Orstom).*

- Tropical systems with a single flood period more or less spread out over the year, followed by a dry period. This system may be further distinguished into:

– transitional tropical systems (an intermediate between tropical and equatorial system) in which the high water period is longer than the lowest water level period (for example the Ubangi in Congo and the Sanaga River in Cameroon, figure 2.3);

– tropical systems where the low water period is slightly more significant than the flood period (the Niger River is a good example of that, figure 2.3);

– Sahelian systems in which the flood period is limited to some months in the year, while the discharge is interrupted for several months (observed in the Ba Tha River at Ati in Chad, figure 2.3). The extreme situation is that of rivers in desert zones where flow is limited to flash floods after storms.

Average discharges of medium and large rivers that accumulate flows from several tributaries are relatively regular throughout the year. Meanwhile, smaller rivers are characterized by large seasonal fluctuations of water levels. These fluctuations reflect the uneven distribution of rainfalls.

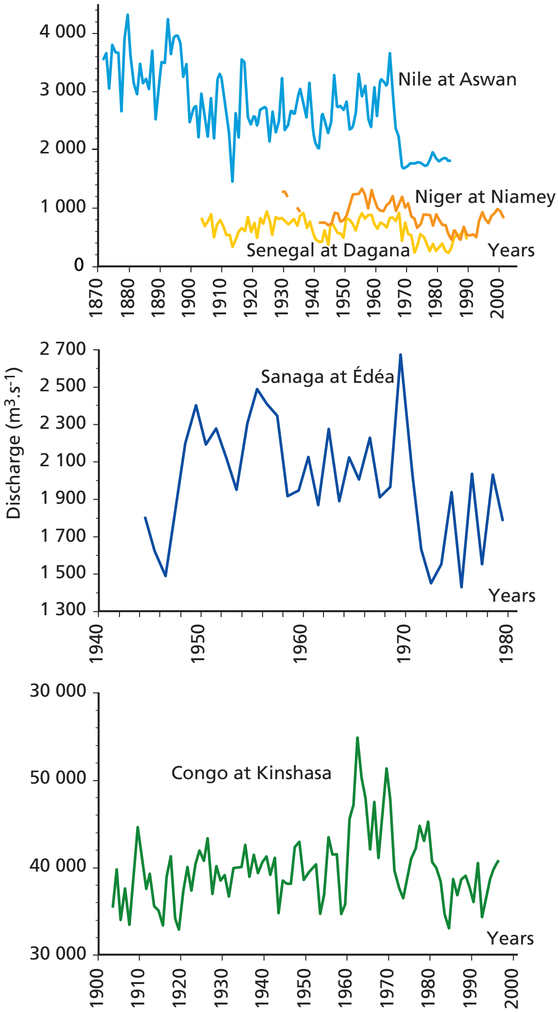
In addition, certain rivers have more or less pronounced low water levels, sometimes with periods during which flow is completely interrupted. Such intermittent rivers, such as the Red Volta River in Burkina Faso or the Baoulé River in Mali, do not offer the same ecological conditions for aquatic fauna as perennial rivers would.

Climatic and hydrological variability over decades and centuries

Numerous studies had focused on the considerable inter-annual variability and irregular distribution of rains and their impact on river discharge, especially since the drought of the Sahel that started in the early 1970s. The annual peaks of precipitation in the Sudano-Guinean region showed a downward trend since as early as 1968. This rarefaction seems to have continued over a period of about twenty years. During the 1980s, the duration of drought in central Africa became more prolonged and large rivers of tropical humid and equatorial zones of Africa were in turn seriously affected by reduced flows. Even if a recent improvement were to occur, it would remain insignificant because annual precipitations are still deficient (Olivry *et al.*, 1995).

Data has been collected since the beginning of the 20th century on the discharges of some large Sahelo-Sudanian rivers such as the Senegal, Niger and the Nile (figure 2.4), as well as several decades of data from other rivers. These data indicate that the recent drought in the Sahel is not a unique phenomenon, but that similar conditions had existed during the 20th century particularly during the 1910s and 1940s. Between 1950 and 1990, the most humid period in the Sahelian region was observed between 1951 and 1970, with a maximum in 1962-1963 (Mahé, 1993; Mahé *et al.*, 1990). The driest years recorded occurred between 1980 and 1990, with a minimum in 1983.

FIGURE 2.4.
Evolution of the average annual discharge of some large African rivers during the 20th century (data from Orstom).



Since 1970 the West African Sahel has experienced a significant drought which appears to correspond to abrupt change (between 1966 and 1970) in the long rainfall series collected since the end of the 19th century (L'Hôte *et al.*, 2002). A similar discontinuity (between 1969 and 1970) was also found for West and Central Africa for the series of regional rainfalls over the period 1951-1989 (Mahé & Olivry, 2001). The Sahel drought persisted into the beginning of the 21st century despite two wet phases in 1994 and 1999 which raised hopes of a remission. The decrease in precipitation observed before and after this disjunction varies between 15 and 30% depending on the zones. One of the first consequences of this decrease in precipitation was a 30 and 60% decline in flow within principal water courses of the region (Olivry *et al.*, 1998). This translates to a decrease of surface water resources which has had consequences for the vegetation cover and has accelerated desertification.

RECESSION OF THE SAHELO-SUDANIAN RIVERS

Variation of rainfall and river flows in the medium term have significant consequences for the evolution of certain continental aquatic ecosystems such as Lake Chad and, more generally, for endorheic lakes. Their hydrological budgets depend principally on supply from tributaries and loss from evaporation.
Lake Chad experienced spectacular changes of the aquatic environment between 1965-1978, with significant consequences for the biology of species and the composition of fish communities (Carmouze *et al.*, 1983; Bénech & Quensière, 1989). The area of the lake decreased from about 25,000 km² in 1965 to only 5,000 km² in the middle of the 1970s, with a decrease of the average depth to 3 m and the transformation from a predominantly lacustrine system to a marsh-type system (see box "From Mega to Marshy Chad").
A comparable situation was observed in Lake Chilwa which dried up in 1968 and then recovered normal water levels between 1969 and 1972 (Kalk *et al.*, 1979).
Lake Naivasha (Kenya) also experienced a period of low levels between 1945 and 1955 (figure 2.5).
Major changes in lacustrine levels have also been observed for other East African lakes. The depth of Lake Turkana for instance decreased by close to 15 m within a century (figure 2.5). Lake Victoria however experienced very high levels in the mid-1960s (see box "Is there a risk of Lake Victoria drying out?"). Lake Malawi, which overflows annually into the Zambezi via the Shire River, experienced an interruption of this connection between 1915 and 1935 when the rainfall fell below normal.

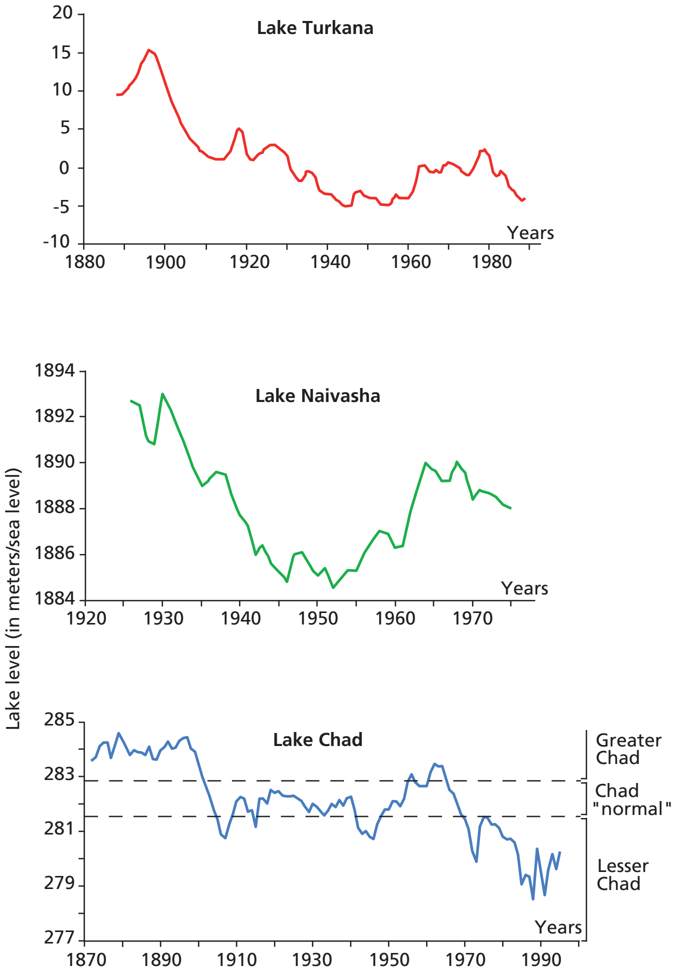


FIGURE 2.5.
Lake depth changes in Lake Turkana (Kolding, 1989), Lake Naivasha (Litterick *et al.*, 1979) and Lake Chad (Olivry *et al.*, 1996).

The Sahel drought had a counterpart in Central Africa, a region also known as "wet Africa" (Laraque *et al.*, 2001). With regards to the equatorial zone, the inter-annual mean discharge of the Congo River is 41,000 $m^3 s^{-1}$ for a recorded period of 86 years, with extreme mean from 55,200 $m^3 s^{-1}$ in 1962 to 33,300 $m^3 s^{-1}$ in 1984. The river was comparatively regular over the entire period up to 1960, while for 1960-1970 exceptional floods were recorded in 1961, 1962 and 1969. The means in the 1970s were closer to normal but with a period of great deficit, centred around 1972-1973, which chronologically corresponds to the beginning of the Sahelian drought. The 1980-1990 period marked a decade of generally diminished river flows, particularly in 1984 (Olivry *et al.*, 1995).

The decrease in river flood discharges is not the only consequence of the drought. There is also a decrease in low water level discharge resulting from depleted groundwater. The reduction of the flow of certain tropical rivers, marked by longer and more frequent interruptions during the low water period, has adversely affected fish communities.

Long-term climatic and hydrological changes

Long-term change in rainfall and the extent of aquatic ecosystems can be reconstructed using various methods (study of sediments, fossil diatoms, etc.) or deduced from ancient climatic fluctuations (palaeoclimates) which are underscored by changes in terrestrial vegetation. Variations in the expansion of dense tropical rain forests which cover regions that receive at least a monthly rainfall of 100 mm, and whose average annual temperature exceeds 24°C without any period of freezing, are useful for the study of climatic changes in geological time.

Climatic changes over millennia

From around 150,000 to 130,000 years ago, Africa experienced colder and more arid periods than present conditions. About 130,000 years ago, a warm phase moister than the present began, and this lasted until about 115,000 years ago, with greater rainforest extent and the deserts almost completely covered with vegetation. A rise of sea level occurred some 140,000 years ago and reached a maximum 125,000 years ago. This phenomenon was accompanied by increased temperatures and rainfall, translating into a major humid period in the Sahara (Petit-Maire, 1994; Leroux, 1994).

Progressive change of the climate has been observed during the last 115,000 years with periods of degradation followed by regeneration of terrestrial environments varying substantially according to latitude. Little is known about the periods between 100,000 and 50,000 years before present (BP). Phases of cooling and drying of the climate led to a cold, arid maximum about 70,000 years ago, Between 50 and 40,000 years BP a dry phase occurred in

IS THERE A RISK OF LAKE VICTORIA DRYING OUT?

Lake Victoria plays a vital role in supporting the millions of people living around its shores. The basin serves as a major source of employment for some 30 million people, of which 80% are engaged in agriculture. For a long time, the lake has been subjected to a high level of eutrophication. This phenomenon is a result of human activities, mainly agricultural development because the surrounding basin is intensely cultivated.

Lake Victoria's water level remained relatively stable from the turn of the 20th century to 1960. In late 1961 and early 1962, the lake received unusual and abundant rainfall and unexpectedly rose 2.5 metres. The water level has remained above average for more than 40 years since 1963. However, *the lake's surface lowered progressively* and the lowest level since the beginning of the 1960s was recorded in 2005 (figure 2.6). The lowering of the lake had economic consequences: ports were closer to closure, and it caused some regions on the lake to institute water rationing.

The lake level became therefore a matter of concern, and a debate rose about the causes of the lake level changes: rainfall variability or human impacts?

The lake typically recharges during the "short rain" (October-December) and "long rain" (February-June) seasons. It seems that the water level of Lake Victoria is extremely sensitive to moderate changes in rainfall (at least 80% contribution to the water budget) over the lake and its catchments (UNEP, 2004b). According to Mangeni (2006) no significant influence on lake level could be deduced from changes in rainfall, evaporation and drought conditions, as these remained essentially about average at least up to 2004. Another study established an annual water balance model of Lake Victoria for the period 1925-2000 (Tate *et al.*, 2004) (figure 2.6). Climate changes scenarios were applied to the lake rainfall inflows series and evaporation data to estimate future water balances of the lake. The scenarios produced a potential fall in lake levels by the 2030s and a rise by the 2080s. On the other hand, Yousef Shahinaz & Amer (2003) pointed out a very close relationship between solar forcing and the level of Lake Victoria (and other lakes).

However, some other hypotheses accused the power stations established on the Ripon Falls, the lake's only outlet, to contribute to the depletion of the lake. In 1954, Owens Falls Dam (later renamed Nalubaale) was commissioned downstream of Ripon Falls to generate hydroelectricity along the Victoria Nile River and became Uganda's largest power station. The Nalubaale power station was recently expanded by Kiira power station located about one kilometre above. Comparison of the trend of the Jinja releases and satellite Lake Victoria height variations was carried out from 1998 to 2004 (Mangeni, 2006). The results indicated that the releases of the dams were no longer based on the agreed operational rule curve after 2001. More water than authorized was being released. Soon after, a consultant also claimed that the power stations were using more water than allowed (Kull, 2006).

The question is not yet completely solved. Independent of the dams' releases, the water levels of the lake seem to be mainly controlled by the climatic balance of the inflows (mainly rainfalls) and outflows. At the beginning of 2007 the water level of Lake Victoria had increased substantially and was still rising due to ongoing rains. This event supports the proponents of climatic variability!

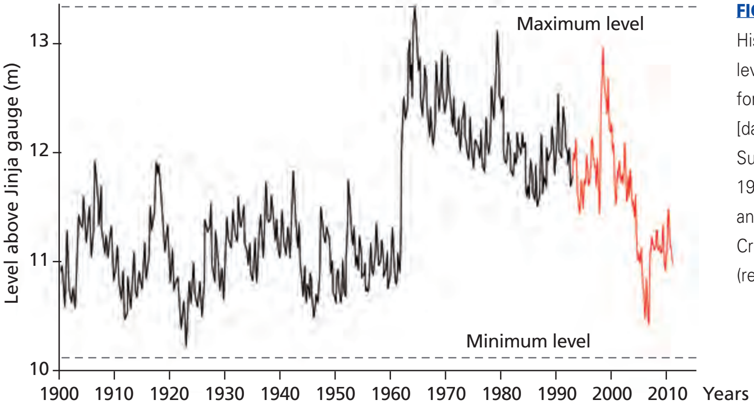


FIGURE 2.6.
Historical water level elevations for Lake Victoria [data from Sutcliffe & Parks, 1999 (black) and Legos: Crétaux *et al.*, 2011 (red).

FROM MEGA TO MARSHY CHAD

The impact of climate through changes in precipitation and enhanced evaporation could have profound effects in river discharges and lakes levels. Lakes for instance are sensitive to climate variability via pronounced changes in storage, leading, in some cases, to drying, changes in their extent, reduced outflow, etc.

Lake Chad provides a very good example of such dynamic systems which are constantly changing in size, shape, and depth. This very shallow endorheic system is particularly sensitive to fluctuations in water budget (rainfall, discharge and evaporation), which occurs both annually and over decades. A Mega Chad probably occurred some 10 000 years ago, covering at least 300 000 km^2 (almost the size of the Caspian sea) (UNEP, 2004a).

More recently, many observations suggest that the level of Lake Chad fluctuated during the 19th and the beginning of the 20th century (figures 2.7 and 2.8).

In the 1960s Lake Chad was, however, the sixth largest lake in the world (25,000 km^2). Since that time, the volume and area decreased rapidly as a response to the Sahelian drought. It is now no more than a small marshy area (less than 1,500 km^2) close to the Chari mouth (see figure 2.9).

There is a debate on the reasons for this low water situation. Is it the consequence of climate change or does it result from human influence through water diversion and extraction for irrigation? Plainly speaking, the climate has without a doubt been the main driving factor. So, in a few decades, the aquatic system completely changed, as well as the aquatic fauna, as the result of "non-anthropogenic" changes.

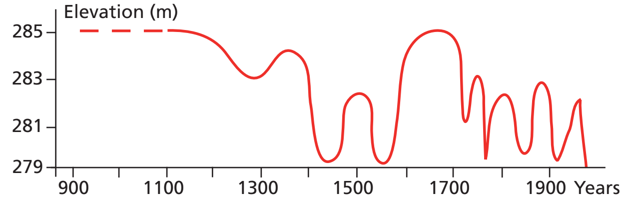


FIGURE 2.7.

Evolution of Lake Chad level over the last millennium (from Maley, 1981).

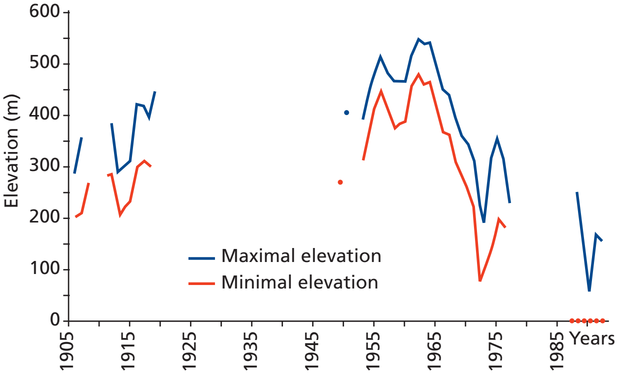


FIGURE 2.8.

Evolution of Lake Chad level over the last century (from Olivry *et al.*, 1996).

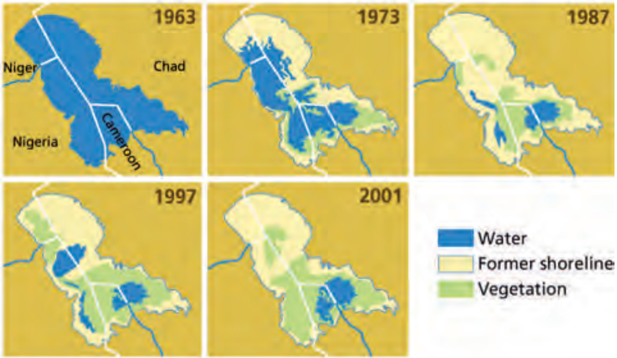


FIGURE 2.9.

Chronology of the reduction of open water affecting Lake Chad (UNEP GIWA, 2004). Maps were taken in January each year and have been sourced from satellite images provided by NASA Goddard Space Flight Center.

the Niger, followed by two humid episodes until 20,000 years BP although in general, the African continent experienced hot and humid conditions between 25,000 to 22,000 years BP with temperature and rainfall slightly above the present.

The past 20 kyears encompass extreme climatic conditions, including the last glacial maximum (LGM) around 18 kyears ago and the early Holocene (10-4.5 kyears BP) when monsoon rainfall in the northern tropics was considerably reinforced in response to orbital forcing.

Lake level records show evidence of several short-term dry periods from 13 kyears BP to present in Africa. The major ones occurred during the following intervals: 11-9.5 kyears BP, 8-7 kyears BP, 6 kyears BP, and 4-3 kyears BP (Gasse, 1998).

The last glacial maximum was characterized by an overall decrease of the average temperatures by approximately 8°C relative to the present for the whole of northern Africa (Frenzel *et al.*, 1992) and more accentuated cold temperatures on the borders of North and South Africa. The ocean level was 130 m below the current level. In the Sahara, the highlands of the Hoggar and Tibesti Mountain ranges received comparatively high rainfall, Meanwhile, low altitude zones and the sub-Saharan zones progressively dried out. The general decrease in rainfall resulted in a decrease in lake levels. For instance, Lake Chad disappeared around 15,000 years BP. Lake Tanganyika was at least 300 m below its present level. River systems were disrupted, an example being the Niger River whose flow was interrupted by dunes in its internal delta. Likewise, the lower valley of the Nile was also invaded by dunes after 17,000 years BP. In East Africa, Lake Tanganyika experienced a phase of regression between 17,000 to 12,500 years BP, with near-total drying of the southern basin and a decrease in depth of some 300 m relative to its current level (Tiercelin *et al.*, 1988). Lake Victoria was also totally different from present conditions some 40,000 years BP. Its lowest levels (75 m below its current level) occurred between 14,700 and 13,700 years BP (Stager *et al.*, 1986) at which time it was alkaline, endorheic, and occupied a very small area. Johnson *et al.* (1996) estimated that Lake Victoria was completely dried out 17,000 years ago, which somewhat perplexes ichthyologists interested in the hundreds of endemic Cichlid species of the lake and in their origins. If complete desiccation occurred, these numerous endemic species may have evolved during the last 12,400 years BP, dating back to the refilling of Lake Victoria which recovered its drainage to the Nile about 12,000 BP.

As a whole, during the last glacial period, vegetation was highly degraded on the African continent with an almost-total disappearance of dense forests except in certain sheltered sites. This led to the formation of savannahs and steppes, and a considerable extension of dune structures especially in the Sahara. Around Lake Barombi Mbo (Cameroon), forest existed in the form of a small island in a semi-arid area (Giresse *et al.*, 1994). However, dense forest was generally replaced by mountain prairies at lower altitudes of 800 to 1,000 m on the Bamileke plateaus (Maley, 1987) due to temperature decreases of about 5 to 6°C. In the Congo basin the savannah expanded progressively to the detriment of the dense humid forest that now exists only in some refuges (highlands and edges of the watercourses) (Colyn, 1987). These changes in climatic conditions and terrestrial environments (figure 2.10) have certainly had an influence on aquatic systems and fish communities although precise data is unavailable at this point.

Past glacial warming was associated with monsoon reactivation. An increase in humidity recurred approximately 12,000 years ago. The Holocene climatic optimum that extended from -9,000 to -6,000 years BP was characterized by a general warming. Rain forest reappeared abruptly in Ghana about 9,000 years BP and, at the same time, there was a decline of highland forests. In Western Africa and the Congo basin the re-colonization by forest may have occurred from refuges in less than a millennium (figure 2.7). There was also an increase in rainfall and a consequent increase of lake levels. The Sahara in particular was well-watered and a multitude of shallow freshwater lakes occupied interdunal depressions; a grass cover developed and grazing herbivores migrated (Petit-Maire, 1991; Petit-Maire *et al.*, 1994). This period was also a period of intensive recharge of the aquifers in the Sahara and the Sahel. Lake Taoudeni to the north of Mali experienced a maximum around 8,000 years BP, while the Niger spread its internal delta to the north of Timbuktu. The Saharan tributaries of the Niger, Senegal and Chad had a quasi-permanent flow. Lakes Ziway, Langano, Abijatta and Shala in the Ethiopian Rift formed a single lake and Lake Abbe in the Dankali depression was 160 m above its current level (Gasse *et al.*, 1980). In southern Africa, climatic optimum is expected to have occurred between 10,000 and 8,000 years BP.

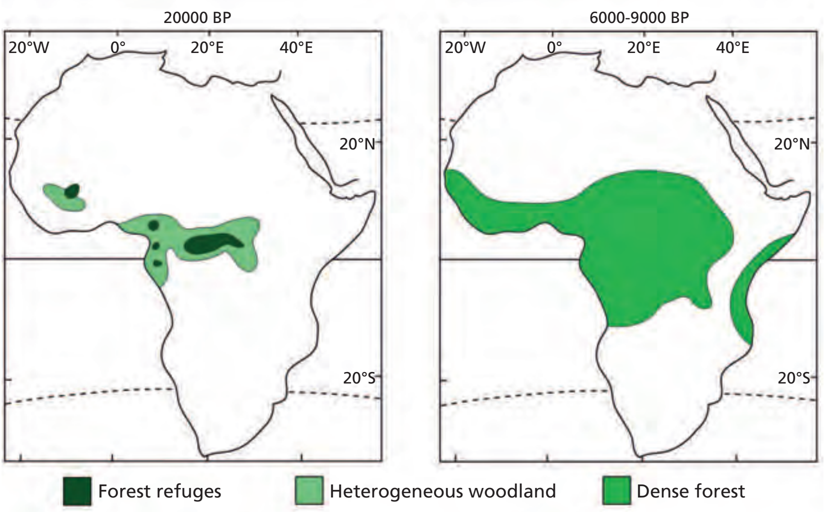


FIGURE 2.10.
Variations of the extent of tropical humid forest during the last glacial cycle (according to Leroux, 1994).

Following the humid phase, rainfall declined in the Sahara although the climate remained comparatively humid until about -4,500 years BP. This marked new climatic changes in Africa with aridification within the Sahara and decline of the hydrologic conditions. The present tendency in the evolution of the climate is seemingly towards a cold scenario with reduction of about 0.01°C per century in global temperatures.

Over the last 20,000 years, the position of the Sahara-Sahel boundary has experienced major fluctuations linked to these climatic variations (figure 2.11).

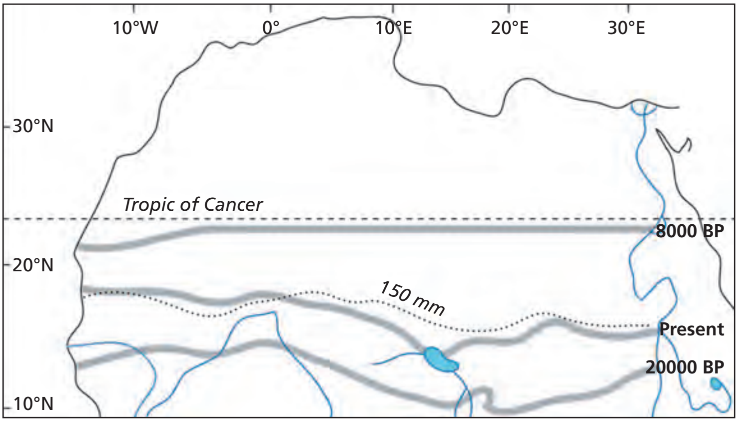


FIGURE 2.11.
The displacement of the Sahara-Sahel boundary over the last 20,000 years (from Petit-Maire, 1994).

RELICT FAUNA IN THE SAHARA

Since the beginning of the century numerous adventurers have brought back fish captured from small water bodies in the Sahara (gueltas, wadis). About fifteen species have been identified (Lévêque, 1990), consisting of several *Barbus* (*B. apleurogramma, B. bynni occidentalis, B. deserti, B. macrops, B. pobeguini*), two species of *Labeo* (*L. niloticus* and *L. parvus*), *Raiamas senegalensis*, two species of *Clarias* (*C. anguillaris, C. gariepinus*), one Cyprinodontidae (*Epiplatys spilargyreius*), and three Cichlidae (*Hemichromis bimaculatus, Sarotherodon galilaeus, Coptodon zillii*). The largest number of species were collected from the Ennedi-Tibesti region, live fish were however captured in Adrar of Mauritania, Hoggar and Tassili N' Ajjer.

Almost all the species, with the exception of *B. apleurogramma* and *B. deserti*, are present in the southern Nilo-Sudanian pools. It is now well established that these species are the relics of a rainy era during which the Chad and Niger basins extended much farther north (see Servant, 1973; Talbot, 1980). The current populations were isolated approximately 5 to 6,000 years ago.

B. apleurogramma is currently only known from Lake Victoria and its tributaries. It is probable that it is a relic type of an older fauna that extended more to the north and that disappeared, partly due to the numerous climatic changes that affected this region for more than 2 million years.
B. deserti on the other hand was found on the versants of Tassili and in Libya.

(see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*.

LAKE SEDIMENTS RECORD CLIMATIC HISTORY

The study of lake sediments allows the acquisition of information relating to the characteristics of aquatic ecosystems during different historical periods, and also to deduce information on the variability of climatic conditions.

In a sediment core realized for Lake Tritrivakely in Madagascar, Gasse *et al*. (1994) and Sifeddine *et al* . (1995) demonstrated a succession of very different environments.

- 36,000 years ago, the climate was humid, the lake was filled with water and the organic sedimentation was owed principally to phytoplankton.
- between 36,000 and 20,000 years BP, progressive aridification of climatic conditions and colonization of the bottom of the lake by peat bog vegetation translate to an important decrease in water levels.
- about 20,000 years ago, during the last glacial maximum, biological production was very weak, with the near-absence of diatoms and of aquatic plants in sediments suggesting partial periods of drying up.
- conditions favourable to aquatic life were re-established at about 14,500 years BP with the presence of organic matter derived from phytoplankton in large abundance. The climate once again became humid with a maximum between 9,000 and 6,000 years.
- the period 6,000 years before present began with the existence of a peat bog, which indicates a period of drying up. This period was followed by a humid period that manifested as a lacustrine type of sedimentation, culminating in the current peat bog which appears linked to the progressive filling up of the lake.

Climatic changes over millions of years

The geographic distribution of large assemblages of vegetation that we currently observe within the African continent date back about 14 million years, *i.e.,* during the time of the positioning of the African continent in its current geographic location. Previously, Africa's location was further south, such that the Sahara was traversed by the equator. 60 million years ago, dense rain forest occupied the whole of North Africa up to the Mediterranean coast (figure 2.12).

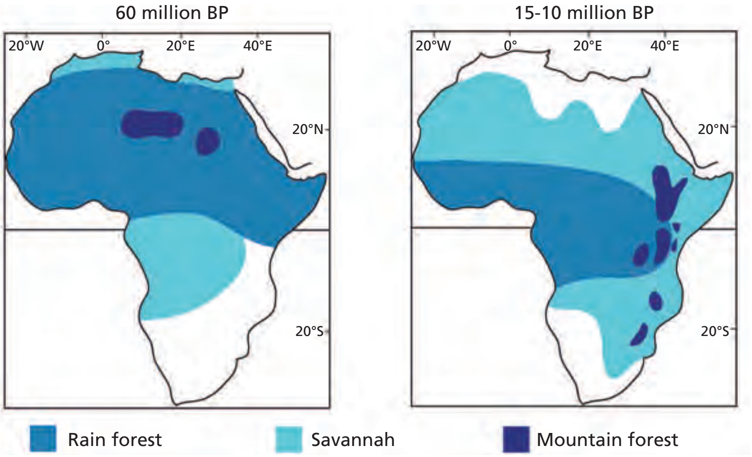


FIGURE 2.12. Distribution of the large assemblages of vegetation during the Tertiary period (from Bonnefille, 1993).

About 6 million years ago, the Earth's climate underwent significant modifications referred to as the "Messinian salinity crisis", linked to the spread of the Antarctic glaciation. The first major arid period in Africa, marked by the extension of the savannahs, dates back 2.5 million years. During the same era, significant cooling appeared leading to the formation of ice caps in the northern hemisphere.

From this period the global climate experienced repeated glacial/interglacial cycles, with a periodicity of about 40,000 years between 2.5 and 0.7 million years ago and a periodicity of 100,000 years over the last 700,000 years. Some 20,000 years ago, the glacial period coincided with the major extension of icecaps. It has been shown that these glacial periods lasted on average ten times longer than the interglacial periods. As a result, past periods of tropical drought lasted ten times longer than wet periods.

The palaeoclimatic history over the last three million years indicates the occurrence of an alternation of dry and wet periods which allowed the restoration of permanent aquatic ecosystems (Bonnefille, 1993). The recent drought in the Sahel is thus not exceptional, and is in accordance with this climate variability, without predicting whether it is a long-term or short-term event.

African fossil fish

OLGA
OTERO

ALISON
MURRAY

LIONEL
CAVIN

GAËL
CLÉMENT

AURÉLIE
PINTON

KATHLYN
STEWART

This chapter illustrates how palaeontology helps to retrace the evolution of African fish, and what can be learned about their palaeobiogeography, adaptation and ancient environment. The first part (1. Africa and fish through geological time) is a presentation of the fish fossil record within the environmental contexts that prevailed in continental Africa through geological time, followed by a focus on the fossils themselves. Using the case study of African characiform fossils, the second part (2. Which fossils? Case study of the African characiforms) illustrates the various kinds of fossils and fossil remains that can be recovered and explains what information fossils can give us. The third section (3. Old groups, old cradles!) focuses on biogeographical information, using the example of one emblematic archaic fish: the lungfish. The fourth part (4. When a marine fish adapts to freshwater) tracks the invasion and extinction of stingrays in the Turkana basin and discusses the still-debated origin of the Nile perch in Africa, to demonstrate the links between fossil fish and their environment, thus giving us information on long-term environmental change. The last section (5. Neogene changes in the African ichthyofauna) is a conclusion concerning the impact of the most recent long-term environmental changes which deeply modified Africa fish faunas, notably the uplift in Eastern Africa and the Saharan aridification.

Africa and fish through geological time

The history of life on Earth started about 3.8 billion years ago. The metazoans (multicellular animals) appeared 545 million years ago, initiating the Phanerozoic eon which literally means the times of visible animals (figure 3.1). Metazoans diversified first in marine waters and then in both marine and continental environments, following the colonization of fresh waters and land by plants. Among these metazoans, vertebrates occupied various available habitats. Their evolutionary history is shaped by the geological and climatic context prevailing on the continent, and on the processes of diversification and extinction.

Here, we present the main issues of the geological and environmental background in which the evolutionary history of fish took place in Africa throughout time (figures 3.2, 3.4, 3.5). The tectonic history reviews the periods of connection and isolation of the continent as well as the latitudinal position of the African plate. Combined with continental topography and global climate, this explains the main features of the environmental conditions that prevailed at a regional scale. We use one emblematic ichthyofauna to illustrate the main features of African fish fauna for each era.

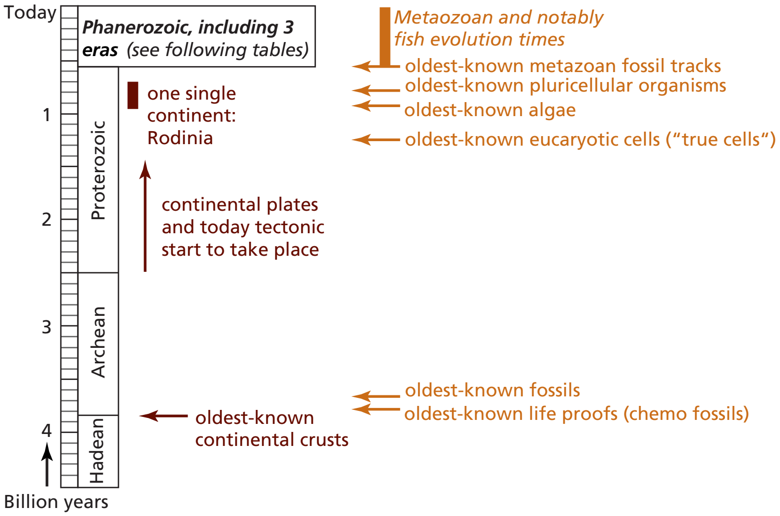
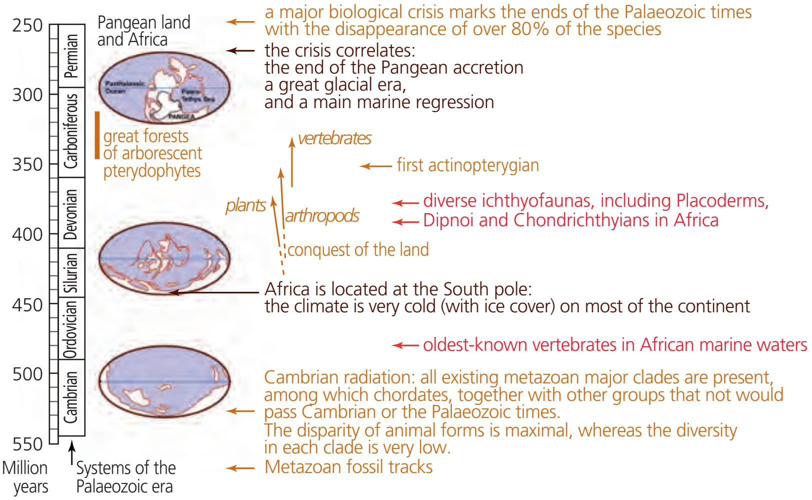


FIGURE 3.1.
Timetable resuming the main aspects of geological modifications and biological evolution through the Pre-Cambrian time.

The Palaeozoic

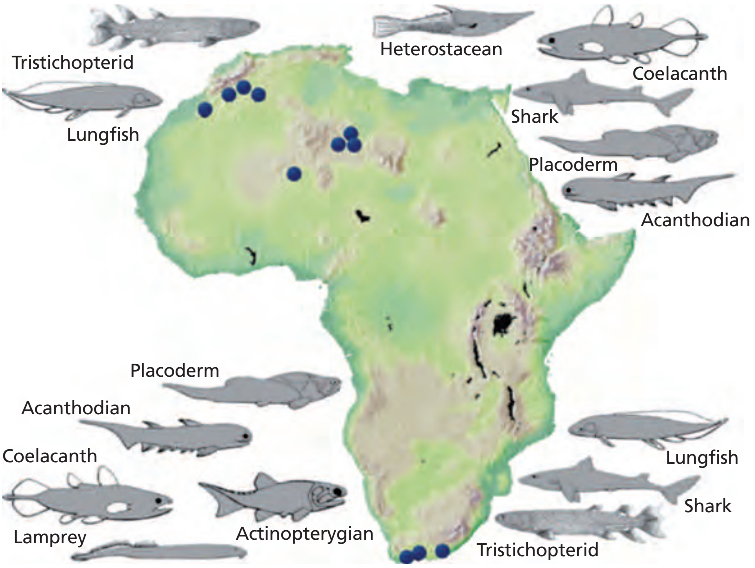
Although some rare isolated vertebrate remains are known in the Early Palaeozoic of Africa, the rise and diversification of major groups of vertebrates occurred during the Middle Palaeozoic era (Silurian and Devonian; figure 3.2). Some of them, such as the armoured agnathan fishes (heterostracans and osteostracans for instance) and the placoderms (armoured jawed fishes), disappeared at the end of the Devonian. Some others, such as the "naked" agnathans (lampreys), chondrichthyans (sharks, rays and chimaeroids), actinopterygians (ray-finned fishes), actinistians (coelacanths), dipnoans (lungfishes) and tetrapods ("terrestrial" vertebrates), had long and flourishing evolutionary histories. These groups now make up the modern vertebrate faunas. Although the actinopterygians currently represent the most diversified group of vertebrates with about 32,000 species distributed in both marine (58%) and freshwater (41%) environments (Nelson, 2006), Middle Palaeozoic actinopterygians were neither diversified nor abundant, and originally were limited to marine waters. So far, the oldest-known putative actinopterygian comes from the Upper Silurian marine deposits of Sweden and China. The earliest presumed freshwater actinopterygians are known from mid-Devonian deposits of Scotland, Australia and Antarctica (see Friedman & Blom, 2006 for a review of the first-known actinopterygians).

FIGURE 3.2.
Timetable resuming the main aspects of geological modifications and biological evolution through the Palaeozoic era.



During the Middle and Late Palaeozoic, present-day Africa was part of the Gondwana landmass, which itself was part of the supercontinent Pangea (figure 3.2). The movements of land masses have been reconstructed on the basis of palaeomagnetic, biogeographic and palaeoclimatic data. This land mass slowly moved in the southern hemisphere and, during the Devonian, central Africa was located near the South Pole (figure 3.2). The polar position of Africa during the Middle Palaeozoic and the climatic conditions related to that position explain the scarcity of the fossil fish record in general and of freshwater fishes in particular during those times. However, some African sites document this astonishing fish fauna which exhibits the last groups of the earliest vertebrates

FIGURE 3.3.
Map of the main sites that have yielded Palaeozoic lower vertebrates with outlines of the animal reconstructions (from Anderson *et al.*, 1999b, modified). Their distribution at the southern and northern borders of the African continent is to be related with the polar position of the continent and the climate induced.



and the early actinopterygian fishes (figure 3.3). A few heterostracans and acanthodians ("spiny sharks") have been recorded in the Silurian of Algeria. Placoderms, acanthodians, chondrichthyans (sharks), actinopterygians and sarcopterygians (lobe-finned fishes) have been found in the Devonian of South Africa (see box "A Late Devonian African fish fauna in South Africa"), Morocco, Algeria, and Libya (e.g., Lelièvre *et al.*, 1993, Murray, 2000).

During the Late Palaeozoic (Carboniferous, Permian), no major diversification is reflected in the fish faunas. The actinopterygians that inhabit the African fresh waters are primitive taxa, notably palaeoniscoid fishes known from the lacustrine and fluviatile deposits of Carboniferous sediments of South Africa (Jubb, 1965a; Gardiner, 1969; Jubb & Gardiner, 1975) and of Permian sediments of South Africa, Namibia, and Zimbabwe (Evans & Bender 1999; for a review see Murray, 2000).

The Mesozoic

During the Triassic and the Jurassic, Pangea started to split apart as it rotated in a global northward movement (figure 3.4). At the end of the Jurassic and first part of the Cretaceous, this resulted in a configuration of the world land masses that would eventually result in the isolation of the Afro-Arabian plate that was to last throughout the Late Cretaceous and most of the Tertiary (figure 3.4). These changes in land and marine connections, and the associated changes in oceanic circulation pattern and climate, produced new conditions for the organisms living at that time, but did not induce any great biotic extinction/radiation events. Lungfishes and other sarcopterygians show a greater diversity of species throughout the Mesozoic era than today, including in African fresh waters. In addition, the diversification of basal teleost fish was rather slow during most of the Mesozoic. Despite the absence of any remarkable biotic crisis at the Jurassic/Cretaceous boundary, the Late Jurassic/Early Cretaceous was a significant time with the initial diversification of crown group teleosts occurring (Cavin *et al.*, 2007a).

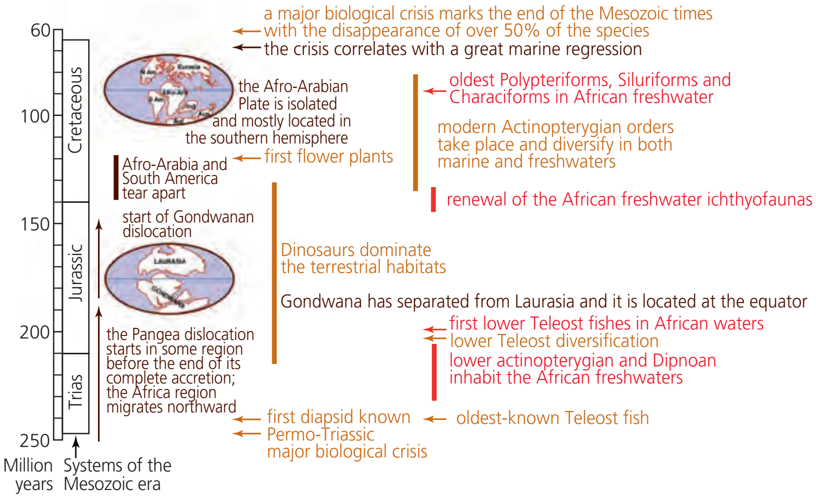


FIGURE 3.4.
Timetable resuming the main aspects of geological modifications and biological evolution through the Mesozoic era.

By the Late Jurassic, fishes had been colonizing the waters of the Earth for well over 300 million years. Although they had already evolved greatly from their early ancestors, the Jurassic fish fauna still would be unfamiliar to people today. Many of the Jurassic fishes were heavy bodied forms with thick scales covered by enamel (ganoin), large mouths, paired fins placed well posteriorly on the body, and heterocercal tails (see box "The Stanleyville Beds assemblage, a typical 'ganoid fish fauna'"). They formed a diverse fauna of ganoid fishes in most regions of the world including non-teleost ray-finned fishes (basal Actinopterygii), essentially the chondrosteans and neopterygians with common semionotiforms, amiiforms, pycnodonts, macrosemiiforms, and lepisosteiforms. Today, only some of them are still represented by a few species: chondrosteans by five genera including *Acipenser* and *Polyodon*; lepisosteiforms by *Lepisosteus* and *Actractosteus*, and amiiforms by *Amia* (Nelson, 2006). The teleosts arose in the Late Triassic and Early Jurassic with stem-group forms of uncertain relationships such as the "palaeonisciforms" and "pholidophoriforms" that formed a dominant component of the African fauna at the end of the Jurassic only.

The "pholidophoriforms" became extinct in the Late Jurassic, and the diverse fauna of ganoid fishes disappeared and was replaced during the Cretaceous by early forms of various teleost lineages including among others clupeomorphs, salmoniforms, osteoglossomorphs, elopomorphs and gonorynchiforms (Murray, 2000), and also probable osteoglossiforms (*Chanopsis*) and lepisosteids (*Paralepisosteus*?). By the Late Cretaceous, most of the modern orders of African freshwater fish diversify in the Afro-Arabian plate, which has become isolated from all the other land masses (figure 3.4). This early stage of the modern ichthyofauna is documented in a few outcrops in northern Africa, including in Morocco which offers one of the richest fish fossil records for this time period, including fossil species of extant freshwater fish orders such as Lepidosireniformes, Polypteriformes and Osteoglossiformes (see Cavin *et al.*, 2010, for a review).

The Cenozoic

The Afro-Arabian plate remained isolated from other continents during most of the Cenozoic, until it finally collided with Eurasia about 18 Myrs ago in the early Neogene (figure 3.5). The Palaeogene freshwater fish fossil record is relatively limited and is concentrated mostly in a few regions, notably the Lower Nile outcrops of the Fayum of Egypt, and in Niger and Nigeria (Otero, 2010). In these areas, outcrops yielded fossils assigned to extant families, and the earliest members attributed to modern genera were identified in late Eocene deposits from Egypt and Libya dated 40 and 34 Myrs ago (Murray *et al.*, 2010). Among a few others, two rich and diverse ichthyofaunas from late Miocene sites have been extensively described: one from the deposits of the ancient Lake Turkana in Kenya (Stewart, 2003a) and one from the Toros-Menalla fossiliferous area of the Djurab desert in Northern Chad (Otero *et al.*, 2010a). These faunas show the relative homogeneity of the African ichthyofauna that existed during the Miocene, at least in the north equatorial zone. The Chadian ichthyofauna resembles the modern Nilo-Sudanian fauna (see box "Toros-Menalla, a Cenozoic freshwater fish fauna 7 Myrs ago"). It

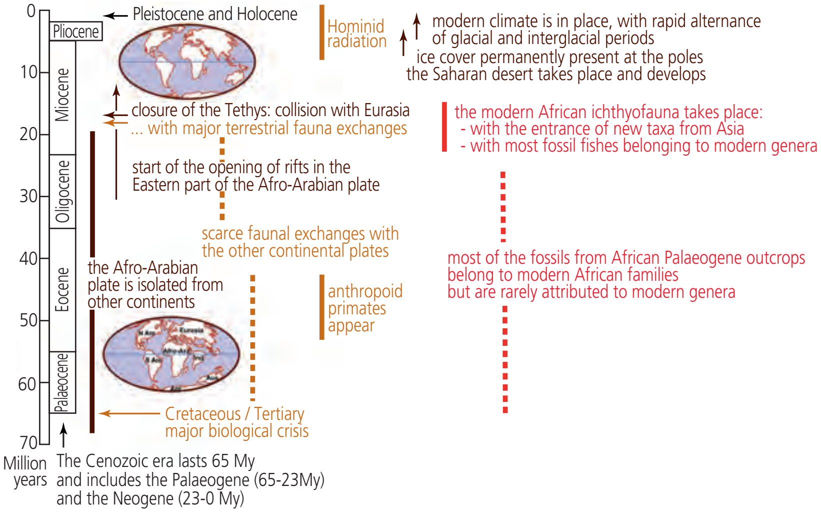


FIGURE 3.5.
Timetable resuming the main aspects of geological modifications and biological evolution through the Cenozoic era.

includes members of modern genera that belong to lineages that evolved in Afro-Arabia since the Cretaceous, and also the Eurasian fish lineages, such as the cyprinids, that have entered the continent by virtue of the tectonic connection of the two land masses. Some other extinct fish were also present and give a peculiar cachet to the Neogene fish fauna when compared to the modern. Finally, the other remarkable feature of the African fish during the Neogene is probably their distribution that was deeply modified notably at the northern margin of the Afro-Arabian plate, including in the Maghreb and into the Arabian Peninsula (see section *How the Neogene times shaped the African fish fauna*).

In any fossil assemblage, the diversity recorded is very fragmentary when compared with a living assemblage. Because of their strong resemblance with the modern fauna, the Neogene assemblages allow an evaluation of what information has been lost. First, due to sedimentary and taphonomical processes, the smallest taxa (such as cyprinodonts) and fishes with fragile bones and minute teeth (like mormyrids) are usually not recorded. This is the case in most of the Chadian outcrops that correspond to fluvio-lacustrine deposits (Otero *et al.*, 2009, 2010a, b). Moreover, the fishes from aquatic environments without a sedimentary record also have no chance to show (or preserve) a fossil record. This is the case for cave fish and taxa living in upstream environments. Meanwhile, fishes with strong ossification or differentiated large teeth and living in the main streams and water bodies have a better chance to be recorded, and their fossil record informs us of their distribution and evolution through time. For instance, this is true of several catfishes and of the Nile perch *Lates*, which are known by skeletal elements, and also of the tiger fish *Hydrocynus* and of the puffer fish *Tetraodon* known by their teeth and tooth plates respectively (Otero *et al.*, 2010a). However, some outcrops with exceptional preservation provide sporadic information on some taxa. This is, for example, the case of fishes described in an extinct family of killifish (Cyprinodontiformes) endemic in late Miocene deposits of

A LATE DEVONIAN AFRICAN FISH FAUNA IN SOUTH AFRICA

GAËL CLÉMENT

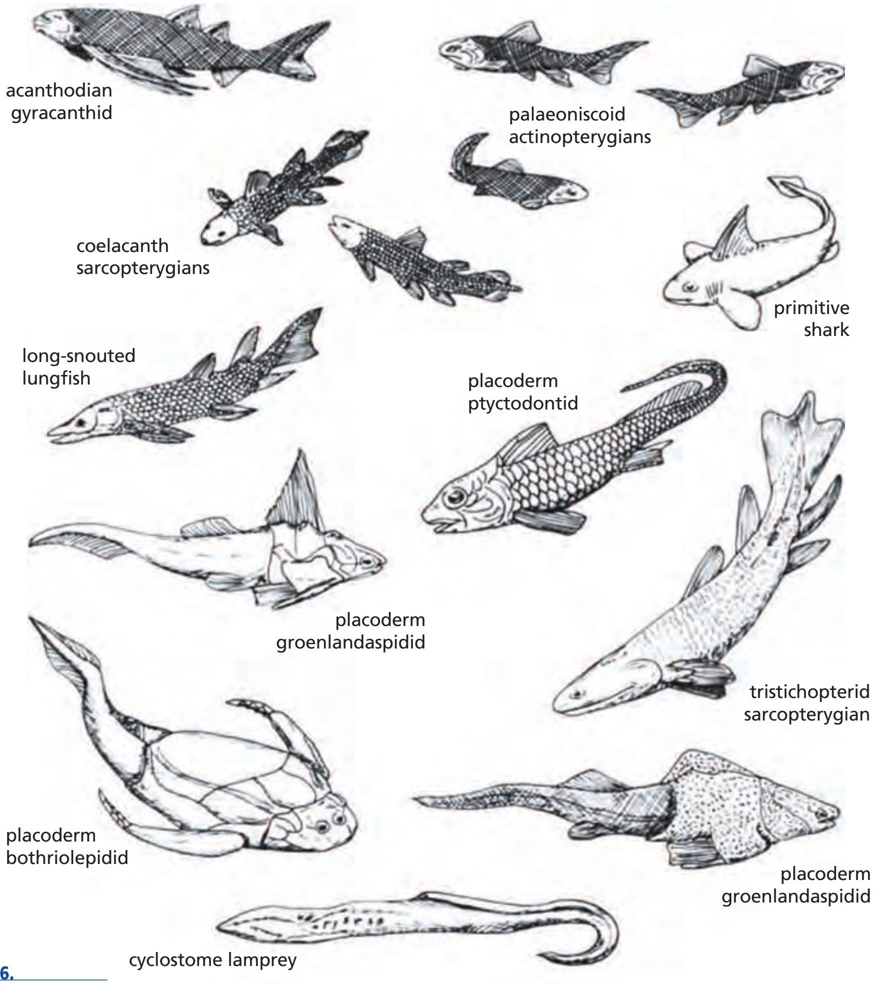


FIGURE 3.6.
The African lower vertebrate fauna at the Witpoort Formation, Witteberg Group, South Africa: drawings of some fossils and reconstructed outline of the animals (modified from Anderson *et al.*, 1999b).

The earliest probable freshwater fish fauna in Africa is the Late Devonian assemblage of the Witpoort Formation in South Africa, where various fishes have been found in black shales interpreted as having been laid down in a stagnant back barrier lagoon, an environment receiving both freshwater and marine sediments.

The fish fauna (figure 3.6) consists of placoderms, acanthodians, unidentified palaeoniscoid actinopterygians, and three sarcopterygian groups, *i.e.*, osteolepiform, coelacanth and lungfish (Anderson *et al.*, 1994; Long *et al.*, 1997). Exquisitely preserved fossil shark and lamprey fossils have also been described from this formation (Anderson *et al.*, 1999a; Gess *et al.*, 2006).

According to Young (1987) and Anderson *et al.* (1999b), this fish fauna, although partly composed of endemic forms, shows more affinities with those of East Gondwana (Australia, Iran) than West and North Gondwana (South America, Maghreb).

THE STANLEYVILLE BEDS ASSEMBLAGE, A TYPICAL "GANOID FISH FAUNA"

ALISON MURRAY & OLGA OTERO

The Stanleyville Beds in the Democratic Republic of the Congo have been assigned a Middle Jurassic age (Aalenian-Bathonian; Colin, 1994). They have yielded one of the better documented Jurassic freshwater ichthyofaunas in Africa with about twenty species (Saint-Seine, 1955).

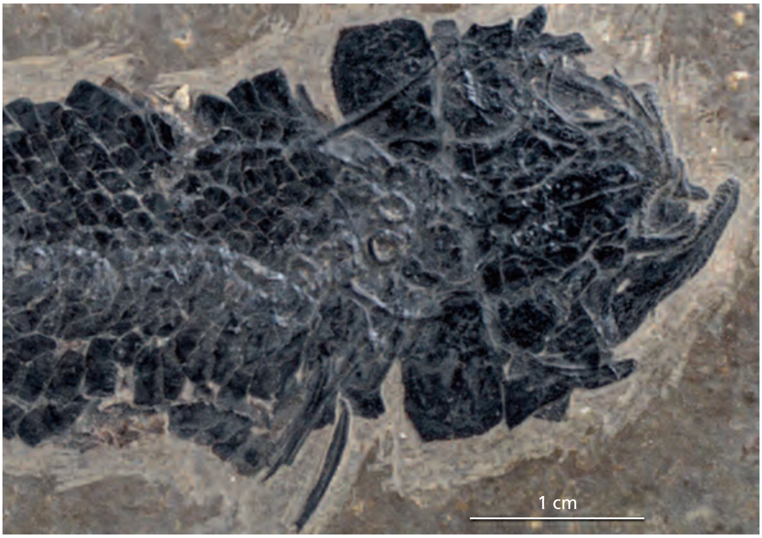
The majority of the fish remains from the Stanleyville Beds are "pholidophoriforms" (figure 3.7) represented by four families and 11 species.

Fishes of the genus *Lepidotes*, once included in the family Semionotidae, but now considered to be a lepisosteiform, two species of coelacanths, and one ionoscopiform have also been recovered (Arratia & Schultz, 1999; Arratia, 2004; Lopez-Arbarello, 2012).

The other fish species from the Stanleyville Beds have been more difficult to place taxonomically. *Macrosemius maeseni* was originally considered to be a macrosemiid, but has since been removed from the group and left in an unknown position, tentatively into the genus *Tanaocrossus* (Bartram, 1977), and *Leptolepis caheni*, originally described as *Paraclupavus caheni*, is also of unknown relationships within the basal teleost lineage.

FIGURE 3.7

One Jurassic fish (*Catervariolus hornemani*) from Stanleyville Formation in the Democratic Republic of the Congo. Note the stout scales covered by shiny enamel (photograph by Lilian Cazes, MNHN/CNRS, Paris).



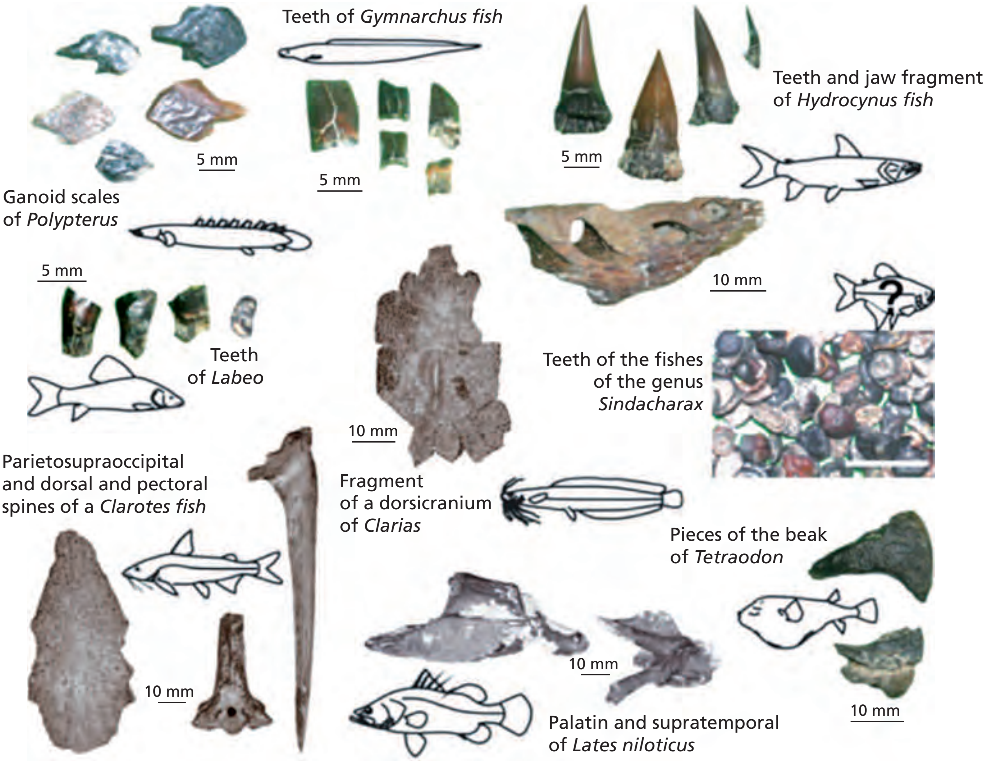
the Lukeino Formation in Kenya (Altner & Reichenbacher, 2015). Indeed, the information available on extinct animals is highly dependent on the geological context and on the ecology and evolution of the animal (Otero, 2010). The case study of the characiform fossils from Africa shows the various kinds of fossils that are available depending on preservation, and how they demonstrate characiform evolution.

TOROS-MENALLA, A CENOZOIC FRESHWATER FISH FAUNA 7 MYRS AGO

OLGA OTERO

This Chadian ichthyofauna includes over 20 species (figure 3.8) (Otero *et al.*, 2006, 2007, 2008a, 2010a; Pinton *et al.*, 2011). Three extinct species belong to the extinct genera *Sindacharax*, *Bunocharax* (characiforms) and *Semlikiichthys*, this last known locally by the species *S. darsao* (acanthomorph). Four extinct species belong to extant genera, among which the catfish *Auchenoglanis soye* and *Mochokus gigas* and the bichir *Polypterus faraou*, are all known only from Toros-Menalla so far. The other fish are either assigned to indeterminate species in extant genera, or are attributed to modern species. They are bichirs (Polypteridae: *Polypterus* sp.), bony tongue fish (Arapaimidae: cf. *Heterotis niloticus*), aba fish (Gymnarchidae: cf. *Gymnarchus niloticus*), mud fish (Cyprinidae: cf. *Labeo* sp.), tiger and tetra fish (Alestidae: *Hydrocynus* sp. and *Alestes*/*Brycinus* sp.), catfishes among which bagrids (cf. *Bagrus* sp.), claroteids (cf. *Clarotes* sp.), clariids (two *Clarias* spp.), mochokids (two *Synodontis* spp.), and some acanthomorph fish such as the emblematic Nile perch (Latidae: *Lates niloticus*), two puffer fishes (*Tetraodon* sp.), and also indeterminate cichlids.

FIGURE 3.8.
Some of the fish fossils from the site TM266 in Toros-Menalla (7Ma, Djurab, northern Chad), with outlines of the body of a modern relative, from Otero *et al.*, 2010a.



Which fossils? Case study of the African characiforms

The order Characiformes is probably best known for containing the voracious South American piranha or the large robust pacu, but it also includes a wide variety of fishes found in Africa, notably the tetras and tiger fish. This group of exclusively freshwater fish arose during the split of western Gondwana and its separation into the land masses of South America and Africa. The relationships between the African and the South American characiform families are still under debate. However, most specialists agree in the composition of four monophyletic African families (Hepsetidae, Citharinidae, Distichodontidae, Alestidae) that evolved and diversified in the fresh waters of the newly isolated African plate during the Late Cretaceous and the Cenozoic, when rifting and volcanism drove the formation of large water basins. When preserved, the sedimentary deposits in intra-cratonic and coastal basins constitute the fossiliferous archives that are sporadically exposed today. In certain cases, they yield freshwater fish assemblages including various types of characiform remains (see box “African freshwater fish localities since the Late Cretaceous: a review”). The fossils are like incomplete messages to decode so they can tell us about fish evolution and the freshwater environment that prevailed or the depositional context that allow their preservation. Most of the past diversity of characiforms is known through their teeth, emphasizing the importance of screening sediments to collect minute remains. It is easy then to realize why taxa with skeletons of similar robustness, but with no differentiated teeth, would have a very reduced, if not entirely lacking, fossil record.

The characiform fish fossil record in Africa

The great differences in the richness of the fossil record of the four African characiform families (Hepsetidae, Citharinidae, Distichodontidae, Alestidae) is not only due to the differences in the diversity of each family, but is also attributable to their differing ecology and skeletal characteristics.

With 119 species, the family Alestidae comprises about half of the modern diversity of African characiforms. This family includes a number of variously-sized fishes from the giant tigerfish, *Hydrocynus goliath*, which often reaches over one metre long, to the smaller “dwarf African tetras”, including the robber fish, *Micralestes*. Most of the characiform fossils found in Africa belong to the Alestidae which also has the highest known fossil diversity among characiforms. With the exception of jaw fragments, their bones are generally not preserved and the alestid fossil record consists of numerous isolated teeth and some scarce jaws. Indeed, all the Cretaceous and Tertiary molariform and multicuspidate teeth collected in Africa are assigned to this family even if they cannot be related to any modern genus. The fossil record for the extant genera consists of *Hydrocynus* and *Alestes* or *Brycinus* teeth. The record starts in the late Eocene in Egypt and Libya (Murray *et al.*, 2010; Otero *et al.* 2015), and they are present in most Neogene outcrops, although in many cases their sampling may depend on using screening mesh (e.g., Otero *et al.*, 2010a).

AFRICAN FRESHWATER FISH LOCALITIES SINCE THE LATE CRETACEOUS: A REVIEW

OLGA OTERO

Continental sedimentation and preservation of deposits depend on environmental conditions such as topography, eustatism (sea level), and climate. The fossiliferous sites do not cover all the different time periods, nor do they cover the continent uniformly in terms of geographical location, leading to many gaps in our knowledge. The various sites also sample different environments, including brackish lagoons and coastal areas as well as freshwater rivers and lakes. These different environmental settings also lead to gaps in the fossil record, as the fishes in each site are most likely to be quite different. Because of these environmental, temporal and geographical differences, there is no continuous record of any particular fish lineage in Africa.

Indeed, the available fish fossil record is generally the exception, and is highly dependent on the fish itself and on the geology and climate (Otero, 2010).

The oldest Cretaceous freshwater localities with fish occur in southern Morocco and Niger. They are probably of Aptian or Albian age and represent a variety of environments including streams and lakes as well as deltaic floodplains. The overlying Cenomanian deposits, both marine and fresh water, are associated with a major marine transgression of the Tethys Sea.

They are predominantly located in North Africa. At some point in the Cenomanian, Morocco, Tunisia, and most of Algeria, Libya and Egypt were under water, and the Tethys Sea reached into Sudan, Mali and Niger through the central area of North Africa (figure 3.9).

Late Cretaceous deposits are also known from West Africa, in the Democratic Republic of the Congo and probably correspond to a shallow lagoonal area with fresh water input.

Marine waters again flooded the lowland areas through North and West Africa, creating a shallow seaway connecting the Tethys to the Atlantic during the Campano-Maastrichtian and again in the Palaeocene (figure 3.9).

These transgressive cycles are documented by many marine deposits and some freshwater fish localities in Niger, Cameroon, Congo and Togo. Also during the early Tertiary, freshwater localities were mostly located in North Africa and Tanzania.

Definite Eocene freshwater localities are found in Egypt, Libya and Algeria with riverine and lacustrine deposits, and in Tanzania, represented by a crater lake deposit (figure 3.9).

Egyptian, Kenyan, Tanzanian and Libyan localities have also yielded Oligocene freshwater fish, along with a few sites in Somalia, Oman and Kenya (figure 3.9, Ducrocq *et al.*, 2010).

Neogene sites are far more numerous and more broadly distributed than the Palaeogene sites in the north equatorial part of Africa, notably in the Great Lakes region southwards to Malawi, in the lower Nile River valley, in Chad, Egypt, and in the Maghreb and Maschrek (figure 3.9).

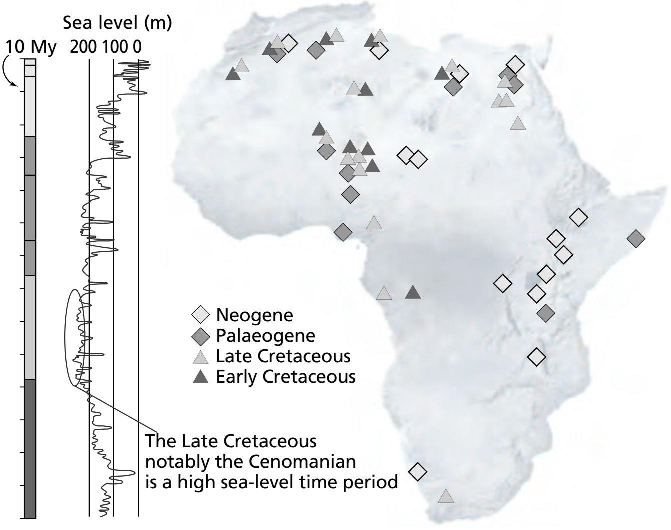


FIGURE 3.9.

African Cretaceous and Tertiary outcrops that yielded freshwater fish sites (most data in Otero, 2010), and the variation of sea level (in meters), relative to modern level, (from Haq *et al.*, 1987).

Moreover, several species have been described in two extinct Neogene genera, *Sindacharax* and *Bunocharax*. The assignment to the family is more tentative/difficult for a few Oligocene teeth from Oman and for the multicuspidate teeth sampled in Cretaceous and Tertiary deposits in Europe (see box "On the tracks of evaders?").

The two families Distichodontidae and Citharinidae number 101 and eight extant species respectively and together form the suborder Citharinoidei. Contrasting with this rich modern diversity, they have a poor fossil record. A small articulated fossil from the Eocene of Tanzania and two incomplete neurocrania from the early Pleistocene of Kenya have been assigned to Citharinoidei. The Tanzanian fossil is the anterior portion of a fish skeleton. It was collected in the site of Mahenge (ca. 45 Myrs) and was named *Eocitharinus macrognathus* (figure 3.10; Murray, 2003a). The Kenyan fossils have been referred to the modern genus *Citharinus*. Finally, a few isolated elements, predominantly teeth, from middle Miocene to Pleistocene deposits in Libya, Chad, Kenya, Uganda and the Democratic Republic of the Congo, have been referred to *Distichodus* sp. (figure 3.10; Stewart, 2001; Otero *et al.*, 2010a; Argyriou *et al.*, 2014). Although the Eocene articulated fossil is the oldest probable citharinoid known, it is at least 50 million years younger than the expected age of the families.

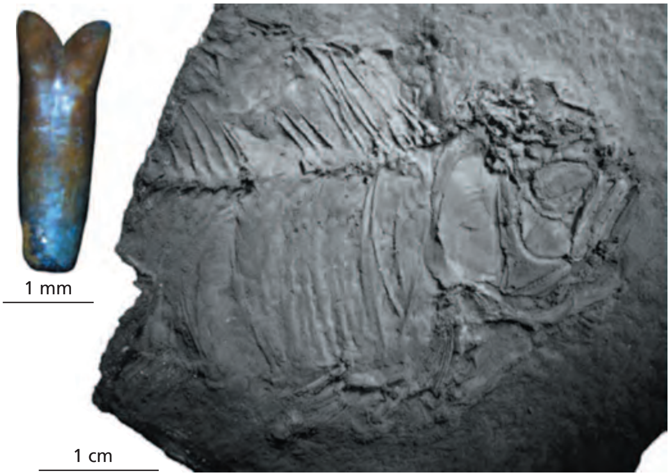


FIGURE 3.10.
Citharinoid fossils and fossil record: *Distichodus* tooth (left) from the Late Miocene of Toros-Menalla (photograph by OO) and holotype specimen of *Eocitharinus macrognathus* (right). Note the discrepancy between the fossil record of the two sister families, notably the age of the first occurrence and the distribution (data as cited in the text).

The final family, Hepsetidae, is known today by a single species (*Hepsetus odoe*, the African pike or Kafue pike). Despite a modern distribution close to that of *Hydrocynus* and characteristic conical teeth, *Hepsetus* has not been reported in the fossil record at all. This is explained by their radically different habitat: *Hydrocynus* occupies larger streams, lakes and flood plains, whereas *Hepsetus* is observed in swift tributaries in the same hydrographical systems. The former group of environments, notably flood plains, is largely susceptible to preservation in the sedimentary record with reduced transport of teeth and bones, whereas the latter environment corresponds to an erosive sedimentary context, in which remains will not be preserved.

Alestidae: the highest fossil diversity observed for an African fish family is revealed by teeth

The fossil record of the tiger fishes, genus *Hydrocynus*, is limited to isolated caniniform teeth and a few jaw elements known from Mio-Pliocene deposits, mostly from the Nilo-Sudanian region (Stewart, 2001). These remains do not bear specific characters and the teeth are attributed to *Hydrocynus* sp. Meanwhile, the remarkable molariform and multicuspidate teeth that characterize the extant genera *Alestes* and *Brycinus*, and the fossil genera *Sindacharax* and *Bunocharax* exhibit various morphologies which reveal a high specific fossil diversity, the highest observed for fish in Africa.

The oldest-known molariform teeth were signaled from Upper Cretaceous deposits in Morocco (Dutheil, 1999a) and from Sudan (Werner, 1993) and from marine deposits in the Ouarzazate Basin in Morocco, considered probably Lower Palaeocene (Cappetta *et al.*, 1978). A number of multicuspid and molariform jaw teeth (figure 3.11) of probably several species referable to extinct genera in Alestidae were collected in late Eocene deposits in Egypt and Libya (Murray *et al.*, 2010, Otero *et al.*, 2015) and in the Oligocene in the Fayum, Egypt (Murray, 2004). Other teeth collected from the Oligocene in Oman exhibit different morphologies, including typically elongated teeth with cusps aligned in one row forming a blade (Otero & Gayet, 2001). A few minute teeth from the Eocene of Egypt and Libya (Murray *et al.*, 2010, Otero *et al.*, 2015) and younger remains have been more narrowly related with the *Alestes*/*Brycinus* species complex. Van Couvering (1977) reported isolated teeth of an "*Alestes*-like" fish from the Daban Formation (possibly Oligocene) of Somalia, from the early Miocene in Uganda, and from middle and late Miocene deposits in Kenya. Moreover *Alestes*/*Brycinus* teeth have been collected in many Neogene sites by screening (Stewart, 2001; Otero *et al.*, 2009, 2010a). The monotypic fossil genus *Bunocharax* was erected by Van Neer (1994) for robust round or elliptical teeth and jaws recovered from middle Miocene to Pleistocene deposits near Lake Albert, Uganda. Finally, many molariform alestid teeth in Mio-Pliocene deposits have been referred to the extinct genus *Sindacharax* in which several nominative species have been identified.

FIGURE 3.11.
Alestid-like teeth from the Oligocene of Egypt, from Murray (2004) modified.

The first species of *Sindacharax* (*S. deserti*), described from Pliocene deposits at Wadi Natrun, Egypt, was first placed in *Alestes* (Greenwood, 1972). With the description of a second species (*S. lepersonnei*) from the Miocene and early Pleistocene Lake Albert-Lake Edward Rift, the two were given a new genus based on isolated teeth (Greenwood & Howes, 1975). The genus was described on the presence of one major cusp and two or three cuspidate ridges on some teeth (those of the inner row of the premaxillary bones), together with unicuspidate and tricuspidate teeth. Hundreds of teeth have since been recovered and reported in many late Miocene and Pliocene sites of the Nilo-Sudanian ichthyoprovince. Varying tooth shapes and cusp patterns, and lack of living relatives of the genus with similar tooth morphology, have led to considerable confusion in the literature (see Stewart, 2001), because as in the living *Alestes*/*Brycinus* fishes, the tooth morphology not only varies according to the species, but also according to their position in the jaws. However, the recovery of several *Sindacharax* jaws with *in situ* teeth from the western Turkana basin sites of Lothagam and Kanapoi (Mio-Pliocene, Kenya), enabled Stewart (2003a, b) to demonstrate the systematic validity of five *Sindacharax* species based on the anatomy of their molariform teeth. There was considerable overlap between the cusp patterns of the outer teeth and the inner third and fourth teeth, but the patterns of the first and second inner teeth were both distinctive (figure 3.12) and consistently identified with a stratigraphic unit or geographic locale within a unit. The five species present in the late Miocene to Pliocene-aged deposits at Lothagam (Stewart 2003a) were: 1) *Sindacharax lothagamensis*, associated with the Nawata Member, 2) *S. mutetii*, associated with the Apak Member deposits; it was larger in size than *S. lothagamensis* and had greater ridging on its inner premaxillary teeth, 3) *S. deserti,* associated with the Muruongori Member deposits, 4) *S. howesi*, associated with the north Kaiyumung Member deposits, and 5) *S. greenwoodi,* associated with the southern Kaiyumung Member deposits (figure 3.12).

FIGURE 3.12.
Teeth of the premaxillae in the Lothagam *Sindacharax* species: inner teeth 1 (left) and 2 (right) in *S. greenwoodi*, in *S. deserti*, in *S. howesi*, and *S. mutetii*; and inner teeth 2 of the premaxillae in *S. lothagamensis*.

On the tracks of evaders?

Olga Otero

Despite the lack of geological evidence of freshwater connections between Afro-Arabia and other continents during the Cretaceous and the Palaeogene, there is biological evidence of faunal exchanges, notably with Eurasia (Gheerbrant & Rage, 2006). These authors identify five to seven vertebrate interchanges, mainly involving mammals. Among other ideas, transitory emergent platforms, part of the Mediterranean Tethyan Sill, have been invoked to explain dispersions of terrestrial animals during times of lower sea levels. In contrast with mammals, the evidence of dispersal events of freshwater fish to or from Afro-Arabia is very scarce. One freshwater sarcopterygian fish has crossed the Tethys to Southern France at the Campano-Maastrichtian (Cavin *et al.*, 2005). A clariid catfish crossed the Tethys to reach Afro-Arabia in the early Oligocene (Otero & Gayet, 2001). Finally, multicuspidate and molariform teeth attributed to characiform fish might be evidence of iterative dispersals of African freshwater alestid fish to Europe. This last scenario has been discussed by researchers at various points.

The oldest multicuspidate teeth in Europe were collected in Campano-Maastrichtian deposits of Provence (Southern France) in Vérane and Les Pennes-Mirabeau (Otero *et al.*, 2008b, figure 3.13) and possibly of Rumania (Grigorescu *et al.*, 1985), in several Eocene localities from France, Sardinia and Spain (Cappetta *et al.*, 1972; Cappetta & Thaler, 1974; Patterson, 1975; De la Peña, 1993, 1995). After that time, the Oligocene characiform record in Europe is limited to *Eurocharax tourainei* (Gaudant, 1979, 1980) known from both the skeleton and the teeth, and the youngest characiforms are known in Miocene deposits in the Iberian peninsula (Gaudant, 1996; Antunes *et al.*, 1995).

While most specialists agree on the West-Gondwanan origin of the order, there has been a debate on the type of environment where Characiformes may have diversified.

From a palaeontological perspective, based on fossil evidence, it has been suggested that the order Characiformes arose in the Early Cretaceous, possibly from marine ancestors (see Otero *et al.*, 2008b). However, the hypothesis of a marine origin was based on some marine Tethyan fish that were attributed to Characiformes. This marine origin scenario has been dramatically weakened since a review of the fish resulted in them being excluded from the order (Mayrinck *et al.*, 2015a, b). Following from that, there is no evidence to doubt the archaeolimny (primary freshwater ecology) of African characiforms. The presence of European characiform fish with multicuspidate and molariform teeth is therefore most parsimonious if it is interpreted as a dispersion event, even in the case of the Cretaceous fish.

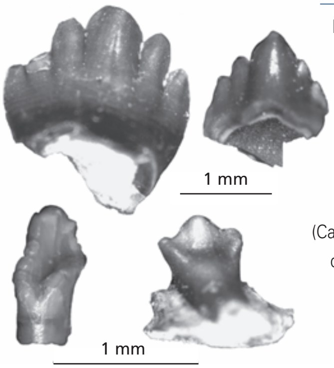


FIGURE 3.13.
Photographs of some of the probable oldest-known characiform multicuspidate alestid-like teeth collected in Europe (Campano-Maastrichtian deposits of Provence, southern France), modified from Otero *et al.* (2008b).

Additionally, there are two main hypotheses to explain the European characiform fossil record: either there were successive, multiple invasions into European fresh waters by characiform fish from the African stock, or the European forms belong to a single clade whose ancestor reached Europe in the late Cretaceous, with multiple lineages subsequently descended from that ancestor. The first hypothesis has the advantage in that it explains the gaps in the European fossil record, in both time and space.

Moreover, the ages of the proposed dispersals correspond to certain of the dispersal events posited based on evidence for terrestrial animals, as well as to discontinuous land routes (Dercourt *et al.*, 2000; Gheerbrant & Rage, 2006). A Campano-Maastrichtian pathway was used by both a sarcopterygian fish and by derived tetrapods to reach Africa. Next, the timing of the highest known diversity in European characiform fishes (Eocene) is correlated with the main dispersal phase of mammals from Africa to Laurasia. Additionally, a putative minor dispersal phase of mammals is correlated with the Oligocene record of European characiform fishes.

Since no phylogenetic study contradicts this second hypothesis as of yet, it is retained as the most probable.

Finally, one primary assumption remains yet untested: are all the multicuspidate and molariform teeth fossil remains of alestid fish? Indeed, most notably when the morphology does not exactly fit with modern alestids, and where there are long gaps in the fossil record, it is safer to attribute a tooth to a characiform indet., while awaiting information (Otero *et al.*, 2008b).

A few articulated skeletal remains, many further evolutionary study perspectives

Besides thousands of teeth, the known fossil record of characiforms also includes a few articulated skeletons. One such fossil, *Arabocharax baidensis*, is known from the Oligocene Baid Formation of Saudi Arabia (Micklich & Roscher, 1990). In Africa, only two fossil species have been reported for the family Alestidae based on articulated remains: the middle Eocene *Mahengecharax carrolli* from Tanzania, based on four specimens (figure 3.14; Murray, 2003b) and the much younger *Alestes junneri* based on three specimens, from probable late Pleistocene deposits of Ghana (White, 1937; Greenwood, 1972).

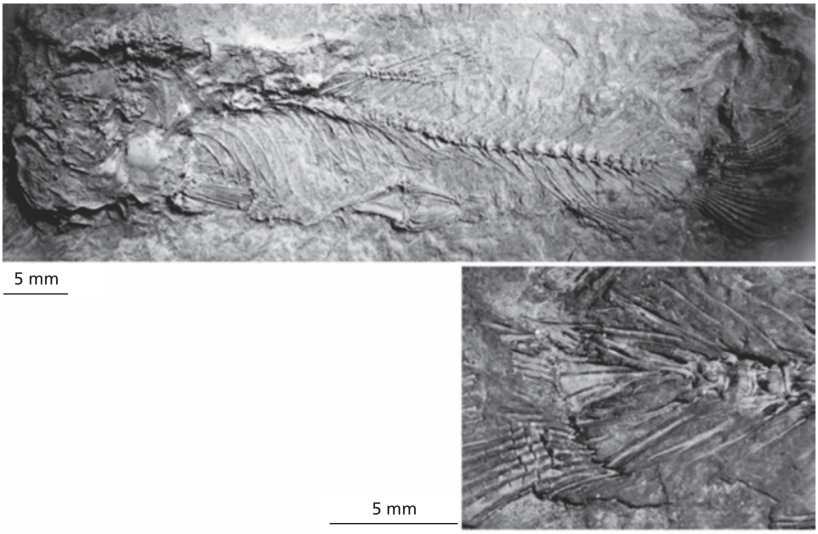


FIGURE 3.14.
Photographs and drawings of the fossils with zoom of the caudal zone of the *Mahengecharax* material.

Attribution of articulated fossils might be thought to be easier than attribution of isolated teeth, but debates are greater for these few skeletal fossils because the interpretation of these remains may influence views on the evolution of the group. Articulated fossils are most often preserved as flattened skeletons, sometimes covered with scales, with the bones lying atop one another, obscuring many details. Because of this, a particular problem may be the inability to readily identify the material. In the case of characiform fish, they show a particular organization of the Weberian apparatus, a complex built from the modification of the first four vertebrae and existing in all ostariophysan fish (the group that includes among others catfishes, carps and minnows). If the Weberian apparatus cannot be identified, the identification of material as belonging to a characiform fish can be controversial. However, with a better understanding of their osteology, we will be able to build a more complete picture of the phylogeny of the group, including the fossils, which is vital for interpreting time scales of evolution and biogeographic history of these fishes. With little material to work with, every new fossil may cause a significant change in our view of the evolution of the group. Moreover, increased use of computed tomography (CT) scanning technology and 3D reconstruction opens new perspectives and allows researchers to revisit historical fossils. So far these techniques have not been used for African characiforms, but there is little doubt that in the next years we will see the exploration of these new data sets.

Old groups, old cradles! The case of lungfishes: a Pangean or a Gondwanan history?

Today lungfishes, or dipnoans, are known by three genera inhabiting the fresh waters of Australia (*Neoceratodus*), South America (*Lepidosiren*) and Africa with four modern species of *Protopterus* (*P. annectens*, *P. aethiopicus*, *P. amphibius* and *P. dolloi*). At first sight this distribution looks typically Gondwanan. We might expect that the modern lungfish lineage originated in Gondwana and that the whole evolutionary history and distribution of the group was restricted to Southern continents. Because of its incompleteness, the lungfish fossil record is rather hard to interpret (see box "The inconsistent state of the lungfish fossil record"). However, it provides a more complex pattern of an evolutionary history that starts over 360 million years ago.

In order to understand the biogeographical evolutionary history of the lungfishes in the context of the break-up of Pangea and then of Gondwana, it is necessary to resolve the phylogenetic relationships between recent and fossil representatives of the group since the Triassic. All studies agree that the South American *Lepidosiren* and the African *Protopterus* are sister genera, grouped together within the family Lepidosirenidae. Most of these studies also agree that both genera split during a vicariant event associated with the opening of the South Atlantic in the Cretaceous (figure 3.16A and 16B). What remains controversial is the relationship between lepidosirenids and the Australian *Neoceratodus* lineage, in Neoceratodontidae. Two main patterns dealing with recent taxa have been proposed, with significant biogeographical implications.

The traditional hypothesis suggests that neoceratodontids are a sister-group of lepidosirenids (figure 3.16B). This solution suggests that both lineages split rather recently, in the Late Jurassic or Early Cretaceous (Martin, 1984), somewhere on the Gondwanan landmass. It explains why recent lungfishes are found only in Southern continents, because crossing the Tethys would have been impossible for these freshwater fishes.

However, during the Cretaceous, neoceratodontid remains are known in Australia, but also in Africa (see above) and in South America. These spatial and temporal distributions do not fit with a vicariant event between the western Gondwanan lepidosirenids (Africa and South America) and the Eastern Gondwanan neoceratodontids (Antarctica and Australia) because neoceratodontids are found on all these landmasses (except Antarctica). Instead it implies that neoceratodontids rapidly dispersed toward Australia, while both other recent lineages remained

THE INCONSISTENT STATE OF THE LUNGFISH FOSSIL RECORD

LIONEL CAVIN

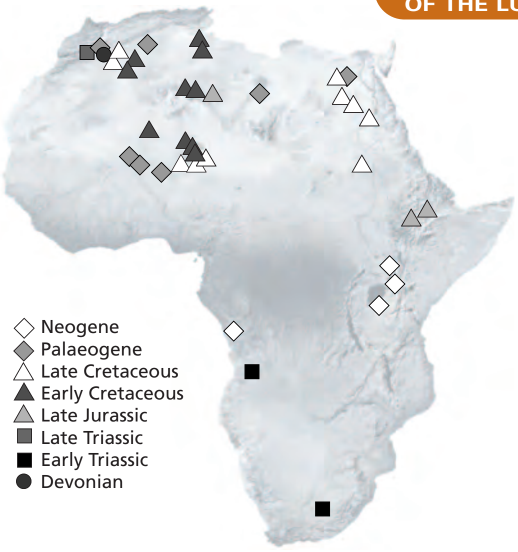


FIGURE 3.15.
The African fossil record of lungfishes in Africa (data as cited in the text).

The lungfish fossil record is odd because it exhibits two very distinctive phases in the evolutionary history of the group. Lungfishes are first known from the Early Devonian, 410 million years ago. They were marine fishes that rapidly diversified worldwide. Their skeleton was heavily ossified and some of them had dermal bones and scales covered with a hypermineralized tissue, cosmine. The function of this tissue, unknown in modern fishes, is still debated. The skull of these first lungfishes was composed of numerous ossifications and their lobed fins were sustained by a central skeletal axis. The latter feature, still present in modern forms, allows lungfishes to be referred to sarcopterygians. Teeth of Devonian lungfishes were arranged in patches of small denticles or fused together forming dental plates.

Few African fossils document this first marine radiation of dipnoans (figure 3.15; Lelièvre, 1995; Campbell *et al.*, 2002). This first marine radiation is of little use to understanding the distribution of modern freshwater Dipnoans.

At the end of the Palaeozoic, in the Carboniferous and Permian, lungfishes were in a way intermediate with those from the second period of their evolution that occurred during the Mesozoic and Cenozoic. This second phase of lungfish history indeed started during the Triassic with forms that were quite different from their Devonian relatives. Skull bones are thinner and develop deeper under the skin, and tooth plates are bigger and more heavily mineralized. As a consequence of these osteological transformations, the fossil record is altered: the fragile ossifications of the skull are rarer as fossils, whilst the tooth plates are more common but are usually found isolated. So, in the Mesozoic, only a dozen taxa are known by both cranial and dental remains and most are Triassic. The African fossil record is also richer in the Triassic whatever few sites are available (figure 3.15). The oldest are an almost complete specimen referred to *Microceratodus angolensis* from the Early Triassic of Angola (Thomson, 1990) and several taxa based on isolated tooth plates in the Early to Middle Triassic in South Africa (Kemp, 1996) and from the Late Triassic of Morocco with *Aranodus atlantis* known by tooth plates and skull remains (Martin, 1979, 1981). It also appears that lungfishes were mainly freshwater fishes in the Triassic. They stay in these palaeoenvironments from that time onwards so that the break-up of Pangea will have a marked impact on their evolution.

In Africa, after the Triassic times, the fossil record of lungfish is poorly diversified.

There is one occurrence from the Late Jurassic-Early Cretaceous in Ethiopia and one from the Late Jurassic in Algeria (Goodwin *et al.*, 1999; Martin, 1984; figure 3.15), both assigned to the same species (*Arganodus tiguidensis*).

Cretaceous lungfishes occur mainly in the Sahara region (figure 3.15). Among them, another *Arganodus* sp. close to contemporaneous forms from the Albian–Cenomanian Itapecuru Group in Brazil (Dutra & Malabarba, 2001) indicates that relationships between Africa and South America are still very close at that time.

Moreover, two species are referred to the modern Australian genus *Neoceratodus* (Martin, 1984), two other species belong to the recent African lineage of *Protopterus*, *Lavocatodus protopteroides* and probably *L. humei* (Churcher & Iullis, 2001), and the genus *Protopterus* itself is reported from the Campanian of Egypt with *P. crassidens* (Churcher & Iullis, 2001).

After that, the Tertiary record of lungfishes in Africa is limited to the genus *Protopterus*, and from the Oligocene onwards, species close to, or belonging to modern species are known (figure 3.15, Otero, 2011).

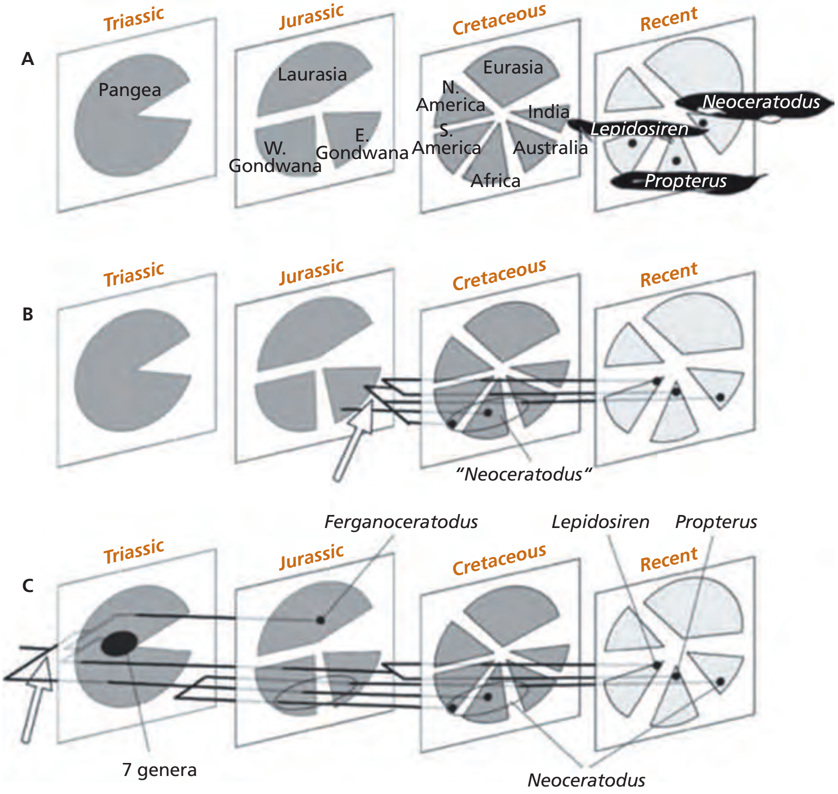


FIGURE 3.16.
The break-up of Pangea and the possible scenarios for lungfish biogeographical history (from Cavin *et al.* 2007b, modified). **A**. Schematic palaeogeographical evolution and modern distribution of lungfishes; **B**. model based on a direct sister-group relationship of the lepidosirenids and *Neocerotodus* (and closely related genera); **C**. model based on a split between the lepidosirenids and *Neocerotodus* that occurred deeper in the phylogeny.

static. The hypothesis of a middle Mesozoic split between lepidosirenids and neoceratodontids is thus not parsimonious. An alternative hypothesis (Cavin *et al.*, 2007b) proposes that the split between both modern lineages is much older than mid-Mesozoic and that several Triassic and Jurassic genera are phylogenetically closer to the *Lepidosiren-Protopterus* lineage than to the *Neoceratodus* lineage (figure 3.16C). According to this pattern, the origin of the neoceratodontid lineage occurred at the end of the Palaeozoic or at the very beginning of the Mesozoic. The split is apparently not associated with a vicariant event related to some kind of geographical barrier, but it occurred at a time of rapid diversification of the group. The diversification produced several genera in Pangea (figure 3.16C, *Ceratodus*, *Ptychoceratodus* in Europe, *Paraceratodus*, *Arganodus* and "*Ptychoceratodus philippsii*" in Africa, *Asiatoceratodus* in Asia and *Gosfordia* in Australia). Then the break-up of Pangea at the end of the Triassic isolated a Northern lineage from a Gondwanan lineage. The northern, or Eurasian lineage, is known by fossil remains from the Jurassic of Kyrgyzstan, China and Thailand (figure 3.16C, *Ferganoceratodus*). This lineage appears to become extinct during the Early Cretaceous. The southern lineage gave rise to the lepidosirenid lineage, which split between Africa and South America. The old neoceratodontid lineage remained on Southern continents then became extinct except in Australia, where they are known by several genera and species during the Tertiary (figure 3.16C).

Bichirs: decline, fall and new rise of a Western Gondwanan fish in Africa

Olga Otero

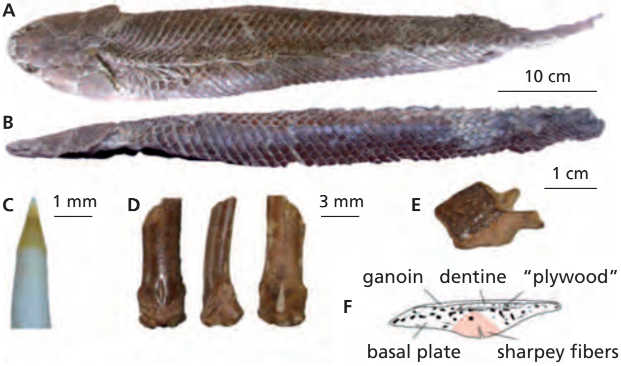


FIGURE 3.17.

Polypteriform fossils: Holotype specimen of the only *Polypterus* fossil species known from articulated material, *Polypterus faraou* in **A.** dorsal and **B.** lateral views (modified from Otero *et al.* 2006); disarticulated fossil remains as generally found in Tertiary outcrops (modified from Otero *et al.* 2015), **C.** jaw tooth, **D.** pinnula with the ganoin anterior cover in front, lateral, and posterior views, and **E.** ganoid scale covered by ganoid and showing the peg (that articulates in a socket in the next scale); **F.** section in a polypteriform scale to show the location of the characteristical plywood structure (modified from Daget *et al.* 2001).

Polypteriforms are the only living members of a very basal actinopterygian group called Cladistia. Today, they are exclusively African and placed in the single family Polypteridae with 17 *Polypterus* species and subspecies and the monotypic *Erpetoichthys*.

Isolated skull-roof bones, scales and spines are found in most of the freshwater outcrops of Africa from the Late Cretaceous to the modern (see box "African freshwater fish localities since the Late Cretaceous: a review", section 2).

They are recognized to belong to polypteriform fish on the basis of their morphology and histology: the pinnulae are the characteristic spine that only these fish exhibit, in front of each of their dorsal finlets; the vertebrae exhibit a typical morphology with closed neural arch and all dermal bones are covered in a layer of ganoin enamel (figure 3.17). Two extinct species have been described on the basis of articulated fossils: *Serenoichthys kemkemensis* from the Late Cretaceous of Morocco (Dutheil, 1999b), and *Polypterus faraou* (figure 3.17A, B) from the late Miocene of Chad (Otero *et al.* 2006).

Several Cretaceous genera have also been erected based on original morphology of the articular head of pinnulae (e.g. Meunier & Gayet, 2000), of scales and of the ectopterygoid (Grandstaff *et al.*, 2012). Moreover, two other fossil species have been described in *Polypterus* on the sole morphology of the scales (Gayet & Meunier, 1996; Werner & Gayet, 1997). The numerous other African fossils, from the Cenozoic, are referred to *Polypterus* sp.

Indeed despite a rich fossil record, little is known about polypteriform evolution in Africa since the phylogenetical relationships of extinct forms remain totally unknown. Until the early 1990s, only fossils from Africa were referred to polypteriform fish. Fossil scales and bones covered by enamel recovered from outside Africa were systematically attributed to other ganoid fish (such as semionotids and lepisosteids).

However, pinnulae and characteristic vertebrae were collected and described in Late Cretaceous and Palaeocene deposits from Bolivia demonstrating their ancient presence on the South American Plate (Gayet & Meunier, 1991). The presence of histological features characteristic of polypteriform scales was then sought and found; it therefore participates in demonstrating the hitherto unsuspected presence of polypteriforms in South America during Cretaceaous and Palaeogene times (Gayet & Meunier, 1991).

Indeed, the scales of living polypterids originally exhibit dentine (like in a tooth) and a bony basal plate with a perpendicular counterplate-like structure (figure 3.17F).

Finally, the other available information on polypteriform evolution is the result of molecular studies and concerns the phylogeny of modern members with estimates of the diversification time (Suzuki *et al.*, 2010; Near *et al.*, 2014). Combined with the fossil record data, a scenario appears for the order (Near *et al*, 2014).

First, they had a flourishing diversity during the Late Cretaceous in both South America and Africa, illustrated by the great diversity of morphology of the pinnulae and also by the size of the taxon that might have reached up to three meters with *Bawitius* (Grandstaff *et al.*, 2012).

Then polypteriform diversity declines on both plates and the lineage goes extinct in South America. In Africa, *Polypterus* and *Erpetoichthys* diverge in the early Tertiary and *Polypterus* diversifies during the Miocene, marking a new radiation phase after a long decline.

Finally, an accurate review of Tertiary dipnoans of Africa suggests that an extinction phase took place during the Palaeogene and was followed by a recent diversification from a refuge located in eastern Africa (Otero, 2011). This hypothesis based on the fossil record fits with the molecular data available so far (Tokita *et al.*, 2005). Decline in diversity followed by a new diversification also occurred in the bichirs which form the other African archaic fish lineage (see box "Bichirs: decline, fall and new rise of a Western Gondwanan fish in Africa"). So far, evidence is still lacking to explain the causes of this common global pattern in the evolutionary history of the two archaic African fish lineages. The Neogene climate modification with enhanced seasonality, with an increasing dry season, has been invoked to give advantage to these relictual fish that are also characterized by their ability to breath air (with lungs) and even to aestivate in the case of *Protopterus* (Otero, 2011).

When a marine fish adapts to freshwater

Tolerance to salt water

Traditionally, scientists have classified fish into three divisions based on their tolerance of salt water (see chapter *General characteristics of ichthyological fauna*). Of particular interest here is the peripheral (tertiary) division, specifically the vicarious and complementary groups. Only recently has the fossil record in Africa become detailed enough to identify both the adaptations to fresh waters in these groups, as well as the geological processes which altered their habitats. Two cases illustrate how palaeontological data document the adaptation of marine taxa to fresh waters in Africa. First, the Dasyatidae has a fossil record in the Turkana basin that documents the adaptation of a marine coastal species to freshwater, and later its disappearance, in association with geological and biotic changes in less than one million years. Second, the fossil record of the family Latidae demonstrates how they evolved from a marine to a mostly freshwater group, notably in Africa, over their ca. 40 Myrs evolutionary history.

Dasyatidae in the Plio-Pleistocene Turkana Basin

Modern freshwater stingrays are assigned to two families: Dasyatidae (stingrays) and Potamotrygonidae (river stingrays). The Dasyatidae is chiefly a marine family; however, it includes some members which inhabit brackish and/or fresh waters (Nelson, 2006). The thorny freshwater stingray *Urogymnus ukpam*, for example, permanently inhabits a lake in Gabon, about 100 km inland from the Atlantic Ocean, and another dasyatid, *Dasyatis garouaensis*, is permanently established hundreds of kilometers upstream in the Benue River. Potamotrygonidae is the only batoid family which is restricted to fresh waters. Potamotrygonid species inhabit rivers in eastern South America, although several species were identified in the Benue River in Nigeria. These latter species were later reassigned to the genus *Dasyatis*, based on the lack of a prepelvic process and the low urea concentration in body fluids, both of which are diagnostic for the family Potamotrygonidae (Thorson & Watson, 1975). Potamotrygonidae are unique among the elasmobranchs in having this osmoregulatory feature, which suggest a long period of evolution in freshwaters, while the Dasyatidae have similar osmoregulatory features to the other elasmobranchs, suggesting that they are fairly recent colonizers of fresh waters. Both the freshwater dasyatids and the potamotrygonids would be classified as peripheral–complementary fish, that is, marine fish which colonized fresh waters.

The fossil record for stingrays is sporadic in Africa, and mainly consists of marine stingrays, so it is rare to find convincing evidence of the transition of stingray groups from marine to fresh waters. In fossil deposits in and around Lake Turkana, northern Kenya, however, there is evidence of marine stingrays colonizing and reproducing over thousands of years in a freshwater inland lake. The modern Turkana basin (including Lake Turkana and the inflowing Omo River) contains highly fossiliferous deposits which date from the early Miocene to the Holocene and have been well studied by palaeontologists and geologists. In the lower Omo River valley, several stingray caudal spines were recovered in the 1930s from lacustrine deposits, in association with other freshwater polypterids, silurids and *Lates*, a percoid (Arambourg, 1948). No other material from marine fishes (or other marine vertebrates for that matter) was recovered. Arambourg (1948) assigned the spines to Potamotrygonidae (*Potamotrygon africana*), the only modern family of stingrays which is completely freshwater, even though it was only known in South America. At least 360 more spines and several teeth were later recovered from deposits in the eastern Turkana basin (Schwartz 1983; Feibel & Brown, 1993). The spines were first found in upper Burgi Member deposits (about 2.0 Myrs), with their last appearance in Okote Member deposits at about 1.5 Myrs (Feibel, 1988; Feibel & Brown, 1993). Feibel & Brown (1993) re-assigned the eastern Turkana and Omo River stingray material to *Dasyatis africana* (figure 3.18A), based on 1) similarities in spines to dasyatids, and in tooth morphology to the modern *Dasyatis* species *D. centroura* and *D. guttata*; 2) the reassignment of the modern African *Potamotrygon* species to *Dasyatis* (discussed above), and 3) the fact that Potamotrygonidae are endemic to South America (Thorson *et al.*, 1983; Thorson & Watson, 1975). *Dasyatis africana* was originally assigned to stingray remains from Cabinda, near the head of the Congo delta in the Democratic Republic of the Congo (Dartevelle & Casier, 1959), but it is not clear if the Turkana stingray material was compared with the Congo material.

Feibel & Brown (1993) have reconstructed the Turkana basin environment associated with the stingray immigration as follows (figure 3.18B): the stingray spines first appeared around 2 Myrs when a large, relatively stable lake system occupied the basin, and continued for about 50,000 years. About 100,000 years later, the lake gave way to a fluvial system with a floodplain dotted by smaller lakes. These lake deposits were filled with mollusc remains and *Dasyatis* spines, and as many modern dasyatids eat molluscs as part of their diet, these were assumed to be a main component of the diet of *D. africana*. After 1.6 Myrs, the lakes became less numerous and more alkaline, and the molluscs began to disappear, along with the stingrays. The drying of the lakes may have been due to climatic or tectonic events. It seems likely that the stingrays disappeared due to the disappearance of their main dietary item, the molluscs.

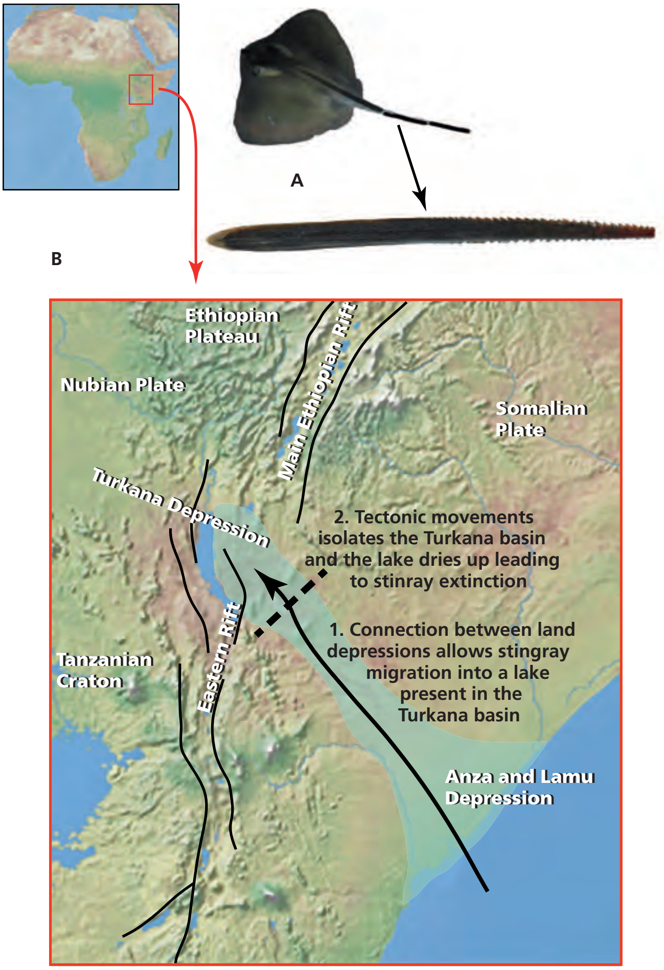


FIGURE 3.18. Invasion of the Turkana freshwaters by a stingray species: **A**: one exemplar of a fossil stingray spine collected in Pliocene deposits from the Turkana basin and its location on a living specimen; **B**. invasion scenario showing the role of the topographical configuration of the Turkana basin and surrounding areas.

This reconstruction indicates that stingrays had clearly established a permanent, breeding population for 500,000 years in the fresh waters of the Turkana basin. The question of their origin was an enigma, as the Turkana basin had been in sporadic indirect contact with the Nile River, but no evidence of stingrays was found in the Nile or its tributaries or associated lake basins. However, based on detailed stratigraphic evidence, Brown & Feibel (1991) have postulated that the ancestral Omo River, which traversed the Turkana basin, was occasionally connected with the Indian Ocean, about 700 km distant, via a presently low lying, sometimes marshy region to the southeast of Lake Turkana. It is not known when the connection ceased to flow. A previous connection between the Turkana Basin and the Indian Ocean must have occurred at least once, as the rostral fragment of a late middle Miocene ziphiid whale was reported in the western Turkana basin, at Loperot (Mead, 1975).

This is some of the first fossil evidence of a chiefly marine family, the dasyatids, moving a considerable distance inland to both colonize a freshwater lake and establish a reproducing, permanent population over a long time span (ca 500,000 years). Either increasing of aridity or tectonic changes caused changes in the lake such that the mollusc population disappeared, followed by the stingrays.

Latid fishes: over 40 Myrs of history from marine to fresh waters told from the phylogeny of modern and extant taxa and the fossil distribution

Modern latid fishes are unequally distributed in two genera: the monotypic *Psammoperca* and the relatively speciose *Lates* genus. Depending on the species, they live either in marine or in fresh waters (figure 3.19). *Psammoperca waigiensisis* is marine and inhabits the Indo-Pacific coastal waters. It overlaps with the widely distributed *Lates calcarifer* which is also found in the Eastern Pacific in coastal marine, brackish and fresh waters, where it has been described to have a catadromous lifestyle (Marshall, 2005). A third marine species (*L. japonicus*) is known from the Japanese coasts and estuaries. In addition to these, nine latid species are known from fresh waters. Two are Asian: *L. lakdiva* from Sri Lanka and *L. uwisara* from Myanmar. Seven are from

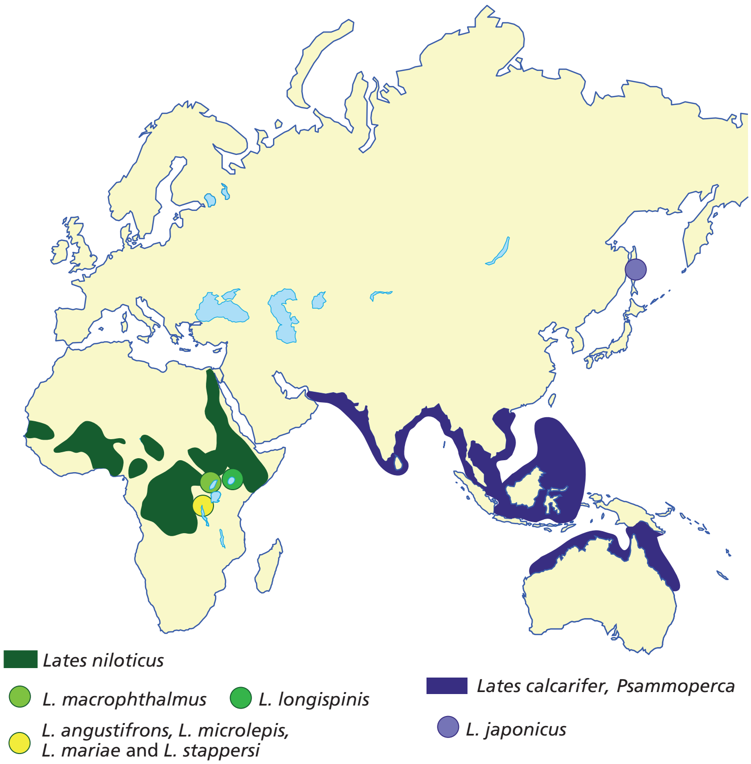
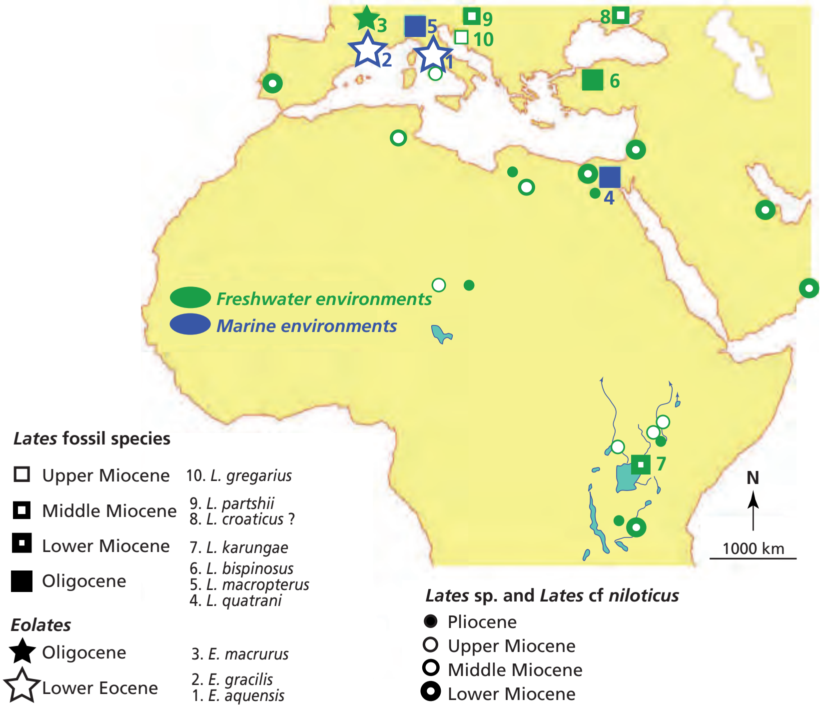


FIGURE 3.19.
Distribution of the species of the two living genera of the family Latidae in African freshwaters and Indo-Pacific coastal waters.

African lakes and streams. Among these, the famous Nile perch, *L. niloticus,* the biggest in size, shows the widest distribution. It is native in the northern and western regions of tropical Africa including Lake Chad, Lake Albert and Lake Turkana, and was also introduced in Lake Victoria and Lake Kioga. The remaining species are endemic in East-African lakes: *L. longispinis* in Lake Turkana, *L. macrophthalmus* in Lake Albert, and *L. angustifrons, L. microlepis, L. mariae* and *L. stappersi* in Lake Tanganyika.

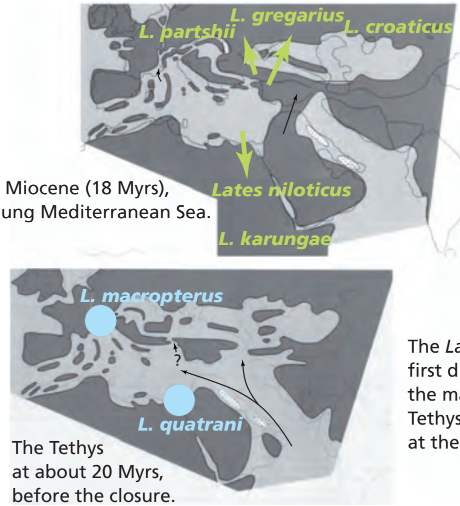
The fossil record starts with extinct fish found in the fossil and paraphyletic genus *Eolates*, which includes two species from lower Eocene waters (ca. 45 Ma) of the European Tethyan coast (figure 3.20). The last record of *Eolates* is known in lacustrine environments from the lower Oligocene (ca. 30 Ma) of South France (Otero, 2004). Extant *Psammoperca* has no fossil record whereas *Lates* includes several fossil species from various habitats in Afro-Arabia and Europe (figure 3.20). The oldest *Lates* species are Oligocene in age and are known from a freshwater environment in Egypt (*L. quatrani*; Murray & Attia, 2004) and a marine environment in Italy (*L. macropterus*; Bassani, 1889). Another freshwater species, *L. bispinosus* (Gaudant & Sen, 1979), is known from Turkey but with an uncertain Tertiary age. During the Miocene, *Lates* fish were present in Western European fresh waters, in Spain and Italy, while fossils assigned to *Lates* sp. or *L.* cf. *L. niloticus* have been recovered from most Miocene and Pliocene outcrops in the Nilo-Sudan, and also from the Maghreb and Arabian peninsula (figure 3.20). With the exception of *L. niloticus*, extant latid species have no fossil record.

FIGURE 3.20.
Occurence of fossil latid fishes with information of the environment of the deposits (data from the review by Otero, 2004, plus the species described by Murray & Attia, 2004 and by Stewart & Murray, 2008).



All clues indicate a marine origin for latid and *Lates* fish: the potential sister groups are marine, and a number of species are found in marine waters.

From the fossil record, the living distribution, and the phylogeny, we can build the following scenario for the history of this family (figure 3.21). The latids have a marine early Eocene (55 Myrs – 40 Myrs) origin with *Eolates*, a fish that inhabited Tethyan waters, at least along the western coasts. A marine origin is also the most parsimonious hypothesis considering that sister taxa are also marine. In the early Oligocene (ca. 30 Ma), an initial freshwater colonization is recorded in Southern France with a species of *Eolates*. At the same time, the genus *Lates* appeared at least along the African Tethyan coast, and, although no fossil has been recovered, the sister-genus *Psammoperca* must have appeared at the same time. Due to its modern distribution and the absence of a fossil record in the Western Tethys, we may hypothesize that *Psammoperca* was present instead in the Eastern Tethys. Next, *Lates* clearly diversified, first in the coastal waters of the Tethys before the closure of this seaway. Following this time, since the early Miocene, *Lates* fishes immigrated into and inhabited the continental freshwaters on both sides of the proto-Mediterranean Sea, in Africa and in Europe (where they may also be occasional invaders), except the *L. calcarifer* lineage. Depending on the range extension of *Lates* westward in Tethyan waters, the *Lates calcarifer* lineage originated in the Indo-Pacific area before the closure of the Tethys, or it invaded the proto-Indo-Pacific waters later, possibly benefiting from the high sea level that linked marine areas creating a connection between the Mediterranean Sea and the Indian Ocean during the Langhian. At the Miocene-Pliocene boundary (ca. 5 Myrs), *Lates* disappeared from European fresh waters and was reduced to roughly its modern distribution. The last representative known so far in Europe is a fossil *Lates niloticus* found at Monte Castellaro, in Italy (Otero & Sorbini, 1999). It probably invaded the Italian peninsula from Africa, during the time of low sea level during the Messinian (between about 7 Myrs and 5 Myrs).



During the Miocene, the *Lates* fishes diversify in the freshwaters of continental masses around the newly formed Mediterranean Sea.

Lower Miocene (18 Myrs), the young Mediterranean Sea.

The *Lates* fishes first diversify in the marine Tethysian waters at the Oligocene.

The Tethys at about 20 Myrs, before the closure.

FIGURE 3.21.
A probable scenario for *Lates* fish diversification.

Neogene changes in the African ichthyofauna

At the very beginning of the Miocene (23 Myrs – 5 Myrs), the Afro-Arabian plate was isolated from the other continents for over 100 Myrs. From this isolation, the inherited ichthyofauna shows an original diversity, with many families endemic in different orders. The Neogene (23 Myrs – present) evolution of the African ichthyofauna is related to the palaeogeographical events within continental Africa and environmental change. Of these, we retain here two of the best documented in the fossil record: first, the connection with Eurasia 20 Myrs ago, that enabled faunal dispersion in both ways between the two continents, and second, the Pliocene development of the Sahara that led to isolation of the North African regions. The influence of palaeogeographical events and environmental change can be estimated in a same family (see box "African fish diversification and geologically-driven events"), but also at the level of the whole ichthyofauna by continuance or disappearance of given taxa.

A main palaeogeographical event: the Afro-Asian connection

The connection of Africa with Eurasia occurred 20 Myrs ago in the early Miocene. It was followed by a disruption of some millions of years due to a marine transgression, and the definitive continental connexion occurred 12 Myrs ago. At each of these events, faunal interchanges occurred between the two plates, notably with mammal dispersal. Among the modern fishes, one can recognize several freshwater families in common on the two continents but a fossil record exists for very few of them. They are the clariid and bagrid catfishes, the cyprinids, and possibly the channids, which are all known to originate in Asia, and thus to conquer the African freshwaters by the presence of a land pathway.

Studies on cyprinid palaeobiogeography agree in placing the origin of the family in Asia. For a long time, the absence of any well-known Miocene fossil record of African cyprinids led some authors to consider that the family entered Africa during the Plio-Pleistocene. Doadrio (1994) hypothesized a freshwater faunal dispersion prior to the Pliocene, based on the presence of African cyprinids that are well-differentiated from the Asian *Pseudophoxinus* and "*Barbus*" (this later taxon includes various monophyletic taxa; the phylogeny has been deeply reassessed during the last decade, e.g. Stiassny & Getahun, 2007, Yang & Mayden, 2010; Zheng *et al.*, 2012;). This fits with the fossil record. Several forms are known in the Upper Miocene including "*Barbus*" from Egypt (Priem, 1914), Tunisia (Greenwood, 1972), United Arab Emirates (Forey & Young, 1999), and "*Barbus*" and *Labeo* from Kenya (Stewart, 2001). Indeed, the finding of an 18 Myr-old cyprinid fish in the early Miocene of Saudi Arabia (Otero, 2001) indicates that cyprinids certainly entered the Afro-Arabic plate from Asia with the first Tertiary continental connection between the two plates, to which a major mammalian migration also corresponds. The fossil teeth resemble "*Barbus*" and these invaders may be the ancestor of some of the modern African cyprinids.

CHANNID PALAEO-DISTRIBUTION: PALAEOGEOGRAPHICAL OR PALAEOCLIMATOLOGICAL CONSTRAINTS?

ALISON MURRAY & OLGA OTERO

The discovery of fossil snakehead fishes in Eocene deposits of the African continent provides us with a convincing example of faunal exchange via a connection between Asia and Africa in the early Cenozoic, before the Burdigalian landmass connection.

Snakeheads are a small family of freshwater fishes, with two genera and about 30 species living today. They are currently found in Asia, Malaysia and Indonesia (*Channa* with about 27 species) as well as in Africa (*Parachanna*, with three species). They are generally piscivorous fish that range in size from about 15 to 180 cm in length (Courtenay & Williams, 2004).

Snakeheads have long been known from the Cenozoic fossil record of Asia and are also known from the Miocene of Europe (Gaudant & Reichenbacher, 1998). Experimental evidence suggests marine waters would be lethal to snakeheads, and so their modern distribution was presumed to be the result of a Miocene invasion of the African continent, with the advent of the land connection between Asia and Africa through Arabia during this time period.

Moreover, snakeheads are known to be successful invaders of new areas, an ability that is aided by their capacity to breathe air through a specialized respiratory organ, which allows them to travel significant distances across land.

Snakeheads are of increasing interest to a wide range of organizations because of their invasive capacities: release of a few fish have allowed breeding populations to become established in the United States. As voracious predators, they have caused great damage to native fish populations, and as air-breathers, they are able to colonize new areas relatively easily by travelling overland (Courtney & Williams, 2004).

The presumed Miocene migration of snakeheads from Asia to Africa has been correlated with increased rain during changing climatic regimes. Indeed, snakeheads are even shown to be sensitive indictors of precipitation, with high rainfall during the warm season being important to their dispersal (Böhme, 2004). While climate change with increase of temperature and waterfall may well have allowed snakeheads to expand their ranges, fossils from the Eocene of Egypt are a conundrum (figure 3.22). These fossils show that snakeheads were in Africa at least 25 million years before the Miocene land route was available to them. How did snakeheads, freshwater fishes that are intolerant of salt waters, become distributed in Asia and Africa long before these two continents were connected with one another in the Miocene?

One answer might be that the group arose much further back in time, when the landmasses were united in the single continent Pangea.

But this would require snakeheads to have evolved considerably before any other derived teleost group, and about 200 million years prior to their appearance in the fossil record.

A Pangean origin of snakeheads is thus not likely.

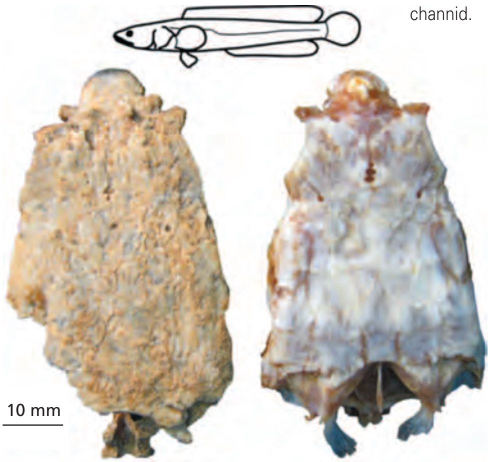
A second suggestion might be that the ancestral snakeheads were able to tolerate marine waters, unlike their modern relatives. However, this idea cannot be tested unless marine fossils are found; there is currently no indication that snakeheads may have migrated through saline waters.

The third, and most likely, scenario is that they used an earlier bridge between Europe/Asia and Africa, in the early Cenozoic. Land connections between Asia and Africa during this time span have yet to be documented by geologists. However, the biological indications are that such a route existed.

More and more precise data on the exchanges would allow testing the various hypotheses: via movement of microplates (McKenzie, 1970); by means of a temporary connection between the Indian subcontinent and East Africa (Krause & Maas, 1990); or by sea-level-controlled discontinuous routes across the Tethys Sea (Gheerbrant & Rage, 2006), which could be combined by rafting under the control of marine palaeo-currents.

FIGURE 3.22.

The skull on the left is the holotype of *Parachanna fayumensis* from Egypt and the skull on the right is *Channa striata* (recent), with outline of a modern channid.



Finally, in the case of the cyprinid fish, the data are congruent with the geodynamic history of the region. However, in other cases, other environmental parameters, notably the climate, seem to have been the main factor that favoured trans-continental exchanges, before the complete land connection (see box "Channid palaeo-distribution: palaeogeographical or palaeoclimatological constraints?"). This is notably the case of the aridification trend that developed in northern Africa in the last 7 Myrs and led to the Sahara desert.

A main palaeoenvironmental change: the Saharan extension

Climate fluctuation and its environmental consequences can be observed at different time scales. For instance when considering the Saharan desert, it was much greener some thousands of years earlier. However, considering a geological time scale, we observe a general aridification trend that started at least at the end of the Miocene with the oldest-known aeolian dunes deposit in the Djurab desert (Schuster *et al.*, 2006, Otero *et al.*, 2011). While short-term variations explain the distribution of some fishes in Saharan oases (chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*), long-term ones may explain the distribution of fishes at the scale of the Saharan belt.

Indeed, until the late Miocene, we know that a homogenous ichthyofauna that resembles the modern Nilo-Sudan one inhabited Africa, at least in the North equatorial zone (Stewart, 2001; Otero & Gayet, 2001). This palaeontological fish continuum extended onto the Arabian plate in the early Miocene (Otero & Gayet, 2001). It finds its roots in the Palaeogene and was enriched by arrivals of fishes from Asia. The systematic similarities between the fossil ichthyofauna and the extant Nilo-Sudan one can be explained because of an ecological continuum and the opportunism of some taxa in conquering new areas by the way of the African hydrographical network (Greenwood, 1983; Roberts, 1975). These differences are largely explained by the geological context that deeply structured the modern distribution of African fish (Pinton *et al.*, 2013).

This ichthyological continuum saw reductions. For instance, the Arabian plate appears to lose its African fish fauna during the Miocene. The comparison of Arabic fish assemblages in the localities of As-Sarrar (Lower Miocene), and Abu Dhabi (Upper Miocene) suggests the loss of *Lates*, an emblematic species that is linked to the existence of a wide hydrographic net (Van Neer, 1994). This could be related to the Saharo-Arabian desert development and/or to the disruption of the drainage network by the East African and Red Sea orogenic phases. Nowadays, *Lates* and *Clarias* are both absent from Arabia and the North of Africa (except along the Nile system); the other taxa typical of the pandemic African fauna are also absent (*Synodontis*, *Bagrus*, alestids, etc.). Furthermore, the extant cyprinids in the Maghreb seem to be of European origin.

The preliminary proposal that desertification or a strong change in the environment was the limiting factor of the continuum, which started its effects during the Miocene, fits with some observations made on mammalian faunas (Thomas, 1979). Nevertheless, the palaeogeographical separation of the African

AFRICAN FISH DIVERSIFICATION AND GEOLOGICALLY-DRIVEN EVENTS

OLGA OTERO & AURÉLIE PINTON

To test in which respect the evolution of freshwater fishes of Africa is dependent on physical modification of landscapes, *i.e.*, connections or disruption between drainage basins that reflects underlying geological and climatic change, we correlate results of phylogeographical works and fossil fish distribution with the current knowledge of African geology chronology (Otero *et al*., 2009; Argyriou *et al*., 2012; Pinton *et al*., 2013). Indeed, we assume that for freshwater fish, basin boundaries constitute barriers to dispersal: they constrain their distribution and strongly influence spatial patterns of fish assemblage composition.

In our studies we focus on three taxa: the catfish genera *Synodontis* and *Carlarius* and the perciform fish *Semlikiichthys*, all present in Afro-Arabia during the Neogene as evidenced by their fossil record: *Synodontis* has existed for at least 18 Myrs and is one of the most widespread catfish within today's African continent (Pinton *et al*., 2013); and *Carlarius gigas* is restricted to the Niger-inner delta whereas it had a wider past distribution including Chad and Libya, while *Semlikiichthys* is an extinct Neogene genus with two species with disjoint distribution, one in the Chad basin and one in Sirt Basin (Libya), Eastern Africa and along the Nile (Otero *et al*., 2009; Argyriou *et al*., 2012). We also include the results of another phylogeographical study that provide results at the continental scale (Brown *et al.,* 2010). Distribution of fossil fish identified at specific level and modern fish phylogeny notably suggest (figure 3.23): 1) the primary role of the Central African Shear Zone that has existed since the Cretaceous and acts all along the Tertiary time period as a main East-West barrier;
2) strong East/West connections between the formatting basins north to the Central African Shear Zone during the early Neogene;
3) sporadic disruptions between Eastern Africa, Syrt Basin and Chad that notably lead to temporary endemism in the later basin; and
4) the probable recent dominant role of the climatic control that drives the modern heterogeneity between the basins during the late Pliocene.

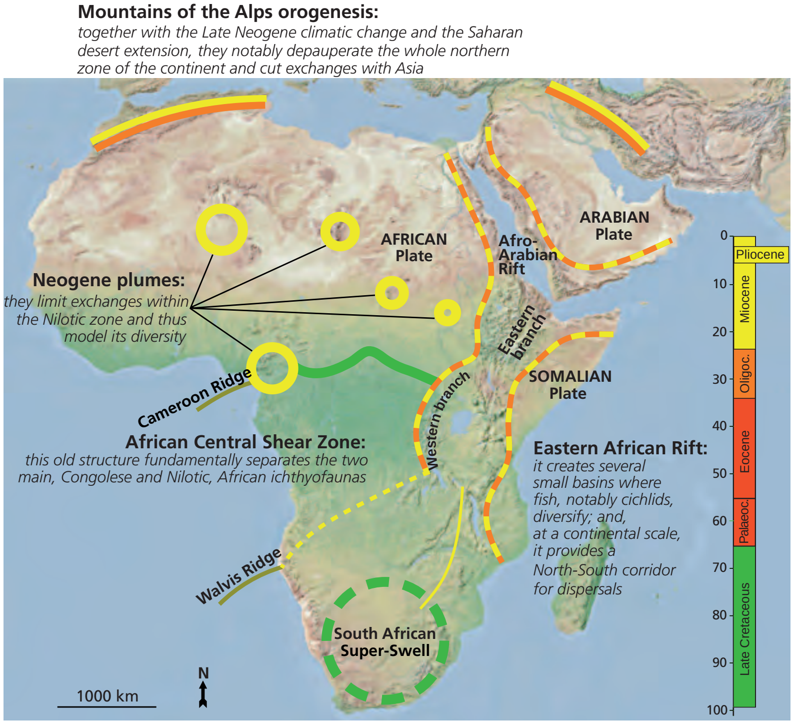


FIGURE 3.23.
Some major African structures that settled in the last 100 Million years and related impact on fish diversity. Colours inform on the time period when each geological structure modified the regional geomorphology and the fish palaeogeography.

and Arabian plates during the Miocene should have enhanced the process or at least made it very patent, because of the disruption of the hydrographical network between the two plates.

During the late Miocene and the Pliocene, endemism and exchanges occur between the sub-basins of the Nilo-Sudan depending on their palaeogeography, but a rather homogenous fauna is maintained.

General characteristics of ichthyological fauna

Christian Lévêque

Didier Paugy

Currently, among nearly 11,000 fresh and brackish water fish species described in the world (Nelson, 1994; Froese & Pauly, 2016), 3,360 species have been described from Africa, belonging to 95 families (Lévêque *et al.*, 2008). Initially, these species were listed in the Check-List of the Freshwater Fishes of Africa or CLOFFA (Daget *et al.*, 1984, 1986a and b, 1991), but since its publication numerous species have been described or placed in synonymy following taxonomic revisions. These revisions also concerned the higher entities (genera, families). Thus, many families have been broken up into several others. For example the old family Bagridae has been divided into three families: Bagridae, Claroteidae and Austroglanididae (Mo, 1991). Conversely, some families who still retained an uncertain status could now be grouped. Thus, genetic studies have confirmed the monophyly of the Cromeriidae and Grasseichthyidae with the Kneriidae within the Gonorynchiformes (Lavoué *et al.*, 2005).

The discovery and description of new species of fish still constitute an important scientific activity in Africa. Rich faunas of cichlids endemic to the Great Lakes of East Africa have not yet delivered all their secrets. Similarly, still poorly-explored areas, such as Angola and some areas including parts of the Congo basin, should still reveal many other species.

In countries where the fish fauna is considered to be relatively well-known, the introduction of new fishing techniques (electro-fishing for example) can lead to the identification of species that had not been captured using traditional techniques alone. Similarly, using new taxonomic tools (*i.e.*, molecular techniques, specific parasitic markers, electrical signals, behaviour, etc.) has facilitated the revision of some taxonomic groups previously based solely on morphology.

For example, we can mention the striking species flock of *Brienomyrus* (Mormyridae) in Ogowe basin in Gabon (Sullivan *et al.*, 2002; Sullivan *et al.*, 2004). At least 41 different forms could be identified, while only five species are described (figure 4.1). However, the specific status of some of these forms remains uncertain. Thus, it is not possible to distinguish the two groups that have different electric waves using only morphological or genetic characters (Arnegard *et al.*, 2005) (figure 4.2).

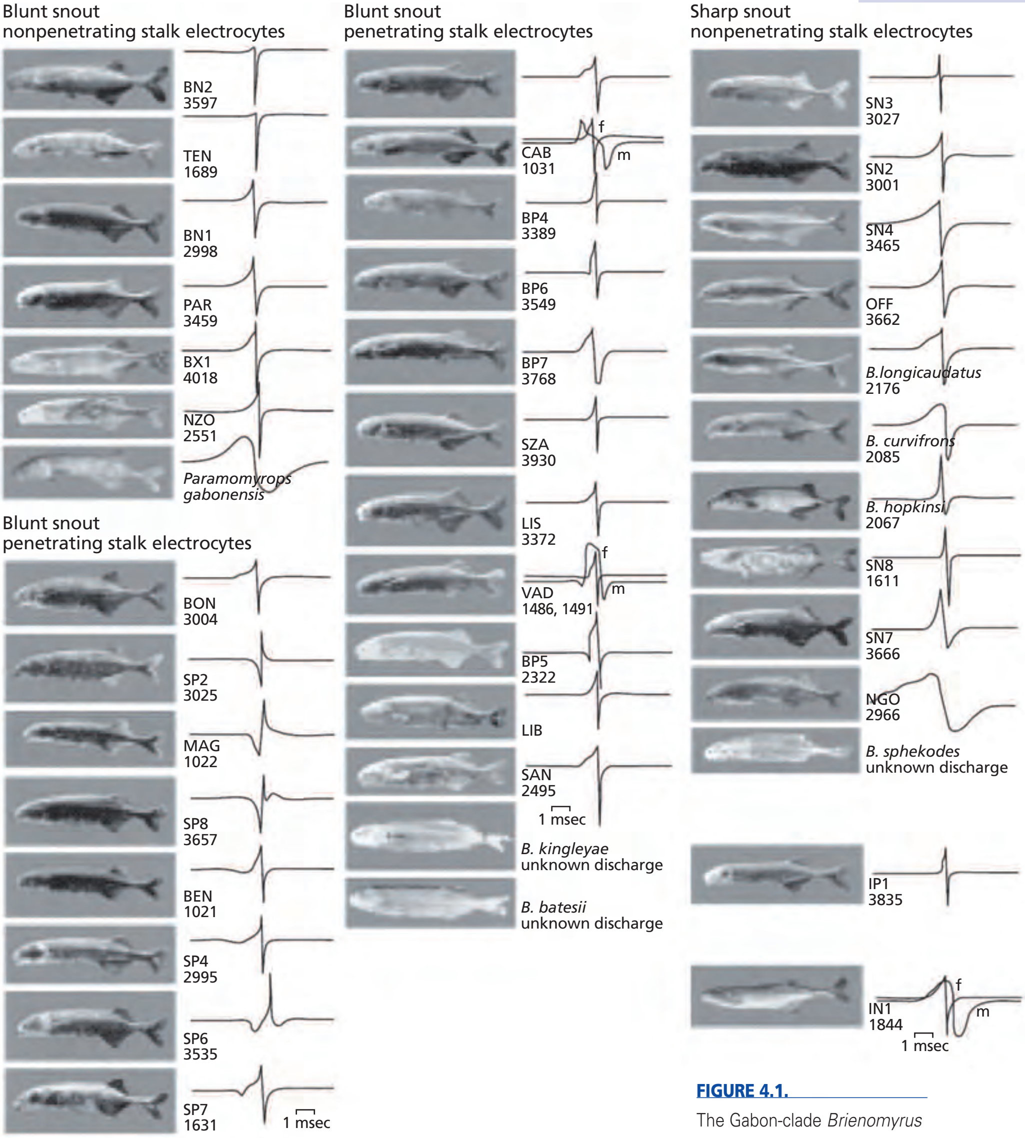


FIGURE 4.1.
The Gabon-clade *Brienomyrus* (from Sullivan et al., 2002).

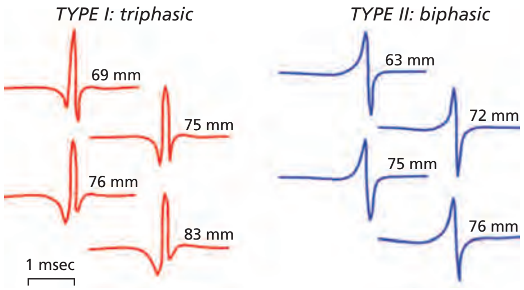


FIGURE 4.2.
Biphasic and triphasic electric organ discharges recorded from different *Brienomyrus* signal forms that cannot be discriminated through genetic and morphologic characters alone.

Composition of the ichthyofauna

Cyprinidae, Alestidae, and a few Siluriformes families constitute the bulk of the riverine fish fauna with Cyprinodontiformes and Mormyridae (table 4.I). The Cichlidae are by far the most abundant with some 1,150 species (more than 2,000 estimated) and about 143 genera recorded, most of them endemic to East African lakes where many species still remain to be described.

Ichthyologists used to distinguish three major groups of fish according to their tolerance of salt water and their ability to disperse across the sea (Myers, 1951):

- the primary division comprises the "primary fish" which are strictly intolerant to salt water and are therefore limited exclusively to freshwaters. They are usually much longer established in continental waters than the other groups. For example, all Mormyrids belong to this group.
- the secondary division includes "secondary fish" rather strictly confined to fresh water but evidently capable of occasionally crossing narrow sea barriers. Many of them are salt-tolerant for short periods. Some species of Cichlidae and Cyprinodontiformes belong to this division.
- the "peripheral" division includes representatives of extant marine families which have colonized inland waters. An example is the genus *Lates* (Latidae), of marine origin, but now widespread in Africa where it has colonized most freshwater habitats. This group includes diadromous fish which are few in African freshwater contrary to what is observed in Europe.

In Africa, 28 out of 94 indigenous families (six families were introduced), are "primary" division fishes and represent about 55% of the recorded species. Another 32% belong to the 3 families of "secondary" division fishes, of which the cichlids alone represent around 30%. The remaining 12% belong to 57 families of the "peripheral" division (table 4.I).

The main feature of African fish fauna is the existence of a high proportion of endemic families (15 of the 28 families belong to the "primary" group) (figure 4.3). They are probably among the most ancient families of fish, given that the African continent has remained above sea level since the Precambrian, more than 600 million years ago. This long period of exundation may explain why Africa has a far more diverse fish fauna than South America, and an unparalleled assemblage of archaic families, such as Protopteridae, Arapaimidae, whose distribution extends far beyond Africa to Australia, Asia and South America, but that have evidently been there for a long time.

The African inland waters house elements of marine origin which either evolved in freshwaters, or moved seasonally or sporadically between the sea and freshwaters: Perciformes, Pleuronectiformes and Tetraodontiformes provide examples.

The number of inland waters fishes of Africa is a little lower than the number estimated for South America. Compared to African fish fauna, there are no Cyprinidae in the South American fauna which mostly consists of Siluriformes

TABLE 4.I.

African fish families with representative in fresh and brackish waters (in orange-brown: introduced families).

Class / subclass ***Orders*** Families	**Division**	**Number of species at least peripheral**	**Number of genera in Africa**	**Number of species in Africa**	**Distribution beyond Africa**
Cephalaspidomorphi					
Petromyzontiformes		41			
01 Petromyzontidae	peripheral		1	1	marine, temperate
Elasmobranchii					
Carchariniformes		8			
02 Carcharhinidae	peripheral		2	2	widespread
Pristiformes				5	
03 Pristidae	peripheral		2	5	widespread, tropical
Rajiformes				27	
04 Dasyatidae	peripheral		4	4	widespread, tropical
Sarcopterygii					
Lepidosireniformes		5			
05 Protopteridae	primary		1	5	South America
Actinopterygii					
Polypteriformes		10			
06 Polypteridae	primary		2	10	fossils in South America
Acipenseriformes				26	
07 Acipenseridae	peripheral		1	1	northern hemisphere, temperate
Osteoglossiformes		217			
08 Arapaimidae	primary		1	1	Asia, Australia, South America
09 Pantodontidae	primary		1	1	endemic to Africa
10 Notopteridae	primary		2	3	
11 Mormyridae	primary		19	203	endemic to Africa
12 Gymnarchidae	primary		1	1	endemic to Africa
Elopiformes		7			
13 Elopidae	peripheral		1	1	widespread
14 Megalopidae	peripheral		1	2	widespread, tropical
Albuliformes				1	
15 Albulidae	peripheral		1	1	widespread, tropical
Anguilliformes		26			
16 Anguillidae	peripheral		1	7	widespread
17 Muraenidae	peripheral		1	1	widespread
18 Ophichthidae	peripheral		3	5	widespread
19 Muraenesocidae	peripheral		1	1	widespread, tropical
Clupeiformes		80			
20 Denticipitidae	peripheral		1	1	endemic to West Africa
21 Clupeidae	peripheral		20	32	widespread
22 Pristigasteridae	peripheral		1	1	widespread, tropical
23 Engraulidae	peripheral		2	2	widespread
Gonorynchiformes		32			
24 Chanidae	peripheral		1	1	Indian Ocean, Western Pacific
25 Kneriidae	primary		4	30	endemic to Africa
26 Phractolaemidae	primary		1	1	endemic to Africa
Cypriniformes		2662			
27 Cyprinidae	primary		41	526	Eurasia
28 Cobitidae	primary		1	1	Eurasia
29 Balitoridae	primary		1	1	Eurasia

TABLE 4.I. (CONT.)

Class / subclass *Orders* Families	Division	Number of species at least peripheral	Number of genera in Africa	Number of species in Africa	Distribution beyond Africa
Characiformes		1343			
30 Hepsetidae	primary		1	1	endemic to Africa
31 Alestidae	primary		13	106	endemic to Africa
32 Citharinidae	primary		3	10	endemic to Africa
33 Distichodontidae	primary		17	92	endemic to Africa
Siluriformes		2287			
34 Ictaluridae	primary		1	1	North America
35 Siluridae	primary		1	1	Eurasia
36 Bagridae	secondary		1	10	Asia
37 Austroglanididae	primary		1	3	endemic to Africa
38 Claroteidae	primary		16	92	endemic to Africa
39 Schilbeidae	primary		5	32	Asia
40 Amphiliidae	primary		12	65	endemic to Africa
41 Clariidae	primary		13	76	Asia
42 Malapteruridae	primary		1	11	endemic to Africa
43 Ariidae	peripheral		3	12	tropical
44 Plotosidae	peripheral		1	2	Indian Ocean, Western Pacific
45 Mochokidae	primary		8	189	endemic to Africa
Esociformes		10			
46 Esocidae	primary		1	1	northern hemisphere, temperate
Osmeriformes		71			
47 Galaxiidae	peripheral		1	1	temperate
Salmoniformes		66			
48 Salmonidae	peripheral		4	6	northern hemisphere, temperate
Atheriniformes		171			
49 Bedotiidae	peripheral		2	11	Endemic to Madagascar
50 Atherinidae	peripheral		2	4	Pacific and Mediterranean
Cyprinodontiformes		805			
51 Aplocheilidae	primary		11	221	South Asia, South and Central America
52 Poeciliidae	secondary		14	83	North and South America
53 Cyprinodontidae	secondary		2	6	North and Central America; Anatolia
Beloniformes		56			
54 Hemiramphidae	peripheral		3	4	widespread
Gasterosteiformes		24			
55 Gasterosteidae	peripheral		1	1	Europe
Syngnathiformes		35			
56 Syngnathidae	peripheral		4	13	widespread
Synbranchiformes		87			
57 Synbranchidae	peripheral		2	2	widespread
58 Mastacembelidae	primary		2	50	Asia
Perciformes		2185			
59 Centropomidae	peripheral		1	7	widespread
60 Ambassidae	peripheral		1	7	Indo-Pacific; east coast of Africa
61 Moronidae	peripheral		2	2	North America; Europe
62 Terapontidae	peripheral		2	4	Indo-Pacific; east coast of Africa
63 Kuhliidae	peripheral		1	2	Indo-Pacific; east coast of Africa
64 Centrarchidae	primary		2	7	North America
65 Percidae	primary		2	2	northern hemisphere, temperate
66 Apogonidae	peripheral		2	3	widespread
67 Carangidae	peripheral		2	3	widespread, tropical

TABLE 4.I. (CONT.)

Class / subclass ***Orders*** Families	**Division**	**Number of species at least peripheral**	**Number of genera in Africa**	**Number of species in Africa**	**Distribution beyond Africa**
68 Leiognathidae	peripheral		2	2	Indo-Pacific; east coast of Africa
69 Lutjanidae	peripheral		1	6	widespread
70 Gerreidae	peripheral		2	3	widespread
71 Haemulidae	peripheral		2	3	widespread, tropical
72 Sparidae	peripheral		2	3	widespread
73 Sciaenidae	peripheral		4	4	widespread
74 Polynemidae	peripheral		1	1	widespread, tropical
75 Monodactylidae	peripheral		1	3	Indo-Pacific; east coast of Africa
76 Nandidae	primary		2	2	Asia; South America
77 Mugilidae	peripheral		6	21	widespread
78 Cichlidae	secondary		154	1047	Asia; South and Central America
79 Pomacentridae	peripheral		1	1	widespread, tropical
80 Clinidae	peripheral		1	1	widespread
81 Blenniidae	peripheral		3	5	widespread
82 Eleotridae	peripheral		11	32	widespread
83 Gobiidae	peripheral		31	59	widespread
84 Kraemeriidae	peripheral		1	1	Indo-Pacifique est
85 Microdesmidae	peripheral		1	1	widespread, tropical
86 Scatophagidae	peripheral		1	1	Indo-Pacific; east coast of Africa
87 Anabantidae	primary		3	34	Asia
88 Osphronemidae	primary		3	3	Asia
89 Channidae	primary		2	5	South Asia
Pleuronectiformes		20			
90 Paralichthyidae	peripheral		1	1	widespread
91 Pleuronectidae	peripheral		1	1	widespread
92 Soleidae	peripheral		4	4	widespread
93 Cynoglossidae	peripheral		1	1	widespread, tropical
Tetraodontiformes		12			
94 Tetraodontidae	peripheral		2	7	widespread
			533	3255	

and Characiformes (table 4.II). Conversely, in Asia Cyprinidae are dominant, the Siluridae (or Siluriformes) abundant, and there are many species of marine origin (table 4.II).

Main sources of taxonomic information

Scientific knowledge of African fish fauna is relatively recent and remains a poorly-explored area. The 10th edition of Linnaeus's "Systema naturae", published in 1758, cited only 13 African freshwater fish species – the ones collected in Egypt by Hasselquist. He died near Smyrna on his way home but his collections reached home in safety, and five years after his death his notes were published by Linnaeus and translated into French, German and English as "Voyages and Travels in the Levant in the Years 1749-1752".

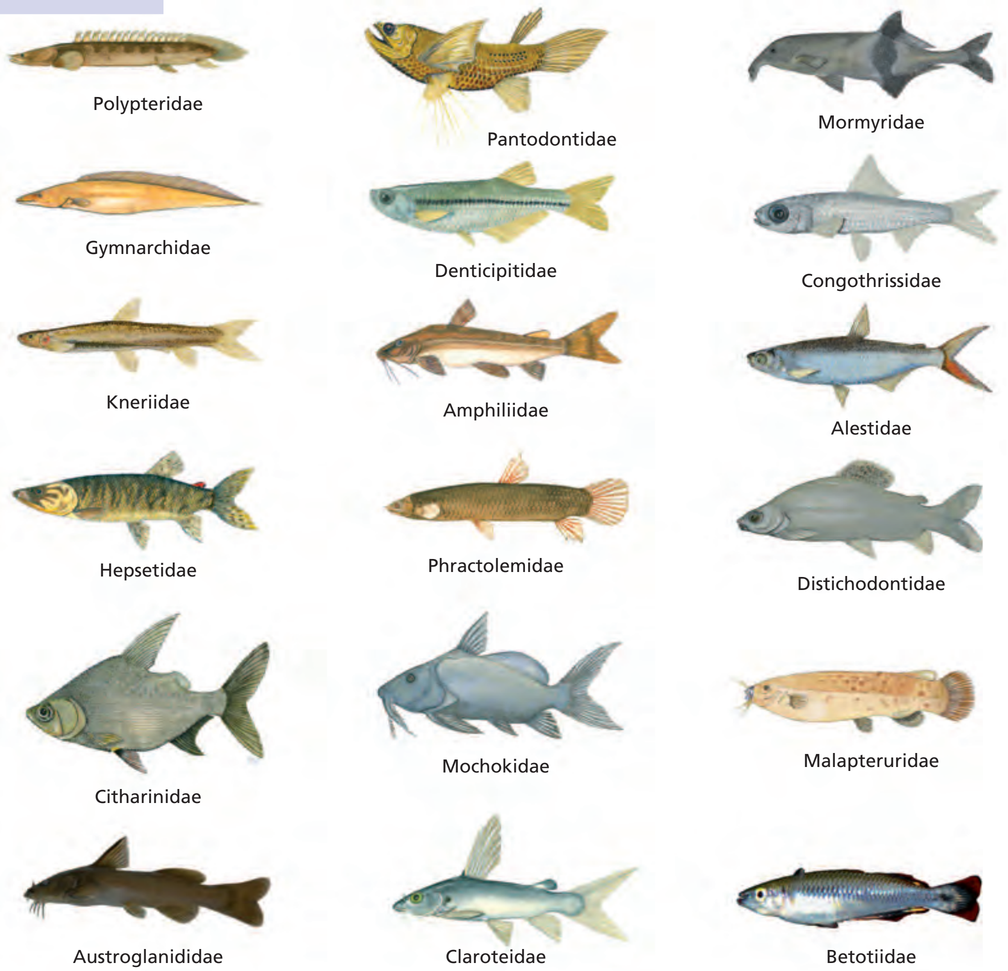


FIGURE 4.3.
Endemic families of Africa.

The true father of modern African ichthyology, Michel Adanson (1727-1806), was a Frenchman who lived in Senegal from 1749 to 1753. Although he published nothing on fishes during his lifetime, he built a large collection in the form of a "herbarium", part of which was given to the Cabinet du Roi in 1756. Another part was deposited at the Muséum de Paris, and the set was used by Cuvier and Valenciennes for their "Histoire naturelle des Poissons" whose 22 volumes were published between 1828 and 1849. About 130 to 140 species of African fresh and brackish water fishes were cited in the work. A third part of Adanson's collection, kept in the family château, was only rediscovered in the early 20th century and was given to the Muséum de Paris in 1939. After Adanson's death, part of his handwritten notes and field drawings were used for the "Cours d'Histoire naturelle" published in 1844-45 (Paugy, 2010a).

TABLE 4.II.
Compared composition of the fish fauna in four representative large basins of Africa (Niger), South America (Mamoré), North America (Mississippi) and Asia (Mekong).

	Mamoré South America	Mekong Asia	Mississippi North America	**Niger** **Africa**
Drainage area (km^2)	159,000	783,000	3,200,000	1,125,000
Length (km)	1,050	4,200	3,780	4,183
Agnathes			7	
Elasmobranches	4	2		**1**
Dipnoi	1			**1**
Chondrostei			6	**4**
Semionotiformes	4		4	
Amiiformes			1	
Osteoglossiformes		3	2	**32**
Anguilliformes			1	
Clupeiformes	4	2	4	**6**
Gonorynchiformes				**1**
Characiformes	138			**35**
Beloniformes	1			
Cypriniformes		168	81	**35**
Siluriformes	146	65		**65**
Gymmnotiformes	20			
Esociformes			2	
Atheriniformes	4		2	
Percopsiformes			1	
Cyprinodontiformes	3	1	1	**23**
Perciformes	21	17	63	**33**
of which Cichlidae	18			**17**
Gasterosteiformes		1		
Synbranchiformes	1	7		**3**
Scorpeniformes			2	
Pleuronectiformes	1	5		**2**
Tetraodontiformes		7		**1**
TOTAL	**350**	**278**	**177**	**242**

Continental level

The only general fish fauna available on a pan-African scale is Boulenger's Catalogue (1909-1916) which is only of historical value at present. A major step forward was the publication of the Check-List of the Freshwater Fishes of Africa (CLOFFA) which provides a current list of brackish and freshwater fish species with full synonymies as well as a full bibliography (Daget *et al.*, 1984, 1986a and b, 1992). The CLOFFA is particularly useful for taxonomists as a major source of information for further taxonomic revisions.

Regional level

For several decades, ichthyologists devoted their research to the inventory of the fish fauna of African continental waters, which allowed the description of many new species. In some cases, their work led to the publication of local or regional inventories and fauna lists. In other cases, regional taxonomic summaries were not yet made. A detailed bibliography of taxonomic publications on African fishes can be found in volumes 3 and 4 of CLOFFA (Daget *et al.*, 1986b, 1991). The websites FishBase (www.fishbase.org) and Faunafri (http://www.poissons-afrique.ird.fr/faunafri/) are, of course, essential tools.

Maghreb

Pellegrin (1921) remains an important reference for the Maghreb. Other works on the systematics and phylogeny of various groups, notably the Cyprinidae, have been published since, but a summary of these works would be welcome (Doadrio, 1994).

Western Africa

Ichthyological inventories for West Africa began in the late 19th century. F. Steindachner from Austria (1870, 1895) as well as A. Günther from Britain, then H.E. Sauvage and J. Pellegrin from France and the Belgian-born British scientist G.A. Boulenger, described numerous species based on the collections that were brought back to them by travellers. A fauna of the freshwater fishes of West Africa written by Pellegrin (1923) summarized the state of knowledge at that time. Later, especially after the Second World War, inventories covered whole basins or regions. These included the following monographies by country or basin: Gambia (Svensson, 1933; Johnels, 1954), Ghana (Irvine, 1947), Upper Niger (Daget, 1954), Chad basin (Blache *et al.*, 1964), Côte d'Ivoire (Daget & Iltis, 1965), Volta (Roman, 1966), coastal rivers of Côte d'Ivoire, Ghana, Guinea, Sierra Leone, Liberia, and Togo (Schültz, 1942; Daget, 1962b; Teugels *et al.*, 1988; Lévêque *et al.*, 1989, 1991; Paugy *et al.*, 1989, 1994; Paugy & Bénech, 1989). The many inventories established later, most notably by teams from Orstom (later IRD) and the Tervuren Museum (Belgium) made it possible to publish an updated fauna of fresh and brackish water fishes of West Africa (Lévêque *et al.*, 1990, 1992; Paugy *et al.*, 2003a, 2003b) which provide the state of knowledge on the taxonomy and distribution of species.

Nile Valley

By the late 18th century, European ichthyologists had begun studying Nile fishes. In 1789, Gmelin cited 17 Nile species based on the collections of Hasselquist (1722-1752) and Forskål (1736-1765). In 1799, Geoffroy Saint-Hilaire accompanied General Bonaparte during his Egyptian expedition and assembled large collections deposited with the Muséum d'Histoire naturelle de Paris. He published the description of *Polypterus* in 1802, and that of other species in 1809. The first overview of Nile fishes was published in 1907 by Boulenger and remains a useful reference.

Lake Tana was the focus of recent work that revealed the existence of a large *Barbus* species flock (Nagelkerke & Sibbing, 2000).

Lower Guinea

The first collections from Cameroon were collected by the German scientist R. Buchholz in the region of Douala and deposited at the Zoologissches Museum der Humboldt Universität in Berlin where they were studied by W.C.H. Peters. Later, Lönnberg of Sweden published the results of collections carried out in the area of Mount Cameroon. Between 1903 and 1913, G.A. Boulenger wrote a summary of the collections made by the American scientist G.L. Bates deposited at the British Museum in London. The Austrian professor K. Haberer also carried out important collections from the Sanaga

River between 1907 and 1909, deposited at the Naturhistorisches Museum in Vienna but described only twenty years later by Holly. In 1930, he published a synopsis of the freshwater fishes of Cameroon. Later, E. Trewavas (1962) examined the crater lake fishes deposited in the British Museum's collections. They were collected in 1948 by the British scientist P.I.R. MacLaren from the southwestern part of the country.

The first specimens from the Ogowe River collected by R.B.N. Walker in 1866 were investigated by British scientist A. Günther of the British Museum. Later, the river was explored in 1874 by Savorgnan de Brazza, who deposited large collections at the Muséum d'histoire naturelle de Paris. Sauvage studied them and later published the first ichthyological inventory of the Ogowe River (Sauvage, 1880). Finally, Mrs Kingsley arrived on the banks of the Ogowe River in 1895 to study the civilizations of Gabon, but she also collected 65 fish species (of which 46 were then unknown). J. Pellegrin continued this work later.

The first collections from the coastal basins of the Congo were carried out in 1929 by French scientist Baudon and deposited at the Muséum de Paris, where they were also examined by J. Pellegrin.

For Lower Guinea (Cameroon, Gabon, Congo), partial contributions had to suffice for a long time: Amiet *et al.*, 1987; Daget, 1978, 1979; Daget & Depierre, 1980; Roman, 1971; Mbega & Teugels, 2003; Thys van den Audenaerde, 1966, 1967; Teugels *et al.*., 1992; Teugels & Guégan, 1994; Mamoneke & Teugels, 1993. But an inventory of N'Tem fauna was nonetheless published (Kandem Toham, 1998) and more recently, an overview of the fresh and brackish water fauna of Lower Guinea was also published (Stiassny *et al.*, 2007a and b).

Congo

The situation is much less favourable for the Congo, for which Boulenger (1901) proposed an initial inventory. Major contributions from the first half of the 20th century came from Nichols & Griscom (1917), Fowler (1936) and Poll (1938). These were followed after the Second World War by major regional contributions such as those by Banister & Bailey (1979), De Kimpe (1964), Gosse (1963, 1966, 1968), Matthes (1964), Poll (1967, 1976), and Poll & Gosse (1963). There are numerous collections from the Congo basin, and it is urgent to summarize and update the available information (Teugels & Guégan, 1994) because this work was not yet realized for the largest African basin. Nevertheless, several recent local contributions (Wamuini Lunkayilakio *et al.*, 2010; Ibala Zamba, 2010) have improved our knowledge of the ichthyological fauna of the Congo basin, which most certainly contains the greatest species diversity.

Angola

Despite Poll's work (1967) over a very limited area, Angola remains a poorly known region in which there remains much to be discovered.

Eastern Africa

The fauna of the East African great lakes is composed in large part of endemic species (Lowe-McConnell *et al.*, 1994). For Lake Victoria, taxonomic data can be found in Barel *et al.* (1977), Greenwood (1980, 1981), Oijen (1991, 1996), Oijen & Witte (1996), Witte & Oijen (1990), Fermon (1997). For Lake Tanganyika, the main sources are Brichard (1989), Coulter (1991), De Vos & Snoeks (1994) and Poll (1986).[1] References for Lake Malawi include Konings (1990), Eccles & Trewavas (1989) and Duponchelle & Ribbink, 2000); for Lake Kivu, Snoeks (1994); and for Lake Rukwa, Seegers (1996).

Zambezi

The fauna of the Zambezi is relatively scarce and is rather well known with the work of Jubb, 1965, 1967; Bell-Cross, 1972, 1976; Gaigher & Pott, 1972; Bruton & Kok, 1980; Skelton *et al.*, 1985; Jackson, 1986; Skelton, 1994; and Marshall, 2011.

East Coast

An exhaustive list of the fish species of the Ethiopian Rift Valley was recently published by Golubtsov *et al.*, 2002. For the East Coast of Africa, Eccles (1992) published a summary of the current state of knowledge, and a detailed inventory was proposed by Skelton (1994).

Southern Africa

In South Africa, the inventory of freshwater fishes began with Burchell's expedition (1811-1812), whose results were published in 1822. A. Smith, who was in charge of the Cape Town museum built in the 1820s, carried out missions inside the country between 1834 and 1836, and published the results of his collections between 1840 and 1845; they included several fish species. During this period, German scientist Wilhelm Peters went on an expedition in what is now Mozambique and described many species. In 1861, France's consul at Cape Town, F. Castelnau, described 21 fish species including some from the Okavango. Several other European scientists, including F. Steindachner of Austria, M. Weber of the Netherlands, and A. Günther and G. Boulenger of Britain, also made significant contributions in the late 19th and early 20th centuries. G.D.F Gilchrist and W.W. Thompson of the South African Museum were the first resident scientists to work on freshwater fishes. They published an initial catalogue between 1913 and 1917. Their successor, K. Barnard (1943), then R. Jubb after the Second World War, pursued the inventory of species with Jubb's 1967 release of "Freshwater Fishes of Southern Africa". Skelton (2001) provides an updated summary of knowledge of this relatively poor fauna dominated by the Cyprinidae.

Madagascar

Malagasy fauna mainly comprises species of marine origin (Pellegrin, 1933; Arnoult, 1959; Kiener, 1963; Stiassny & Raminosoa, 1994). If species that only penetrate fresh water occasionally are excluded, known species would number around sixty (de Rahm, 1996; Sparks & Stiassny, 2003).

NOTE 1

[1] The site http://www.destin-tanganyika.com/ also provides a fully updated overview of the ichthyological fauna of Lake Tanganyika.

Taxonomic revisions

Many taxonomic revisions of African fishes at the continent level have been published during past 30 years: Among the main works, we can list:

- **Mormyridae**: phylogeny of the family (Lavoué, 2001); phylogeny of the Gabon-clade Brienomyrus (from Sullivan *et al.*, 2002)
- **Alestidae**: *Alestes* and *Brycinus* (Paugy, 1986); *Hydrocynus* (Paugy & Guégan, 1989); Hubert *et al.*, 2005
- **Cyprinidae**: Neobolines (Howes, 1984), *Labeo* (Reid, 1985)
- **Bagridae**: in Africa, the Bagridae are now separated in three: Bagridae, Claroteidae and Austroglanididae (Mo, 1991)
- **Claroteidae**: *Chrysichthys* (Risch, 1986); *Auchenoglanis* and *Parauchenoglanis* (Teugels *et al.*, 1991)
- **Schilbeidae**: *Schilbe* (De Vos, 1984; 1995)
- **Mochokidae** : *Synodontis* (Poll, 1971); *Microsynodontis* (Ng, 2004); phylogeny of *Synodontis* (Pinton *et al.*, 2012)
- **Clariidae**: *Clarias* (Teugels, 1986; Hanssens, 2009) and *Heterobranchus* (Teugels *et al.*, 1990)
- **Malapteruridae**: *Malapterurus* description of 11 new species; a new genus *Paradoxoglanis* with 3 new species (Norris, 2002),
- **Cyprinodontiformes**: Poeciliidae (Huber, 1999; Ghedotti, 2000), Aplocheilidae (Murphy & Collier, 1997; Murphy *et al.*, 1999).
- **Cichlidae**: *Oreochromis* and *Sarotherodon* (Trewavas, 1983), *Tylochromis* (Stiassny, 1989)
- **Mastacembelidae**: *Aethiomastacembelus* and *Caecomastacembelus* grouped into a single genus *Mastacembelus* (Vreven, 2001; 2005)
- **Channidae**: *Parachanna* (Bonou & Teugels, 1985).

It is now possible to keep track of developments in the identification of fauna in real time by consulting reliable specialist sites.

Geographical distribution and affinities of African freshwater fishes

CHRISTIAN LÉVÊQUE

DIDIER PAUGY

The present day composition and distribution of the fish fauna are the result of a long and complex history. They have been shaped by millions of years of changes in the global water cycle and the dynamics of freshwater systems. The dual processes of speciation and extinction have interacted with climatic and geological events that have isolated fish populations and/or provided opportunities for migrations and colonization of new habitats.

The understanding of the zoogeography of African fish has prompted several surveys since the beginning of the century. Ideas have evolved substantially according to progress made in regional inventories and taxonomic information (see chapter *General characteristics of ichthyological fauna*). However, some fundamental questions remain challenging. What are the driving factors responsible for the colonization of the continent and the differentiation of the fish fauna in several provinces (biogeography)? What are the affinities of the African ichthyofauna with the other continental faunas? Ichthyologists try to answer these and many other puzzling questions with unflagging pleasure!

Patterns of fish distribution and ichthyological provinces

At the continental level, African ichthyofauna is not distributed homogeneously and the current distribution is a result of:

- the climatic history and geological events that have shaped the current hydrographic systems. In the past, they permitted interconnections between river basins, as well as the temporary or permanent isolation of certain aquatic systems;
- the process of speciation which depends on the duration of hydrographic isolation and of the evolutionary potential of species;
- the ability of fish to disperse and the existence of refuge zones during drought period;
- the size of the catchment area and the diversity of aquatic habitats available for fish which subsequently determine the composition of the communities observed;
- the consequences of diseases that may have affected fish population, even if this type of impact is still very poorly documented.

TABLE 5.I

Presence/absence of families of fish in the African ichthyologic provinces (shown on figure 5.1) belonging to "primary" and "secondary groups ".
Abbreviations for provinces: Maghreb (Mag); Nilo Sudan (NS) including sectors Eburneo-Ghanaian (EG), nilotic (Nilo), Abyssinian (Aby); Upper Guinea (UG); Lower Guinea (LG); Congo (Con); Zambezi (Zam); Angola (Ang); Eastern coast (East); Ethiopian area (Ethio), including Ethiopian Rift Valley (ERV), Lake Tana (Tan), Coastal Red Sea (CRS) and Nilotic group (Nilo); Karroid (Kar); Cape (Cape); Madagascar (Mad).

Families	**Mag**	**NS**		**UG**	**LG**	**Con**	**Zam**	**Ang**	**East**	**Ethio**				**Kar**	**Cape**	**Mad**
		EG	*Nilo*							*ERV*	*CRS*	*Tan*	*Nilo*			
Protopteridae		●	●	●	●	●	●		●				●			
Polypteridae		●	●	●	●	●							●			
Denticipidae					●											
Arapaimidae			●		●								●			
Pantodontidae					●	●										
Notopteridae		●	●	●	●	●										
Mormyridae		●	●	●	●	●	●	●	●				●			
Gymnarchidae			●										●			
Kneriidae			●		●	●	●	●								
Phractolemidae					●	●										
Hepsetidae		●	●	●	●	●	●	●	●							
Alestidae		●	●	●	●	●	●	●	●				●			
Distichodontidae		●	●	●	●	●	●	●	●				●			
Citharinidae		●	●		●	●			●				●			
Cyprinidae	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
Cobitidae	●															
Balitoridae												●	●			
Bagridae		●	●	●	●	●	●	●	●				●			
Claroteidae		●	●	●	●	●	●	●	●				●			
Auchenoglanididae		●	●	●	●	●	●	●	●				●			
Austroglanididae														●	●	
Schilbeidae		●	●	●	●	●	●	●	●				●			
Amphiliidae		●	●	●	●	●	●	●	●				●			
Clariidae	●	●	●	●	●	●	●	●	●	●		●	●	●		
Malapteruridae		●	●	●	●	●	●						●			
Mochokidae		●	●	●	●	●	●	●	●				●			
Cyprinodontiformes	●	●	●	●	●	●	●	●	●	●	●		●			●
Bedotidae																●
Channidae		●	●	●	●	●										
Latidae			●			●							●			
Synbranchidae				●												
Nandidae		●		●	●											
Cichlidae	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●
Anabantidae		●	●	●	●	●	●		●					●	●	
Mastacembelidae		●	●	●	●	●	●	●	●							
Tatraodontidae		●	●		●	●							●			
Number of families	**5**	**24**	**27**	**23**	**29**	**27**	**19**	**16**	**18**	**4**	**3**	**4**	**22**	**5**	**3**	**3**

FIGURE 5.1. The main ichthyological provinces of Africa (from Lévêque, 1997a and Paugy, 2010b).

On the basis of the distribution of the various families and fish species (table 5.I), ichthyologists have currently recognized the existence of ten large ichthyological provinces, inhabited by particular fish communities (Lévêque, 1997a; Paugy 2010b) (figure 5.1):

- **Maghreb province** has a depauperate fish fauna which has little affinity to tropical fauna and is primarily made up of Cyprinidae (Doadrio, 1994);
- **Nilo-Sudan province** extends from the Atlantic up to Ethiopia. It includes the major river basins of the Sahelian zone: Nile, Chad, Niger, Volta, Senegal, Gambia, and Cross Rivers in the south-west (Lévêque *et al.*, 1991; Paugy *et al.*, 2003a; b). Historically, Lake Victoria was also included into this province which is characterized by the presence of a great number of families. It can contain two sub-provinces: Eburneo-Ghanean to the west, characterized by a couple of endemic species (Teugels *et al.*, 1988), and Nilotic (Paugy, 2010b) to the east which is impoverished compared to the others (Hugueny & Lévêque, 1994; Paugy *et al.*, 2003a, b and Paugy, 2010b);
- **Upper Guinea** includes coastal basins from Kogon River in Guinea to Nipoué River at the border of Ivory Coast and Liberia. The families of fish represented are more or less similar to the Nilo-Sudan province, although species composition is very different. Many taxa are endemic to that area which exhibits affinities with the Lower Guinea and Congo (Lévêque *et al.*, 1989; Paugy *et al.*, 2003a; b);

- **Lower Guinea** covers the region from the coastal rivers of Cameroon and Gabon to the mouth of Congo and comprises a rich and diverse fauna (Teugels *et al.*, 1992; Mamoneke & Teugels, 1993; Stiassny *et al*. 2007a; b);
- **Congolese province** includes the entire Congo River basin that is the largest in Africa. Fish faunas of Lakes Kivu and Tanganyika are sometimes in this province. Its fauna is the richest in the continent, although rather poorly known in regards to systematics and distribution of species;
- **Angolan province** includes the coastal drainages of Angola which are inhabited by a characteristic ichthyofauna (Poll, 1967). Currently, this is probably the most poorly-known province;
- **Zambezi province** including the Zambezi and the Okavango basins has a moderately rich fish fauna (Jackson, 1986; Skelton, 1994);
- **East coast province** extends from coastal basins flowing towards the Juba River to the Zambezi (Eccles, 1992; Skelton, 1994);
- **Ethiopian Rift Valley (ERV) or Oromo province** includes all the central and northernmost lakes of the ERV and the Awash River (including Lake Abbe) (Paugy, 2010b);
- **Coastal Red Sea (CRS) province** includes the small coastal basins that flow into the Red Sea. Its fauna, very poor, is close to that of the Near East (Paugy, 2010b);
- **Cape province**, restricted to the rivers of the Cape Fold Mountains, the Amatolas and the Drakensberg, has a rather poor fauna with predominance of Cyprinidae (Skelton, 1994);
- **Karroo province**, centred upon the Orange basin, mainly includes Cyprinids (*Barbus* and *Labeo umbratus* group), as well as southern rock catfishes (*Austroglanis* species) (Skelton, 1993);
- **Malagasy province** remains an enigma for biogeographers. The fauna (135 species, predominantly endemic) is moderately rich. Most of the species belong to widely distributed peripheral families having affinities with Indian Ocean marine province. (Stiassny & Raminosoa, 1994; Sparks & Stiassny 2003).

Finally, due to their endemicity, we consider all the great lakes of East Africa as separate provinces. In most of them, the main fish fauna is constituted by species flocks (Cichlids in Lakes Victoria, Kivu, Tanganyika, Malawi, etc. and Cyprinids in Lake Tana).

In regards to species richness and diversity, the composition of the ichthyofauna within these ichthyoprovinces (table 5.II) has shown that some families have a wider distribution and a greater relative importance than others. That is the case, namely, for Mormyridae, Cyprinidae, Mochokidae, Cichlidae.

The East African Lakes (Victoria, Tanganyika, Malawi, Kivu) and to a lesser extent the lakes of the Rift Valley are inhabited by species that are unique to each lake. The term species flock is sometimes used for these monophyletic groups of species coexisting in the same environment. These large lakes are unique

TABLE 5.II

The composition of the ichthyofauna in representative rivers of the major ichthyological provinces. Nile, Chari and Lake Chad (Cha), Niger and Volta according to Lévêque *et al.*, 1991; Konkouré (Konk) according to Lévêque *et al.*, 1989; Jong according to Paugy *et al.*, 1990; Sassandra (Sass) and Bandama (Band) according to Teugels *et al.*, 1988; Ogowe according to Stiassny *et al.*, 2007a, b; Awash according to Paugy, 2010b; estimates for Sanaga (Sana), and Congo according to CLOFFA (Daget *et al.*, 1984, 1986a, 1991); Ruaha according to Eccles, 1992; Zambezi (Zamb) according to Jackson, 1986; Orange-Vaal (Oran) according to Skelton, 1986. Provinces NS: Nilo-sudan; UG: Upper Guinea; EG: Eburneo-Ghanean; LG: Lower Guinea; EC: Eastern; ERV: Ethiopian Rift Valley; Co: Congolese; Zz: Zambezi.

Basins ***Provinces***	**Nile** *NS*	**Chad** *NS*	**Niger** *NS*	**Volta** *NS*	**Konk** *UG*	**Jong** *UG*	**Sass** *EG*	**Band** *EG*	**Sana** *LG*	**Ogowe** *LG*	**Rufiji** *ET*	**Awash** *ERV*	**Congo** *CO*	**Zamb** *ZZ*	**Oran** *KA*
Dasyatidae			1						1				1		
Protopteridae	2	1	1	1				1		1			3	1	
Polypteridae	3	3	4	3	1		1	1	1	1			9		
Anguillidae	1										1			4	
Denticipidae			1												
Clupeidae	1		5	3			1	1	1	3			13	3	
Arapaimidae	1	1	1	1									1		
Pantodontidae			1						1	1			1		
Notopteridae	1	1	2		1	2		1	1	1			2		
Mormyridae	15	14	27	16	10	13	8	10	16	21	6		109	10	
Gymnarchidae	1	1	1	1											
Kneriidae	1		1	1						2			15	4	
Phractolaemidae			1										1		
Hepsetidae		1	1	1	1	1	1	1	1	1			1	1	
Alestidae	8	11	16	15	4	7	7	8	12	18	6		55	8	
Distichodontidae	7	10	14	8	1	4	3	4	7	11	3		48	2	
Citharinidae	2	3	4	3			1	1			1		3	4	
Cyprinidae	25	23	35	24	16	13	17	18	39	28	16	6	128	45	8
Cobitidae	1														
Bagridae	2	2	3	3					2		2		3	1	
Claroteidae	5	6	13	4	4	6	4	3	7	9			26	1	
Austroglanididae															1
Schilbeidae	5	5	5	6	2	2	2	3	5	3	3		13	3	
Amphiliidae	1	1	5	3	4	2	1	1	3	8	1		25	1	
Clariidae	7	8	14	7	4	5	3	7	8	16	1	1	28	8	1
Malapteruridae	1	1	2	1	1	1	1	1	1	1			2	1	
Mochokidae	15	12	26	13	8	5	5	3	7	15	6		82	10	
Ariidae			3	1											
Cyprinodontiformes	7	8	23	9	8	8	6	10	20	52	5	2	59	8	
Channidae	1	1	2	1		1	1	1	1	2			2		
Latidae	2	1	1	1	1	1	1	1	1				1		
Polycentridae			1							1					
Gobiidae			3	?		1	1	3	2	2	1		3	2	
Eleotridae	1	1	5	1	3	3	1	1	1	2	1		4		
Cichlidae	10	10	17	9	15	16	8	9	7	23	3	1	90	28	2
Anabantidae	2	4	4	1	1	1	1	1	3	3			15	2	
Mastacembelidae		1	3	1	1	3	1	1	4	2	1		23	2	
Tetraodontidae	1	1	1	1									4	?	
Cynoglossidae			1						1	1			1		
Soleidae			1												
Number of families	**28**	**26**	**37**	**29**	**19**	**20**	**22**	**25**	**26**	**26**	**16**	**4**	**32**	**23**	**4**
Number of species	**129**	**131**	**249**	**139**	**86**	**95**	**75**	**91**	**153**	**228**	**57**	**10**	**771**	**149**	**12**

and exceptional sites for the study of speciation. They have been compared to natural laboratories. No equivalent situation exists in South America where the family Cichlidae is also well represented.

Moreover, these East African Lakes are inhabited by a diversified ichthyological fauna (table 5.III) whose origin depends on the hydrographical systems to which they were previously associated: the Nile for Lake Victoria, the Congo for Lake Tanganyika and the Zambezi for Lake Malawi. In Lake Tanganyika, species flocks also exist for groups other than Cichlidae: Mastacembelidae, Claroteidae (*Chrysichthys*) and Mochokidae (*Synodontis*) (De Vos & Snoeks, 1994). In Lake Malawi there is also a species flock for Clariidae (*Bathyclarias*) (Anseaume, 2007).

TABLE 5.III

Composition of the ichthyofauna of the East African Great Lakes (int.: introduced).
Data for Cichlidae drawn from CLOFFA IV (Daget *et al.*, 1991).
For other species: Coulter, 1991 (Lake Tanganyika); Ribbink & Eccles, 1988 (Lakes Malawi and Victoria); Lévêque *et al.*, 1991 (Lake Turkana).

Lakes	**Tanganyika**		**Malawi**		**Victoria**		**Kivu**		**Turkana**	
Families	Species	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Genera
Protopteridae	1	1	1	1	1	1			1	1
Polypteridae	2	1							1	1
Anguillidae			1	1						
Clupeidae	2	2					1 int.	1 int.		
Arapaimidae									1	1
Mormyridae	6	6	9	7	8	6			2	2
Gymnarchidae									1	1
Kneriidae	2	1								
Alestidae	7	5	2	2	5	2			9	4
Distichodontidae	3	1							1	1
Citharinidae	1	1							1	1
Cyprinidae	35	8	16	5	22	5	5	2	12	6
Auchenoglanididae	1	1							1	1
Bagridae	1	1	2	2	2	1			2	1
Claroteidae	15	7							1	1
Schilbeidae	2	1			2	3			1	1
Amphiliidae	2	2	1	1	3	2	1	1	1	1
Clariidae	9	4	15	3	6	3	2	2	2	2
Malapteruridae	1	2							2	1
Mochokidae	13	2	2	2	3	2	1	1	3	2
Cyprinodontiformes	2	2	3	3	8	5			2	1
Latidae	4	1			1 int.	1 int.			1	1
Cichlidae	250+	54	800+	59	500+	15	17	2	9	5
Anabantidae	1	1			1	1				
Mastacembelidae	13	1	1	1	1	1				
Tetraodontidae	1	1							1	1
TOTAL	**374+**	**106**	**853+**	**87**	**563+**	**48**	**27**	**9**	**55**	**36**

Intercontinental affinities of African fish

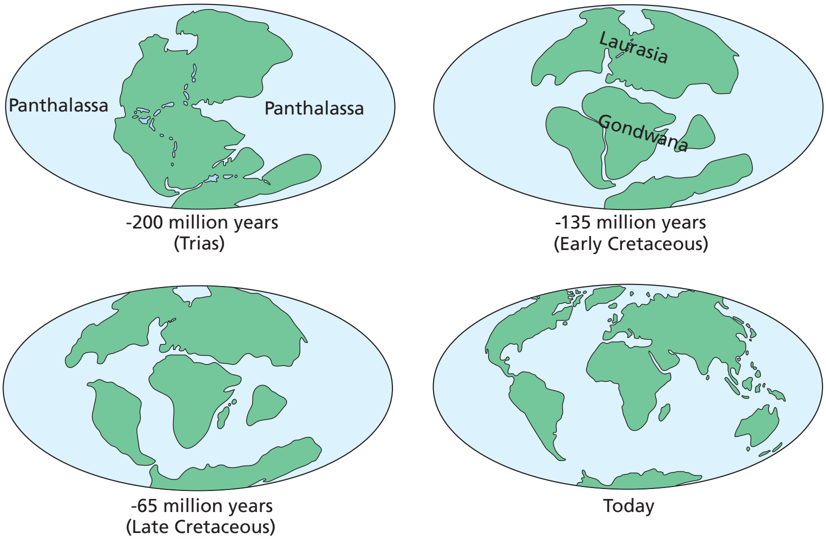
The precise number of extant fish species remains to be determined. However, since Linnaeus' listing of 478 species of teleost fish in 1758, our knowledge has increased considerably and some global estimates are available. The Catalog of Fishes established by Eschmeyer (2005) provided an estimate of 27,300 valid fish species, with a prediction of about 31,500 species when all inventories are completed (Berra, 2001). In September 2005, 28,900 species were already listed in FishBase. Nelson (2006) suggested a total of almost 28,000 species (freshwater and marine), which is 51% of the 54,711 then recognized living vertebrate species. The eventual number of extant fish species may be projected to be close to, conservatively, 32,500 (Nelson, 2006). At the global scale, the fresh and brackish water fish belong to 207 families, 2,513 genera and approximately 15,100 species (table 5.IV).

TABLE 5.IV.
Fresh and brackish water fish species richness by continents or large sub-continental units (from Lévêque *et al.*, 2008).

	Freshwater		Brackish water		Total	
	Families	Species	Families	Species	Families	Species
Africa	48	2,945	66	295	89	3,240
Asia	85	3,553	104	858	126	4,411
Europe	23	330	36	151	43	481
Russia	28	206	28	175	40	381
Oceania	41	260	74	317	85	577
North America	74	1,411	66	330	95	1,741
South America	74	4,035	54	196	91	4,231
Total		**12,740**		**2,322**		**15,062**

African ichthyofauna has close affinities with that of South America (Characiformes, Cyprinodontiformes) and Southeast Asia (Notopteridae, Bagridae, Clariidae, Schilbeidae, Channidae). Why do certain families of fish exhibit a vast distribution and occur on continents that have been long separated from each other? This geographical distribution can be explained both by geological events and the evolutionary history of fish.

At the end of the Triassic period, approximately 200 million years ago, all continents were joined in a "super-continent", Pangea, referred to as Gondwana in the south and Laurasia in the north (figure 5.2). In the mid-Jurassic (approximately 150-160 million years), Gondwana began to separate in two parts: an Eastern part (Madagascar, the Indies and Australia) and a Western part (Africa and South America). In the Lower Cretaceous (125 million years) South America started to separate from Africa, but this separation was not completed until the Late Cretaceous (approximately 100 million years). At the beginning of the Eocene epoch, 40 million years ago, Africa, still joined to Arabia had become an island. India was encroaching upon the Asian continent during the Eocene, pushing up the Himalayas. Finally, in the Miocene, approximately 17 million years ago, Africa and Arabia came into contact with the Asian continent at the vicinity of Turkey and Iran.



-200 million years
(Trias)

-135 million years
(Early Cretaceous)

-65 million years
(Late Cretaceous)

Today

FIGURE 5.2.
Reconstitution of the location of the continental masses from early secondary era (according to Cloud, 1978).

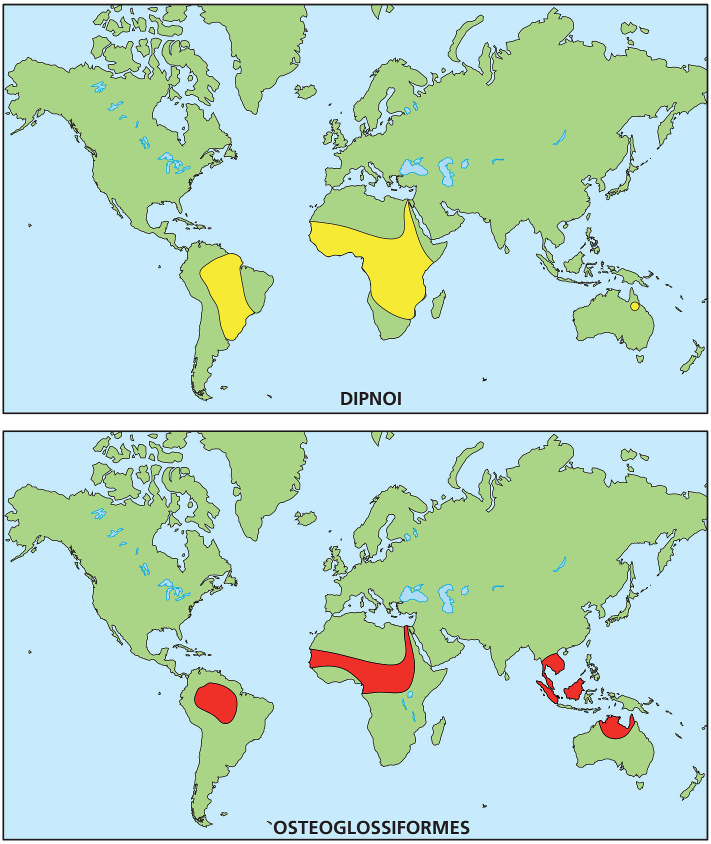
For many ichthyologists the majority of the larger groups of taxa (order and family) which make up the current African ichthyofauna were already established at the end of the Cretaceous (see chapter *African fossil fish*). Actually, South America and Africa have great taxonomic affinity even though their fauna had a different history after isolation (Maisey, 2000). The study of fossils provided evidence that part of the African ichthyofauna was already differentiated in the mid Jurassic *i.e.*, at the beginning of the fragmentation of Gondwana. Representatives of certain fish families in the formerly united continents could thus subsist and evolve independently. This is one of the explanations for the existence of families with a worldwide distribution.

Several fish lineages appear to have a Gondwanan origin *i.e.,* members of the lineage were present on Gondwana prior to fragmentation. Consequently, they have widespread distribution with living representatives and/or fossils present on different continents.

The order Osteoglossiformes is one of the best-known example of widespread distribution among freshwater fish (figure 5.3). It is now represented by one African species (*Heterotis niloticus*), three South American species (*Arapaima gigas*, *Osteoglossum bicirrhosum* and *O. ferreirai*), and by a genus (*Scleropages*) occurring in Australia (*S. jardinii* and *S. leichardti*) and in Southeast Asia (*S. formosus*). Fossils belonging to this family were also discovered in Asia and North America

Dipnoi (lungfishes) (figure 5.3) is a monophyletic group that first appeared in the Devonian and diversified in the Mesozoic (Lundberg *et al.*, 2000). It is now represented by the family Protopteridae with four living species of *Proptopterus* in Africa. The family Lepidosirenidae from South America is closely related and is represented by the genus *Lepidosiren* (one species, *L. paradoxa*). This group is also closely related to Neoceratodontidae today

FIGURE 5.3.
Global distribution of Dipnoi and Osteoglossiformes.



represented by one living Australian species (*Neoceratodus forsteri*). Several fossils of Dipnoi especially those of *Protopterus* have also been discovered in various parts of the world, particularly in South America and Africa.

The Polypteridae (bichirs and reedfishes or ropefishes) also had a large distribution. Today, however, living species occur only in Africa while fossils have been identified in South America (see box "Polypterids").

The distribution of the Cichlids in Africa, Madagascar, India, South and Central America (figure 5.4) may also be explained by a Gondwanan origin. Fossil remains of this group have also been found in Europe. The order Characiformes is generally regarded as the most primitive among Ostariophysi with four families known in Africa and 15 in South America (figure 5.5). Fossils of Characiformes have been uncovered in Europe (Serrasalmidae), but it is not known why they did not survive or spread into Asia or North America.

The Otophysi (superorder Ostariophysi) is a monophyletic group that includes very speciose families in freshwater: the Siluriformes (catfishes), Gymnotiformes (knifefishes), Cypriniformes (minnows) and Characiforms (characins) whose current distribution present some interesting contrasts (figure 5.5). They do not

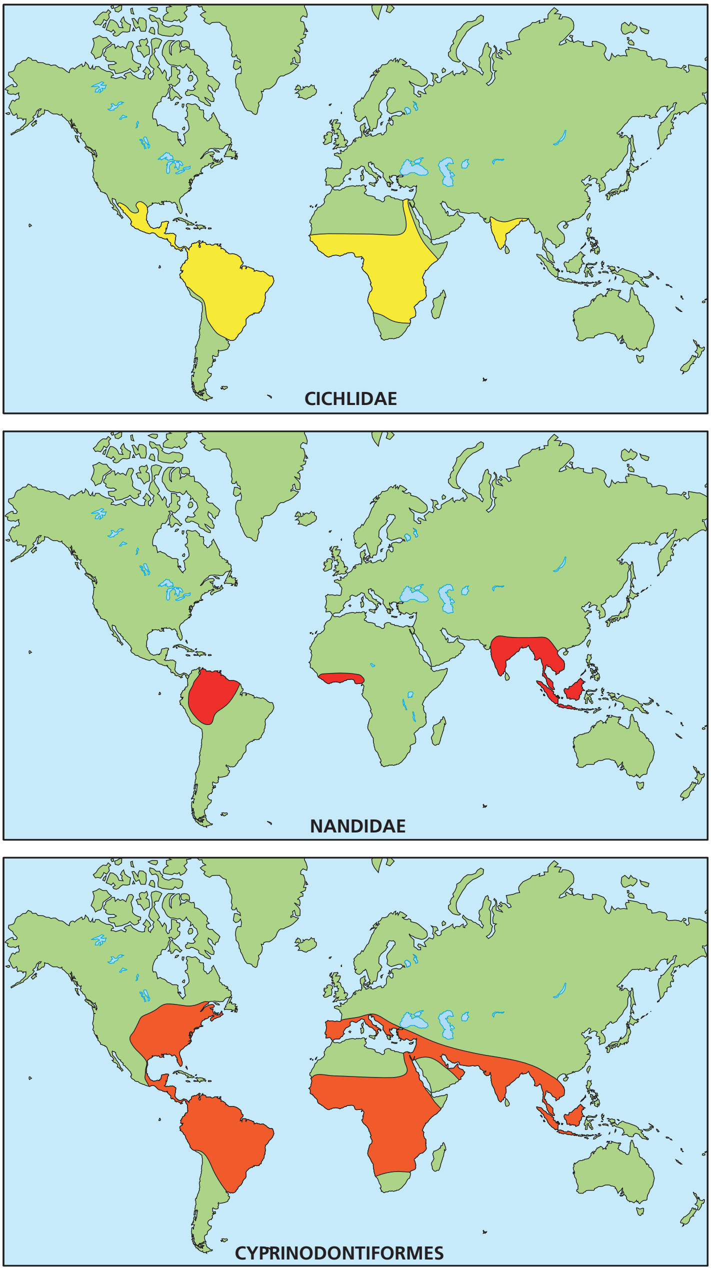


FIGURE 5.4.
Global distribution of Cichlidae, Nandidae and Cyprinodontiformes.

occur in Australia, Madagascar or the West Indies. Recent molecular studies supported the hypothesis that Cypriniformes are the sister group to the remaining three orders (Saitoh *et al.*, 2003). The divergence time of cypriniforms from the otophysan stock has been estimated at 250 Myrs ago (Kumazawa *et al.*, 1999).

POLYPTERIDS

FRANÇOIS MEUNIER

American polypterids!

Of uncertain origin (but probably close to the Palaeonisciformes), Polypterids have long been considered typically African fishes, and modern species are related to the continent's tropical regions. Moreover, the somewhat ancient Polypterid fossils were limited to scattered and unconnected remains (scales, vertebrae and finlet rays, skull fragments). Up to the late 1980s, they had only been found in different beds dating from the Tertiary and mid Cretaceous (Greenwood, 1972, 1984) that cover their current zone of geographic distribution; only a single mention, in Tunisia (Greenwood, 1974), was clearly located outside this area. The single known complete Polypterid fossil in Africa was found a short time ago in Chad, in a recent fossil bed of about 7 million years of age (Otero *et al*., 2006). Owing to the paucity of the fossil record, the origin of this group of fishes as well as their geological history thus long remained a mystery.

In fact, recent studies based on palaeohistological techniques and scanning electron microscopy on one hand, and the collection of more or less complete new fossils on the other hand, have revolutionized these traditional views. First, in 1986, scales, vertebrae, and finlet rays were described in a Niger bed in In Becetem from the Senonian, *i.e.,* some 75 million years, which places them significantly earlier (as most of the then-known fossil remains came from the end of the Tertiary). The greatest surprise came from the discovery in 1991, in several fossil beds in Bolivia (South America) dating from the late Cretaceous/early Tertiary, of scattered remains that were incontestably from Polypteridae. They consisted of scales whose structure was comparable on all points to those of modern Polypterids or African fossils, with the presence in particular of a characteristic orthogonal structure between the dentin and the bony basal plate. In addition, these scales are accompanied by finlet rays and vertebrae whose morphology and histological characteristics are typical of Polypteridae. As these beds were located outside the western zones of the Brazilian Shield, there remained an enormous gap between these sites and the African provinces. The gap was bridged in 2001 with the discovery of Polypterid scales, finlets, and vertebrae (Dutra & Malabarba, 2001), in eastern Brazil, more precisely in an Albian-Cenomanian bed (100 million years) in the state of Maranhão, east of the mouth of the Amazon.

An American or African origin?

As Polypterids are typically freshwater species and the Bolivian remains were found in continental sediments, this discovery implies that the origin of this Osteichthyes family predates the opening of the southern Atlantic ocean, when South America and Africa were still connected, *i.e.,* more than 110 million years ago (figure 5.2). Moreover, at this time, the morphology of American Polypterids was probably similar to that of modern Polypterids, as the Bolivian species also had finlets. Alas, none of the American fossils, nor most of the African ones, have connected skeletal elements, and the cranial bones are too rare or incomplete to permit reconstruction. Nonetheless, it is possible to imagine that the ancestors of the Polypteridae family may have been "American"!

Siluriformes (figure 5.5) are present on the various continents, but whereas three families (Bagridae, Clariidae and Schilbeidae) (figure 5.6) are common to Africa and Asia, there are no families in common between Africa and South America. Their origin, as that of Cypriniformes (figure 5.5) is still debatable.

Actually, the understanding of Otophysan biogeography has been a matter of debate since the beginning of the 20th century. Asia, where the group is the most speciose, was long considered to be the centre of origin of the Cypriniformes. However, current evidence argues for a hypothesis that the Cypriniformes, and probably also the Siluriformes, originated in South America and migrated to Asia in the late Jurassic (ca 150-160 Myrs ago) along the northern shore of the Thethys sea (Briggs, 2005). Diogo (2004) also supported the

That said, several relatively well-preserved fossils (Sereno *et al.*, 1996) composed of articulated skeletal elements were found in a fossil bed aged 93 million years in Morocco.
A first fossil, named *Serenoichthys kemkemensis* (Dutheil, 1999), whose head is not known, as well as a second species currently being described, with bodies that are shorter than modern Polypterids, allow reconsideration of the region of origin of these animals. Africa has the advantage once again, more so given that the Polypteridae family appears to have diversified further there compared with America, at least based on current palaeontological knowledge!

A Polypteriform fish named *Bawitius* is known from various isolated bones (maxillae, ectopterigoid and many scales) from the Kem Kem beds or Bahariya bed (Grandstaff *et al.*, 2012; Cavin *et al.*, 2015).
Some histological characteristics of scales allow a closed linking of *Bawitius* to the Polypteridae family. But it cannot be considered as a true Polypteridae because of the discontinuous ganoine layer of its scales (Meunier *et al.*, 2016).
Nevertheless this taxonomic proximity is an argument to favour an African origin of the polypterid family.

Peculiar Polypterids!

Indeed, two African fossil beds from the end of the Cretaceous, 87 million years for In Becetem in Niger (Gayet & Meunier, 1996) and 95 million years for Wadi Milk in Sudan; (Werner & Gayet, 1997), contain many disarticulated Polypterid bones, particularly scales and most especially spiny rays from finlets. Analysis of theses rays show that some are rather similar in form to existing species, while others are very different.
Some of these rays are clearly asymmetrical, which implies that they did not move in the animal's plane of symmetry.
Rather, they probably deviated from this plane, as is the case today with the 'pinecone fish', a Pacific marine species. Unfortunately, since no complete fossil (with articulated bones) has been found, it is difficult to draw the precise "portrait" of this animal, other than a hypothetical frontal view (Gayet *et al.*, 1997).
In fact these asymmetric bony rays have been misinterpreted; they probably are pectoral rays (as siluroid spiny pectoral rays) that could belong to a short non-anguilliform polypterid!
In any case, the presence of these rays with highly varied morphologies implies that at the end of the Secondary era, Polypterids showed significant diversification in Africa that is much greater than that observed today.

Parallel histories

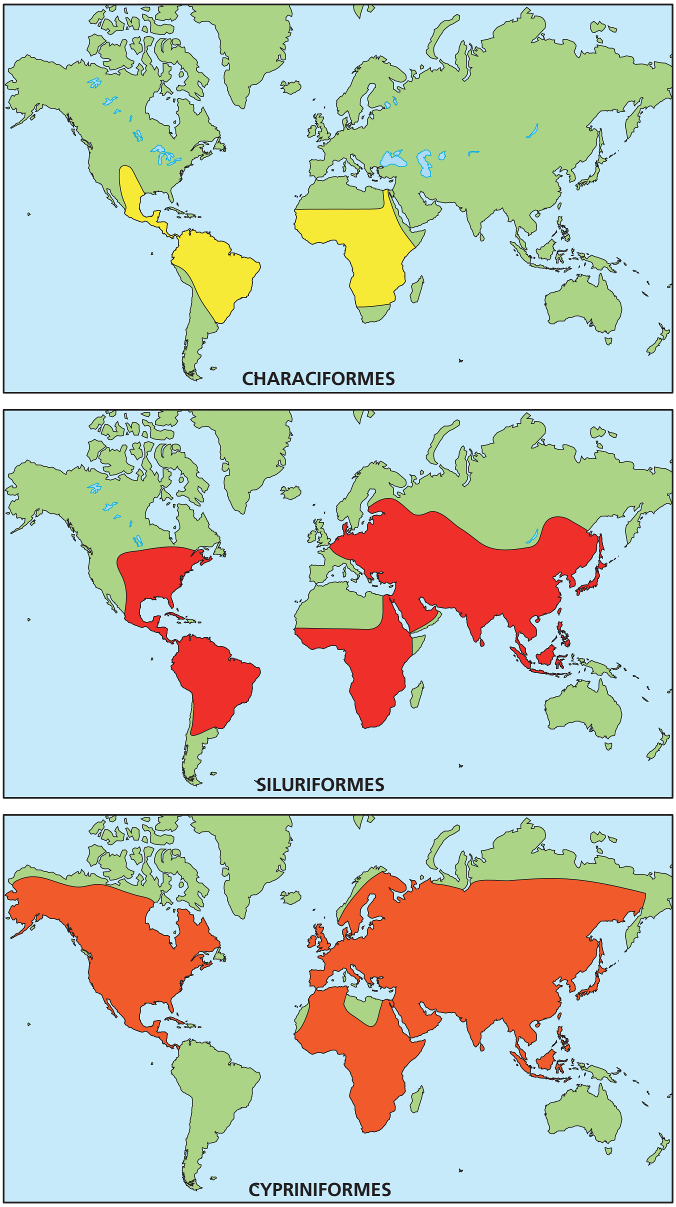
At the end of the Cretaceous, the rivers of the clearly separated South America and Africa hosted a second group of "primitive" fishes, the Lepisosteids. The latter are undoubtedly of slightly more recent origin than the Polypterids. Curiously, Lepisosteids have totally disappeared from Africa but remain present in North and Central America. Meanwhile, as we have seen earlier, Polypterids only remain in Africa and have disappeared from Latin America.
What are the biogeographic events that are behind these two histories from the start of the Tertiary (Gayet *et al.*, 2002)? The discovery of new fossils may provide answers to this question.

origin of catfishes in the South American region during the late Cretaceous period, at a time when there were still some remaining Pangean connections between Gondwana and Laurasia. Then catfishes would have dispersed to other areas with some subgroups migrating via predrift dispersion to Laurasian regions. (Sullivan *et al.*, 2006)

Continental drift explains why the ichthyological fauna of the Indian sub-continent is very similar to that of Africa and why certain groups have very strong morphological resemblances. It is observed in particular that the family of Notopteridae (figure 5.6) is represented in Africa by two species with broad distribution: *Xenomystus nigri* and *Papyrocranus afer*; the latter is close to the Asian genus *Notopterus* which is represented by four species in South Asia.

FIGURE 5.5.

Global distribution of Characiformes, Siluriformes and Cypriniformes.



Other families have a distribution limited to Africa and India. These include families belonging to the orders Siluriformes (Bagrids, Schilbeidae, Clariidae); Mastacembelidae, also referred to as spiny eels (figure 5.6); certain groups of Cyprinidae; Perciformes such as Channidae with the genus *Parachanna* in Africa and the genera *Channa*, *Micropletes* and *Ophicephalus* in Southern Asia; Anabantidae, with the African genera *Ctenopoma* and *Sandelia* and the Asian species of the family Belontiidae.

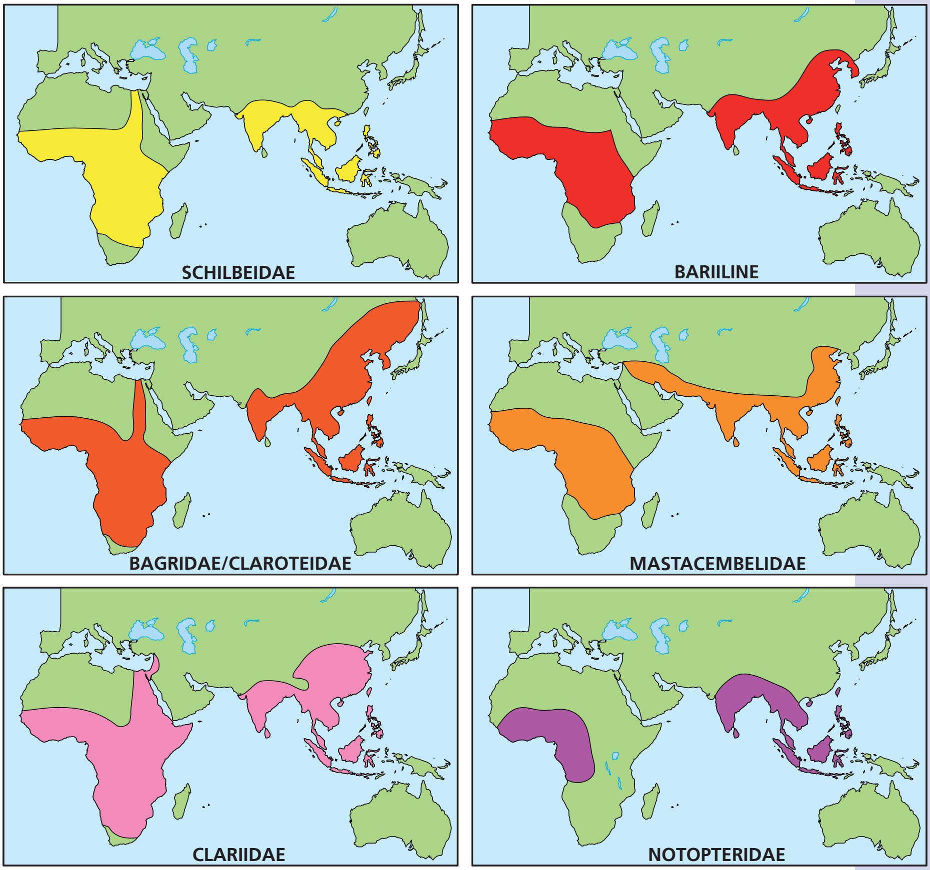


FIGURE 5.6.
Global distribution of Schilbeidae, Bariiline, Bagridae/Claroteida, Mastacembelidae, Clariidae and Notopteridae.

What can we learn from fossils?

African fish fossil remains are very few and are unequally distributed geographically (most are from the Nile valley). However, a certain number of rich and relatively ancient (Cretaceous) fossiliferous layers have enabled to a certain extent the demarcation of the ichthyological history of Africa (Egypt, Sudan, Niger, and Morocco). Western Africa and Southern Africa remain very poor in fossil remains and thus the available information for deduction of evolution and distribution of African species is reduced. Moreover, identification of fossil remains in general does not go beyond the genus level.

Fish fossils are often found during excavations targeting reptiles or mammals and are thus maintained in certain anonymity, particularly for Africa and Asia. The materials are often fragmented and incomplete and remain insufficiently studied whereas they deserve to be re-examined in the light of new palaeoichthyology techniques, which would undoubtedly make it possible to infer the palaeobiogeography of higher taxa. It should be noted that Pleistocene fossil remains are the most numerous remains collected for Africa in comparison to other continents. This is may be due to several studies that have been carried out from this period for the reconstruction of primate history (see chapter *African fossil fish*).

One of the difficulties faced by palaeo-ichthyologists has been to decipher fossilized material due to the fact that fossils are generally dislocated from the layers of their continental origin (after their death, the animals are transported, furled and, after the destruction of non-mineralised tissue, the bones are dispersed and found in detrital accumulation). Moreover, it is often difficult to attribute an isolated bone, even a fragment, to a precise species, genus, or even family. Museums therefore possess abundant, unstudied disparate material. However, in a certain number of cases, the bones are sufficiently characteristic for a more precise systematic positioning either by their morphology (jaw of lungfish, finlet of bichir), or their histology (scales of *Polypterus*).

Some important results deserve mention. In particular, the most ancient fossils (table 5.V) belonging to the genera *Protopterus* and *Polypterus* (from the beginning of the Cretaceous for the former and mid Cretaceous for the latter). Incidentally, remains of *Lates* have been found in sediments belonging to Lakes Victoria and Edward basins, where the species was no longer present until its recent reintroduction.

Remains of Osteoglossiformes, such as Mormyridae, are rare and belong to the late Miocene era. Cyprinidae of the genera *Labeo* and *Barbus* date beyond the mid Miocene. Characiformes fossils are represented by several genera within three families; one of these Characidae comprises 6 genera of which *Alestes* and *Brycinus* are the only living representatives while the others are completely extinct. *Sindacharax* and *Bunocharax* have however been excavated from the lower Miocene.

Among Perciformes, the family Latidae occupies an important place in African continental fauna. The first Latidae goes back to the beginning of the Miocene, from around the large lakes, in Libya and near the Nile delta. Cichlidae is widespread and comprises two subfamilies in Africa (Tilapinae and Haplochrominae). Their fossils are difficult to link to current forms although the first species date back to the lower Miocene from Uganda and Kenya. Another group of highly specialized osseous fish, Tetraodontidae (puffer fish) was described from the lower Pliocene from the Great Lakes region. Last but not least, a fauna of diversified freshwater fish possessing strong affinities to that of tropical northern Africa has been uncovered in deposits from the end of the Miocene from Tunisia, (Greenwood & Howes, 1975). Fossil remains of the genera *Lates*, *Clarias*, *Heterobranchus* and *Polypterus* were also identified in sediments from the beginning of the Eocene from the southern slope of the Algerian Atlas (Mahboudi *et al.*, 1984). These observations thus affirm that at a certain time tropical ichthyofauna reached the banks of the Mediterranean, whereas at present fish fauna is very poor in the Maghreb. In fact, it is possible to show the existence of a dense forest as well as mangroves along the northern coast of Africa at the beginning of the Eocene, 60 million years ago, a time at which the equator was located 10° to 15° higher than at present. Remains of Cichlidae similar to certain known species from West and Central Africa dating from the end of the Miocene (5 to 10 million years) were also discovered in Algeria (van Couvering, 1982), which shows that tropical fauna was previously present in North Africa.

TABLE 5.V

Fossil remains from African fish observed from various geological times
(summarized from results of Lévêque, 1997a; Murray, 2000 and Stewart, 2001).(Myrs: million years).

Geological era Myrs ago	**Eocene** 54-36	**Oligocene** 36-23	**Miocene** 23-6	**Pliocene** 6-1.8	**Pleistocene** 1.8-0.01	**Holocene**
Orders/Families						
Alestidae	●	●	●	●		
Bagridae					●	
Cichlidae		●	●	●	●	
Clariidae			●	●	●	
Cyprinidae					●	
Cyprinodontiformes		?				
Mochokidae			●			
Mormyridae					●	
Genera/Species						
Alestes deserti				●		
Alestes junneri					●	
Alestes sp.		?	●	●	●	●
Anguilla anguilla					●	
Arius sp.					●	
Auchenoglanis sp.			●	●	●	
Bagrus docmak				●		
Bagrus sp.			●	●	●	
Barbus altianalis					●	
Barbus bynni					●	
Barbus sp.			●	●	●	●
Bunocharax sp.				●	●	
Chrysichthys macrotis				●	?	
Chrysichthys sp.					●	●
Citharinus sp.					●	
Clarias gariepinus					●	
Clarias lazera					●	
Clarias mossambicus					●	
Clarias sp.			●	●	●	●
Clarotes laticeps				●	●	
Clarotes sp.			●	●	●	
Dasyatis africana				●	●	
Distichodus sp.			●	●	●	
Eaglesomia eaglesomei	●					
Gymnarchus niloticus				●	●	
Gymnarchus sp.			●	●	●	
Heterobranchus sp.			●	●	●	●
Heterobranchus bidorsalis				●		
Heterotis sp.			●	●	●	
Hydrocynus sp.				●	●	
Hyperopisus sp.				●	●	
Kalyptochromis hamulodentis			●			
Labeo sp.			●	●	●	
Lates karungae			●			

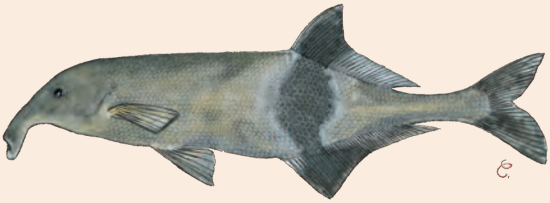
TABLE 5.V (CONT.)

Geological era Myrs ago	**Eocene** 54-36	**Oligocene** 36-23	**Miocene** 23-6	**Pliocene** 6-1.8	**Pleistocene** 1.8-0.01	**Holocene**
Genera/Species						
Lates niloticus			●	●	●	
Lates rhachirhincus			●	●	●	
Lates sp.			●	●	●	●
Lepidosiren paradoxa				●		
Macfadyena dabanensis		●				
Nderechromis cichloides			●			
Nkondobagrus longirostris				●		
Oreochromis harrisae				●		
Palaeochromis rousselleti			●			
Palaeochromis darestei			●			
Palaeodenticeps tanganyikae	●					
Palaeofulu kuluensis			●			
Parachanna sp.				●	?	
Polypterus bichir ornatus					●	
Polypterus sp.	●		●	●	●	
Protopterus aethiopicus					●	
Protopterus polli			●			
Protopterus sp.	●	●	●	●	●	●
Sarotherodon martyni			●			
Sarotherodon sp.					●	
Semlikiichthys rhachirhinchus			●	●		
Schilbe sp.			●			
Sindacharax deserti				●	?	
Sindacharax greenwoodi				●	●	
Sindacharax howesi				●		
Sindacharax lepersonnei			●	●		
Sindacharax lothagamensis			●	●		
Sindacharax mutetii				●		
Sindacharax sp.			●	●	●	
Singida jacksonoides	●					
Synodontis frontosus					●	
Synodontis schall					●	
Synodontis sp.			●	●	●	●
Tetraodon sp. nov..				●		
Tetraodon sp.				●	●	
Tilapia crassispina					●	
Tilapia fossilis					●	
Tilaîa melanopleura					●	
Tilapia nigra					●	
Tilapia sp.			●	●	●	●

Biogeography and past history of ichthyological faunas

Christian Lévêque

Didier Paugy



Ichthyological faunas established themselves and evolved as a consequence of the history of the aquatic systems they occupy. At various timescales, certain basins were colonized from other basins, and such colonizations were sometimes followed by selective extinctions resulting from geological and/or climatic events. The genesis and continued existence of aquatic habitats depend on two main factors: their morphology, which may change over the long term as a result of erosion or tectonics; and their hydrologic budget, which is dependent on precipitation, evaporation, infiltration, and for which slight changes may lead in the short or medium-term to either the drying out or expansion of the aquatic milieu in question, depending on the basin's shape. Simultaneously, some species were able to give rise to others, and these speciation events often explain the presence of centres of endemism.

Biogeography is the discipline that seeks to explain the distribution of organisms and the relationships between the areas of distribution of different species, by attempting to reconstruct the series of events that led to the present situation. To describe the relationships between the establishment of faunas and the spatio-temporal history of the physical systems, scientists need to draw up the most exhaustive inventories possible for different regions.

How do fish disperse?

Given that the large majority of fishes cannot tolerate exundation, the colonization of new habitats is made possible by the existence of connections between basins. Even if hydrographic systems are currently isolated, such connections may have existed in the past, allowing faunistic exchanges.

Connections between river basins

The great similarity between the faunas of the Nile and Chad Basins is undoubtedly the result of connections that existed between the two basins during a humid period that is difficult to date (Lévêque, 1997a). Meanwhile, a connection still exists between the Chad and Niger basins. When water levels are high, some of the waters of the Logone, a tributary of the Chari, spill westward into the Mayo-Kebi depression, cross the Gauthiot falls, and empty into the Benue, a tributary of the Niger River.

The regressive erosion that led to the capture of certain watercourses was probably the most important means of interbasin exchanges for "primary" fishes. Indeed, there are several known examples of river captures in Africa, and this phenomenon must have been rather common even if it did not always leave identifiable traces. The Boucle du Baoulé, a tributary of the Senegal in Mali, resulted from the capture of the Baoulé – formerly a tributary of the Niger – by a small tributary of the Bakoye, in turn also a tributary of the Senegal (Michel, 1973). The history of the Zambezi is particularly complex, marked by many changes in its course as well as captures that are at the origin of the present-day basin (Skelton, 1994; Thomas & Shaw, 1988).

Certain fish species were also able to colonize other basins using connections that were created via estuaries. As Sydenham (1977) notes, the Ogun River is connected to the Niger by a fine network of lagoons that stretch from Benin to the Niger delta. When several rivers empty into closed lagoons, as is the case on the West African coast, the large drop in salinity that occurs temporarily when water levels are high renders possible the circulation of species that are usually salt-intolerant.

Other means of dispersal

The distribution of a few species could also be explained by variations in seawater levels that led to changes in coastal zones. For example, Bioko island (formerly Fernando Poo), now separated from Africa by a 60-metre-deep narrow sea channel, hosts identical – though more limited – fauna as the continent facing it. Some 18,000 years ago, when the sea level was 110 m lower than today, there was apparently a connection between hydrologic systems, and the island's current fauna was isolated when the sea level rose (Thys van den Audenaerde, 1967).

It has been suggested several times that birds and mammals could transport fishes from one site to another. Although this has never been truly proved, the resistant eggs of certain Cyprinodontiformes living in temporary ponds can probably be transported by different animals (birds, mammals), in their feet, fur, or feathers. In the same way, some cases of fishes being transported during tornadoes have been reported, and these events are known as "rains of fishes".

Falls as zoogeographical barriers

Depending on their size, waterfalls can represent impassable barriers for fishes, such that isolated populations upstream remain protected from any competitors. This situation can explain the existence of endemic species in higher courses, as shown by Daget (1962b) in some watercourses in Guinea. Waterfalls allow species to move downstream, but not upstream (table 6.I). Another example is of the Gauthiot falls on Mayo-Kebi, which connects the Chad basin to the Niger basin. In this case, all the species of the Logone are present in the Benue, and there is no endemic species in the Chad basin. On the other hand, Niger species (*Cromeria nilotica*, *Arius gigas*, *Synodontis ocellifer*, *Citharidium ansorgii*, etc.) that are present in the Benue have never been observed in the Chad basin, as they are unable to pass the Gauthiot falls (Daget, 1988a). A comparable situation can also be seen with the Murchinson rapids on the Shire River connecting Lake Malawi to the Zambezi, which prevent species from the Zambezi's lower watercourses to climb back into Lake Malawi (Banister & Clarke, 1980).

TABLE 6.I

Number of fish species upstream and downstream of falls in upper reaches of the Niger River (Tinkisso) and of the Senegal River (Bafing) in the Fouta-Djalon, Guinea (from Daget, 1962b).

	Tinkisso downstream	**Tinkisso** upstream	**Bafing** downstream	**Bafing** upstream
Mormyridae	1	0	1	0
Alestidae	1	0	0	0
Distichodontidae	3	0	0	0
Cyprinidae	6	3	11	10
Bagridae + Claroteidae	1	0	0	0
Schilbeidae	1	0	0	0
Amphiliidae	0	1	2	1
Clariidae	0	0	2	0
Mochokidae	2	2	2	0
Cyprinodontiformes	2	1	3	2
Cichlidae	2	1	3	1
Eleotridae	0	0	2	2
Total	19	8	26	16

What do we learn with fossils?

African fish fossil remains are scarce and unevenly distributed geographically (with most information coming from the Nile valley.) The information that can be gleaned from investigating the evolution and distribution of species is thus limited, especially considering that the identification of fossil remains rarely goes beyond genus level.

A few major findings should nonetheless be underscored. In particular, the oldest fossils found belong to the genera *Protopterus* and *Polypterus,* both considered very ancient. Fossil remains of *Lates* were also found in sediments from the basins of lakes Victoria and Edward, from which the species had disappeared until its recent reintroduction.

African Alestidae also accounted for a few fossils, most of which were found in deposits from the end of the tertiary (Miocene, Pliocene) or the start of the Quaternary (Upper Pleistocene) (White, 1937; Greenwood, 1972; Greenwood & Howes, 1975). In France, however, in deposits from the lower Tertiary (Eocene) of the Paris and Languedoc basins, several ancient teeth related to the genus *Alestes s.lat*. (Cappetta *et al.*, 1972) were found, which suggests that a tropical fauna could have existed in that latitude and at that time period. As for the Characiformes, while there are no fossil remains, it can be estimated that in the Mesozoic, there were two sub-families, the Characinae (*Alestes junneri*) and the Sarrasalminae (*Sindacharax deserti*, *S. lepersonnei*). The latter went extinct fairly rapidly, while the Characinae continued to evolve, giving rise, among others, to the modern genera *Alestes* and *Brycinus* (Paugy, 1986) (see also chapter *African fossil fish*).

Biogeographical scenario for northern tropical Africa

At the beginning of the Miocene, approximately 20 million years ago, a rather uniform ichthyofauna occupied tropical and subtropical Africa. Some taxa with large distributions in tropical Africa are probably witnesses of this period when the interconnection between drainage basins was probably more extensive: *Schilbe mystus, Clarias gariepinus, Hydrocynus vittatus, Brycinus macrolepidotus, Hepsetus odoe, Coptodon zillii, Sarotherodon galilaeus*. The tectonic events of the Miocene period modified the hydrographic system. One of the major events was the formation of the Rift Valley some 15 million years ago, which resulted in the rise of mountain ranges and the isolation of formerly connected aquatic basins. In West Africa, also during the Miocene, tectonic movements caused the uplift of Fouta-Djalon and the Guinean ridge. Moreover, the Quaternary was a period of great climatic instability with numerous glaciations (21 cycles during the last 2.3 Myrs according to Hamilton, 1988), marked by arid periods in Africa, whereas the interglacial periods were more humid. It resulted in a succession of expansions and regressions of aquatic systems and extinction of fish populations (see box "Refuge zones theory").

The fish inventories carried out in north tropical Africa (Lévêque *et al.*, 1989, 1991; Paugy *et al.*, 1989, 1994; Teugels *et al.*, 1988, 1992) and the search for ichthyological provinces (Hugueny & Lévêque, 1994; Paugy *et al.*, 1994) enabled the identification of three ichthyological provinces (Nilo-Sudan, Upper Guinea, Lower Guinea) as well as two large groups of fish species (Lévêque, 1997a):

- species that colonize most of the Nilo-Sudan basins and which, for the most part, are absent from the Congo basin;
- species that are essentially represented in the coastal basins of Upper and Lower Guinea, and which have many similarities with the Congo fauna.

The current Nilo-Sudanian fauna has a pan-African fauna origin that existed during the Pliocene (between 2 and 5 Myrs) when the Congo and Chad basins

REFUGE ZONES THEORY

The refuge zones theory was initially developed for forest environments (Haffer, 1982), then applied to organisms such as birds or fishes. It was based on the observation that the distribution of organisms is not solely explained by current ecological conditions, but is also accounted for by climate changes during the Quaternary, characterized by alternating dry and humid periods. This resulted in a series of extensions and regressions of the forest which, during dry periods, would only be confined to limited zones where forest species could survive.

These refuge zones functioned as allopatric speciation centres from which species could recolonize new areas when conditions became favourable once more. The dispersal rate varies depending on the species and if the last regression phase is not yet too old, some of the species still remain confined to the refuge zone or its neighbouring zones.

These zones would then be characterized by a high degree of endemism.

By analogy, this theory can be applied to aquatic organisms, given that forest refuge zones were apparently sufficiently humid to allow the existence of aquatic biotopes where fishes could survive. This, of course, does not preclude the possibility that other refuge zones such as lakes may have existed for fishes during dry periods.

were not isolated. In many respects, this fauna is close to the Congolese one. In another way, at an unspecified time, exchanges took place between the Nile and the Chad basin, whose fauna is very similar. However, the Chad basin is still in contact with the Niger via the Mayo-Kebi and the Niger itself was probably a refuge zone which served as a reservoir for the recolonization of the Senegal, Gambia, Bandama, Sassandra and Comoé, Volta and Ouémé basins, after long periods of aridity during which these rivers were partially dry. Studies of genetic variability of the populations of *Oreochromis niloticus* for example have indicated that this species drew its origins from the Nile basin and then dispersed into West and East Africa (Pouyaud & Agnèse, 1995).

Species from the Upper and Lower Guinean provinces have different origins. The coastal basins of Upper Guinea were isolated from the Nilo-Sudanian basins during the Miocene with the uplift of the Guinean ridge and Fouta-Djalon, and several species are vicarious forms of Sudanian species. But another group of fishes colonized coastal rivers by northwards migration from the Congo basin, along the West African coast (figure 6.1). This colonization of the coastal basins occurred gradually and probably involved waves of migrations. The presence of species in common or that are very closely related between the Upper and Lower Guinean provinces, with affinities to Congolese fauna, support this shared origin. For example, *Ichthyborus quadrilineatus* of Upper Guinea is close to *I. monodi* of Lower Guinea and *I. ornatus* of the Congo basin. *Sarotherodon melanotheron* has a continuous distribution along the coast from the Democratic Republic of the Congo to Mauritania. Other species such as *Mormyrus tapirus*, *Marcusenius mento*, *Brienomyrus brachyistius* and *Mormyrops caballus* are present in the Upper and Lower Guinean provinces, and several other species are observed in a more or less sporadic way on the West African coast (Lévêque, 1997a).

According to palynological data (Maley, 1989), part of the provinces of Upper Guinea and Lower Guinea were forest refuge zones during the last dry periods (figure 6.2). They could also have served as refuge zones for fishes, which would explain the great wealth and endemism in these zones. Some observations also suggest that a refuge zone may have existed for fishes on the southern border of Ghana and Côte d'Ivoire.

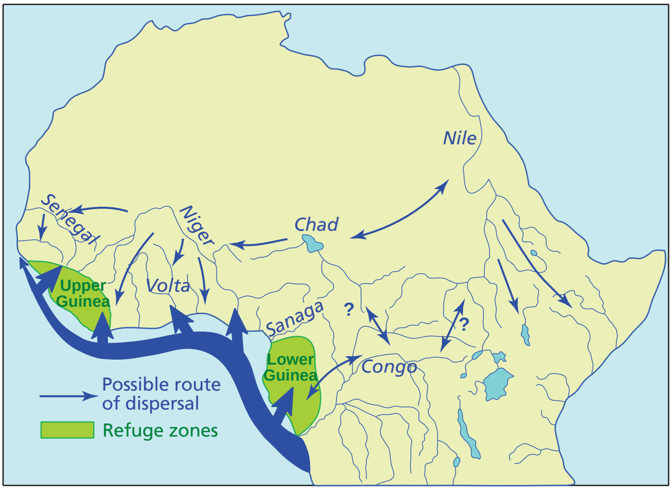


FIGURE 6.1.
Possible post-Miocene biogeographic scenario for fish assemblages of north tropical Africa (redrawn from Lévêque, 1997).

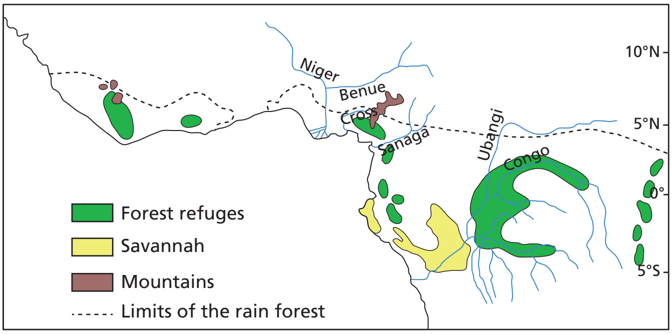


FIGURE 6.2.
Distribution of the main lowlands forest refuges in equatorial Africa during maximum of the last arid phase (about 18,000 years BP (from Maley, 1991). The modern conditions (forest boundary, included savannah) are adapted from White, 1983.

Biogeographical scenario for North Africa

At a more recent time period, the presence of ichthyological fauna with tropical affinities in the Sahara (see box "Fish of the Sahara: witnesses of a wetter past") is explained by climate fluctuations during the recent Quaternary (table 6.II). Once again, the presence of such fauna is accounted for by the existence of physical connections with basins in the south.

TABLE 6.II

Occurrence of fish species in different regions of the Sahara (from Lévêque, 1990).
1: Adrar (Mauritania); 2: Tunisia and South Algeria; 3: Hoggar; 4: Tassili N'Ajjer; 5: Ghat; 6: Tibesti; 7: Ennedi; 8: Borkou.

Regions Species	Adrar Mauritania	Tunisia and South Algeria	Ahaggar Algeria	Tassili Algeria	Ghat Libya	Tibesti Chad	Ennedi Chad	Borkou Chad
Polypteridae								
Polypterus senegalus								●
Cyprinidae								
Barbus apleurogramma							●	
Barbus occidentalis						●		
Barbus callensis			●	●	●			
Barbus macrops	●		●			●	●	
Barbus pobeguini	●							
Labeo niloticus						●		
Labeo parvus						●	●	
Raiamas senegalensis						●		
Clariidae								
Clarias anguillaris	●			●				
Clarias gariepinus				●		●	●	
Nothobranchiidae								
Epiplatys spilargyreius								●
Poeciliidae								
Poropanchax normani								●
Cichlidae								
Hemichromis bimaculatus		●		●			●	●
Sarotherodon g. galilaeus	●							
Sarotherodon g. borkuanus						●	●	●
Coptodon zillii		●	●	●		●	●	

The Maghreb province, found between the African and European tectonic plates, plays host to families with a tropical distribution (Cichlidae, Clariidae), and others of holarctic origin (Salmonidae, Cobitidae). For Doadrio (1994), three biogeographic zones can be distinguished in Africa (figure 6.3):

- the Atlantic zone in the north-west, characterized by the presence of Cyprinidae such as *Labeobarbus* and *Varicorhinus*, and Cobitidae;
- the Mediterranean zone characterized by the Cyprinidae *Pseudophoxinus* and *Barbus s.s.* as defined by Howes (1987), which are absent from the rest of Africa;
- the tropical zone in the east, including the artesian wells of the Sahara (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*), where one finds Cichlidae (*Haplochromis, Hemichromis*, tilapias) and Clariidae (*Clarias*).

According to Doadrio (1994), the North African region could have had connections with Asian faunas and the Iberian peninsula during the Cenozoic. The fish fauna is different from that of Europe, and the presence of African taxa that are similar to Asian forms such as *Pseudophoxinus* and *Barbus s.s.* (*Barbus callensis* for example) could suggest an Asian connection during the Oligocene and (or) lower Miocene. Connections with the Iberian peninsula could be more recent and date back to the upper Miocene, when the Mediterranean dried up. Moreover, some species of the Iberian peninsula and Greece are closer, from a phylogenetic standpoint, to north African (*Barbus callensis*) and Asian species than to European *Barbus* species (Doadrio, 1990).

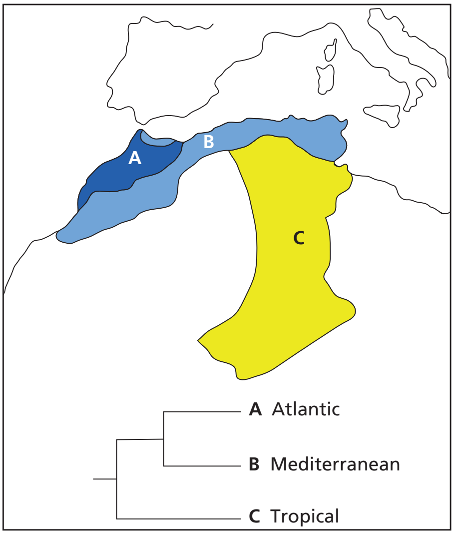


FIGURE 6.3.
Biogeographical zones in North Africa (redrawn from Doadrio, 1994).

The existence in North Africa of four endemic species from the genus *Labeobarbus*, similar to the large *Barbus* of West Africa, seems to argue in favour of an ancient origin with African roots for this genus.

FISH OF THE SAHARA: WITNESSES OF A WETTER PAST

Several tropical fish species have been collected in the ponds of central Sahara (Lévêque, 1990). The most varied fauna is found in the region of Borkou-Ennedi-Tibesti, similar to that found in the Nile and Chad basins (*Barbus bynni occidentalis*, *Barbus macrops*, *Labeo niloticus*, *Labeo parvus*, *Raiamas senegalensis*, *Clarias gariepinus*, *Hemichromis bimaculatus*, *Sarotherodon galilaeus*, *Coptodon zillii*).
It has now been shown that during the first wet period of the Holocene, the Chad basin extended to the foot of the Ennedi-Tibesti, whose then-functional hydrographic systems emptied into the Chad (Talbot, 1980).
The region's fauna is thus a remnant of the Chad basin's ichthyofauna which persisted in precarious conditions after the deterioration of the climatic situation. Populations were probably isolated around 5,000 to 6,000 years ago, which was not enough for them to become differentiated.
The much poorer fauna of the Hoggar is thought to be the relict of the Niger fauna, given that this part of the Sahara was well-irrigated during the Holocene by a dense network of rivers that have now dried out.
At the start of the Holocene there were even large tropical lakes in central Sahara (Riser & Petit Maire, 1986) and numerous fish fossil remains have been found (Daget, 1959b, 1961; Gayet, 1983).
It appears that the poverty of modern ichthyological fauna is the result of a lack of sufficient aquatic habitats that could serve to a certain degree as refuge zones.
The presence of *Barbus apleurogramma* in the Ennedi is surprising, as this species is only known today in Lake Victoria and its tributaries. It is possible that it may be the relict of a more ancient fauna, some of whose representatives could have then disappeared from Nilo-Sudanian rivers.

Biogeographical scenario for Central Africa

The Congo basin, which covers approximately 4 million km², appears to have existed long before the Pleistocene. During the Mesozoic, it was invaded by marine water which left behind sediments and fossils. From the end of the Miocene to the beginning of the Pliocene, the Congo basin became endorheic and a large lake occupied the central basin. Then, before the beginning of the Pleistocene, the basin was captured (most probably in the area around Kinshasa or Brazzaville) by a coastal river flowing into the Atlantic and became the lower Congo. The marshy zones of the western half of the basin where lakes Tumba and Mai-Ndombe are located are possibly the remains of this large lake (Beadle, 1981).

At different periods, there were connections between the Congo basin and adjacent basins. As such, a tributary of the Nyong could have been captured by the Dja, a tributary of the Sangha River (Congo basin). There could also have been temporary and difficult-to-date connections with other coastal rivers of the ‘Lower Guinea’ province such as the Ogowe River, as well as with Angolan rivers (Cuanza, Cunene) by the Kasaï River. Likewise, the Ivindo, the main tributary of the left bank of the Ogowe River, appears to have had been in contact with the Ntem River before being captured by the Ogowe River.

Interactions within the Chad basin may have taken place during very wet periods. Species such as *Coptodon zillii* and *Sarotherodon galilaeus* (Thys van den Audenaerde, 1963) or *Clarias albopunctatus* (Teugels, 1986) may have colonized the upper sections of the Chad basin via tributaries of the Ubangi River.

Biogeographical scenario for South Africa

The tropical freshwater dispersant fishes of East and Southern Africa comprise a similar assemblage of relatively low diversity. The fauna is dominated by barbin cyprinids with aplocheiloid killifishes and tilapine cichlids being notable elements of the East Coast and eastern Zambezian Rivers. A radiation of serranochromine cichlids highlights the Zambezian fauna. In the East Coast Province, centres of elevated biodiversity include the Ruaha basin and the north-Tanzanian coastal catchments.

Skelton (1994) provided a biogeographical scenario for South Africa based on a reconstructed history of hydrographic development (figure 6.4) and on the basis of the current distribution of species. The model proposes that the fauna developed in two main arenas (eastern and western) and that drainage development within these arenas resulted in modern day faunal composition.

At the beginning of the Tertiary period (stage a), three large hydrographical systems existed. The Western basin corresponded to the upper course of the

FIGURE 6.4.

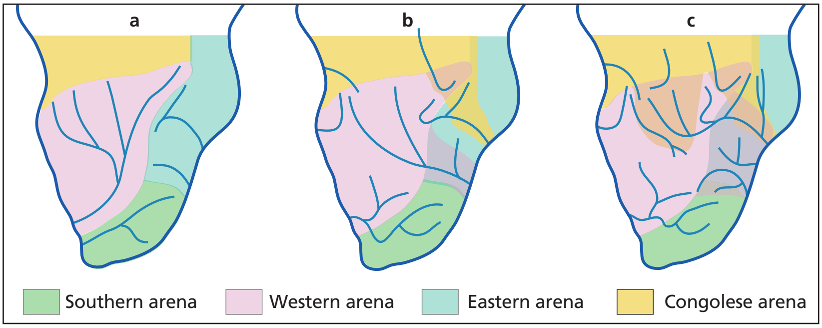
Biogeographic model for Zambezian freshwater dispersant fishes.

(a) Early Tertiary; (b) Mid-Tertiary; (c) Late Tertiary (redrawn from Skelton, 1994).

(a): in the early Tertiary the freshwater fish faunas of southern Africa became established in four evolutionary arenas;

(b): by the mid-Tertiary there were infusions of western and Congolese fauna into the eastern arena, and marginal infusions of Congolese and southern fauna into western arena;

(c): by the late Tertiary there was a second infusion of western fauna into the eastern arena and further infusion of Congolese fauna into the western arena. Minor faunal infusions occur along contact zones of the faunal arenas e.g. western/eastern elements into the southern arena (redrawn from Skelton, 1994).



Zambezi, Cunene, Kafue, and the Okavango basin, which were the tributaries of a river that at the time flowed southwards and discharged on the Western coast of Africa. Its mouth corresponded to the current mouth of the Orange River. The southern basin corresponded to the current upper course of the Orange River. The Eastern basin, which included the mid- and lower Zambezi, Limpopo and Shire River, was then in communication with the Congo basin until the formation of the Rift Valley lakes. Fauna of the Western, Southern and Eastern basins thereafter evolved independently for several million years and then differentiated.

During the mid-Tertiary Period (stage b) the Western basin was divided due to river captures and tectonic movements, and its course was diverted towards the east coast of the upstream reservoir whose fauna attests to its past connection with what is the current Limpopo basin. In the south, the hydrographical system of the Orange River was reconstructed by a merger with southern sections of the lower course of the precedent western basin, causing a mixture of fauna. Connections were also established between the Congo basin and the northern part of the eastern basin.

At the end of the Tertiary period (stage c), intrusions of species of the Congo basin were accentuated, even in the western sector. The capture of the upper Zambezi by the middle course of the Zambezi during the Plio-Pleistocene caused an extension of the western fish fauna towards the east, and an isolation of the Okavango basin which is currently endorheic. The Limpopo and Save basins separated in the eastern sector and their fish fauna is currently a mixture of Western and Eastern elements.

Madagascar

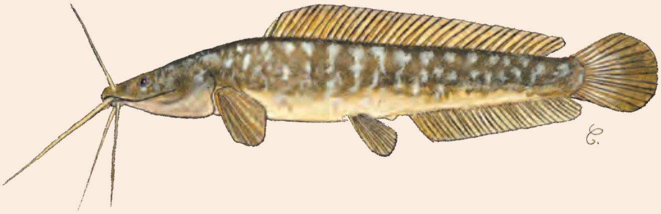
Madagascar's freshwater fish fauna contrasts with that of continental Africa (Sparks & Stiassny, 2003). Of a total of 135 native fish species, 84 are endemic to the island itself. Many new species have been described during the last decade and many more are awaiting identification.

The origin of the freshwater fish fauna remains unclear. The fish fauna is deprived of Cypriniformes, several Siluriformes as well as important Afro-Asian families such Notopteridae, Anabantidae, and Channidae. Ancient groups such as *Polypterus*, *Protopterus* and Arapaimidae are also missing (De Rahm, 1996). Most of the species belong to widely distributed peripheral families. Many of the major groups of freshwater fish present in Africa, as well as those present in Africa and Asia (anabantids, bagrids, clariids, mastacembelids, notopterids, etc.), are absent in Madagascar (Stiassny & Raminosoa, 1994). Noteworthy is the absence of primary freshwater families such as the cyprinids, characins and mormyrids. Only three secondary freshwater families (Aplocheilidae, Cichlidae and Poeciliidae) have been recorded from the island. Many Malagasy species are phylogenetically basal within their respective families, and the ichthyofauna is apparently of relict nature.

The inclusion of Madagascar in the African region is hence mainly a function of geographical propinquity, as its ichthyofauna has more in common with those of Australasia and India than with those of mainland Africa.

Thus, the family Aplocheilidae and the cichlid subfamily Etroplinae are common to Madagascar and India (Murphy & Collier, 1997; Stiassny *et al.*, 2001; Sparks, 2008). The remaining Malagasy cichlids have no obvious sister-group relationship to the family's currently recognized lineages and are regarded as the plesiomorphic sister-group of all other cichlids (Stiassny & Sparks, 2006). The sister taxa of the endemic atheriniform family Bedotiidae are the Australasian families Melanotaeniidae and Pseudomugilidae (Stiassny, 1990; Sparks & Smith, 2004). It cannot be decided on the basis of available evidence whether the closest relatives of the endemic siluriform family Anchariidae are to be found on the mainland of Africa or in India (Mo, 1991; Ng & Sparks, 2005). Madagascar's nominal *Pantanodon* species are the only freshwater fishes whose nearest relatives are of African provenance. In light of these data and given the generally recognized basal nature of Madagascar's endemic freshwater fishes, the island is clearly host to a relict Gondwanan ichthyofauna. Most of the island's freshwater fishes are diadromous or peripheral taxa, many of them widely distributed throughout the Indian Ocean region. The most mysterious aspect of the Malagasy ichthyofauna is the absence of lungfish and osteoglossoids. It is clear from the fossil record that both lineages were present on the Indo-Malagasy island prior to its scission in the late Cretaceous and it is difficult to envisage a scenario that would account for their selective extinction and the survival of the teleost lineages currently present on Madagascar. The absence of the lineages that dominate the ichthyofaunas of mainland Africa from Madagascar is most parsimoniously explained by their relatively recent invasion of Africa [Cyprinidae; Mastacembelidae; Anabantidae] or their absence from the region of Gondwana that ultimately gave rise to India, Madagascar and Australasia.

Diversity of African fish: heritage of evolution



Christian Lévêque

Didier Paugy

Jean-François Agnèse

The present African ichthyological fauna took shape over time. It is a biological heritage, the product of a long history of evolution, marked by periods during which life diversified, but also punctuated by dramatic events and major "disasters" that led to the extinction of many species.

Knowledge on the speciation processes for African fishes have seen much progress in recent years, thanks mainly to advances in molecular biology as well as international attention focussing on the East African Great Lakes, where hundreds of endemic Cichlidae species are threatened by extinction even as they represent a unique model for the study of speciation.

Review of theories of evolution

From creationism to transformism

In the early 17th century, scientists viewed organisms as fixed. In accordance with the sacred Judeo-Christian texts, it was believed that the earth had been populated some 6,000 years earlier, and that the living creatures of that time were faithful copies of the ones created by God. This led to the emergence of so-called creationist theories.

Subsequent advances in knowledge rapidly showed that the age of the planet had been vastly underestimated and that flora and fauna had changed considerably over time. Briefly speaking, in the early 19th century, Lamarck questioned the "fixed species" dogma and proposed a new concept, transformism, which upended the prevailing ideas. Lamarck hypothesized that all of an individual's characters could be transmitted to its offspring, including those it had acquired over its lifetime. This hypothesis, based on the postulate that acquired characters could be passed on, was widely discussed and – rightly – called into question. Half a century later, Darwin proposed another transformist theory that recognized the existence of intraspecific variability, as opposed to the 'typological' concept of the species, that made natural selection the driver of evolution. In other words, in a population living in a given set of environmental conditions, only the fittest individuals for that environment would participate effectively in reproduction.

The existence of mutations was discovered in the early 20th century, and a new theory (mutationism) developed, according to which mutations were the sole driver of evolution. Although it was abandoned quickly, the inclusion of mutations nonetheless remained a major event in the history of evolutionary theories.

The synthetic theory of evolution

The synthetic theory of evolution takes into account the two notions that mutations led to variability, and that natural selection, with every generation, selected the genotypes that were most suited to living and reproducing in a given set of conditions. In a way, the theory is a summary of the Darwinian and mutationist approaches. In an environment that perpetually changes, organisms are forced to adapt by finding physiological or morphological solutions to the problems posed by changes in the physical system they inhabit or risk extinction. Changes in certain factors of the environment such as temperature or salinity may be behind such adaptations. But these innovations may also come about from the appearance of new habitats or new ecological niches that organisms can colonize, and in which they will evolve and diversify to maximize the use of available food resources.

Mechanisms of speciation

Contrary to the beliefs of some creationists, species do not appear spontaneously. Speciation is the phenomenon by which a species gives rise to two or more distinct species, called sister species. This process is also known as cladogenesis. Not only does speciation lead to new species; it also gives rise to new groups, and the history of evolution and the appearance of different phyla is the result of this speciation.

The mechanism behind speciation implies two essential and distinct steps:

- on one hand, the appearance and spread of a mutation within a population;
- on the other hand, genetic isolation of that population from the other populations as a result of this mutation.

The genetic mutations or chromosomal recombinations that frequently occur lead to a genetic diversity that could allow species to adapt to changes in the environment. Many of these mutations are lethal or unfavourable for the individual, and are eliminated by natural selection. Others are neutral and will be maintained or eliminated at random. Only a small fraction will be advantageous. Among these, a few will lead to the emergence of a new species.

Mutations as the driver of evolution

Life begins at the molecular level, and the origins of the diversity of organisms and the adaptive potential of species should be sought at this level of infraspecific variability. Each individual belonging to a species or sub-species is slightly different genetically from all other individuals, and this genetic diversity is the necessary condition for the biological diversity that allows species to carry out alternative strategies that are their adaptive response to changes in the environment. Intraspecific variability is not restricted to the genetic component, but is expressed as a range of different phenotypes.

Mutations at the molecular level

A mutation occurs at the genetic level. It is a change in the structure of the DNA molecules forming the genes which are the main building blocks of heredity. In most organisms, genetic information is found in chromosomes which are a long chain of deoxyribonucleic acid (DNA) carrying hereditary characteristics and biological information needed for cell, organ, and tissue function. The different variants of genes are known as alleles. An individual's full set of genes is its genotype, which serves, in a way, as the initial capital that can be used by the individual in different ways depending on the conditions in the physical system it inhabits.

Cell division or mitosis allows the creation of two daughter cells that are similar to the mother cell. In principle, the copies of chromosomes and genes are identical, but "errors" may occur in the order of the nucleic acid sequence during DNA duplication. These spontaneous genetic mutations create new gene variants or alleles. Genetic diversity within a species is a function of these alleles.

If a gene controls the production of a certain molecule, it may produce a different one after a mutation. These genetic mutations can be lethal, in which case there are no consequences. On the other hand, if the individual is viable and fertile, the mutations are transmitted to the descendants of that individual, and can manifest as evolutionary transformations, such as a change in morphology. They may also be undetectable at this level, and/or affect physiological, biochemical, or behavioural processes.

Given the high number of genes, mutations are not rare, but many of these mutants are not viable, nor are they visible in the phenotype (in which case the mutations are called neutral). Only after a veritable obstacle course that eliminates many of the mutants will the survivors have a chance to create a population that is large enough to become established and sustainable. For species that reproduce sexually, that is, 95% of organisms, a mixing of the population's genes occurs during reproduction, and new genotypes appear while others go away.

Up to about ten years ago, electrophoresis was the technique most commonly used to reveal the polymorphism of proteins and thus a gene's allelic differences in order to assess genetic diversity. Nowadays it is possible to analyse a gene's structure, and DNA polymorphism can be revealed using increasingly powerful molecular biology techniques. Like the human genome, several fish genomes have been or are currently being sequenced (fugu, *Danio*, carp).

Chromosomal recombinations

Mutations can also occur during mitosis via changes in chromosome structure. Each species has a fixed number of chromosomes, but all or part of a chromosome may break or, on the contrary, fuse, thus changing the chromosome set (or karyotype). This can range from simple inversions of some arms to a reduction in the number of chromosomes (figure 7.1).

In fishes, this evolution in the number and shape of chromosomes is particularly spectacular in the Cyprinodontiformes, for which it has been shown that

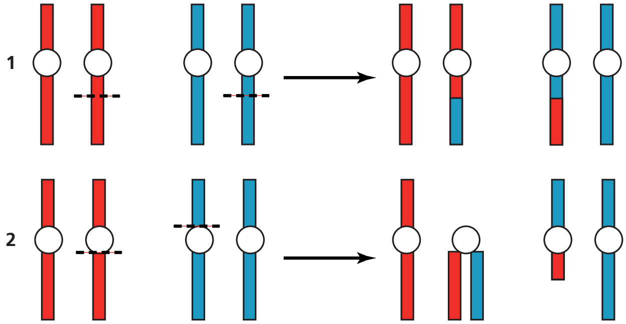


FIGURE 7.1.
Evolution of chromosome form through changes in chromosome structure.
1: translocation;
2: centric fusion.

there are numerous species that are morphologically similar but have different karyotypes, preventing them from creating hybrids (see the work of Scheel, 1968). In the *Aphyosemion*, the haploid number varies from n = 24 (the basic number, according to Scheel) in *A. rectoogoense* to n = 9 in *A. christyi*. There is an especially interesting example of speciation with a reduction in chromosome number from 15 to 13, 11, 10 and 9 pairs respectively, in the series *Aphyosemion melanopteron-cognatum-schoutedeni-elegans-christyi*. The phenotypes of these species are very similar and they cannot be identified using metric or meristic characters alone. They are only distinguishable based on the colouring of adult males. These differences were initially attributed to intraspecific polymorphism until the investigation of their karyotypes and hybridation experiments showed that they were distinct species in terms of reproduction.

Polyploidy that manifests as a significant increase in the number of chromosomes is not rare in fishes compared with other vertebrates. This phenomenon appears to have played a major role in particular in the evolution of the karyotypes of the Cyprinidae family. It was also shown recently that some of the large African *Barbus* species were hexaploid and possessed 148-150 chromosomes (see chapter *Taxonomy and systematics*, table 8.I). Polyploidization can also be induced experimentally in certain fish species (Don & Avatlion, 1988a and 1988b).

Speciation and environmental variability: natural selection

A population is a collection of individuals that can interbreed and have shared genetic properties. A species can be composed of a single population, or of several populations that are more or less geographically isolated (in which case the term "metapopulation" is used).

The principle of natural selection involves two complementary processes: the existence of hereditary genetic variability, and a phenomenon that selects for the most successful individuals in terms of reproduction in a given type of environment. In theory, each species is adapted to a type of environment, but all the individuals in a population are not strictly identical on a genetic and phenotypic level. Owing to genetic polymorphism, the individuals of a population can respond in different ways to the constraints imposed by the environment.

When conditions change, the genotypes that produce the phenotypes most suited to the new constraints have an adaptive advantage and are selected in subsequent generations. Generally speaking, natural selection rewards the characters that provide an advantage to the organisms in question.

While genetic mutations favour the appearance of new phenotypes on an individual level, natural selection is what allows the mutant genes controlling these innovations to spread in the population provided that these mutants are fitter for survival and reproduction. Should this not be the case, the mutation has little chance of spreading and may even totally disappear if the environmental conditions do not change.

Thus, natural selection is a process that concerns each individual of a population. It implies:

- the presence of variability between the individuals in this population, in terms of performance or phenotypic characteristics (colour, growth rate, resistance to anoxia, swimming speed);
- that these characters can be transmitted hereditarily;
- that they have a significant influence on the reproduction or survival rate.

Selection essentially affects gene frequency. Any gene controlling adaptations that reinforce the chances of reproductive success will be favoured, and its frequency can then increase over generations.

Current ecosystems have undergone numerous changes in the past, under the influence of climate change and geological history (see chapter *Variability of climate and hydrological systems*). Thanks to genetic diversity, species were able to use new strategies as their adaptive response to changes in the environment. In some cases, particularly when the populations of the same species were isolated geographically, the desire to adjust to the environment's characteristics led to the appearance of new species. Speciation can thus be considered a fortunate result of a population's adaptation to its environment.

Mechanisms of speciation: how do species appear?

As all species evolved from a common ancestor, ancient species gave rise numerous times to two or more daughter species. What circumstances surround the process of subdivision that we call speciation? Two theories have been the subject of fierce debate: the allopatric theory (speciation in "another place"), which states that geographic isolation is needed for speciation to occur; and the sympatric theory (speciation in "the same place") which states that isolation is not necessary (figure 7.2).

Allopatric speciation

In this traditional model, populations of the same ancestral species with a continuous distribution become geographically isolated from the rest of the species. In the absence of genetic exchanges between these populations, they evolve independently and give rise to new species that cannot interbreed. It follows geological or climatic events that favoured the fragmentation and isolation of populations of the same species. It's obviously the most common situation. The majority of hydrographic basins are currently isolated from each other, and act as virtual islands wherein populations of the same species can evolve independently of each other. If the isolation lasts long enough, populations can diverge until they become different species.

A limited case of allopatric speciation is that of peripatric speciation. In simple terms, this is speciation that occurs in small populations that are isolated on the edge of a species' area of distribution. One example of peripatric speciation is that of species closely related to *Brycinus imberi*. Three endemic species are known in limited zones on the edge of the distribution zone for *B. imberi*: *B. abeli* (Ubangi), *B. carolinae* (upper Niger), *B. nigricauda* (Cess, Côte d'Ivoire) (see chapter *Taxonomy and systematics*). These three species are very similar to *B. imberi* in terms of morphology, and are differentiated mainly by colour (Paugy, 1986).

Parapatric speciation refers to speciation that takes place in an environment where genetic exchange can occur but is highly limited as a result of, for instance, the presence of a geographic cline or environmental segregation. A well-known example is that of *Sarotherodon melanotheron* which is distributed all along the West African coast, and for which there are three sub-species that are relatively well-demarcated geographically but which can be in contact on the edges of their distribution areas (see box "Genetic differentiation of *Sarotherodon melanotheron* populations").

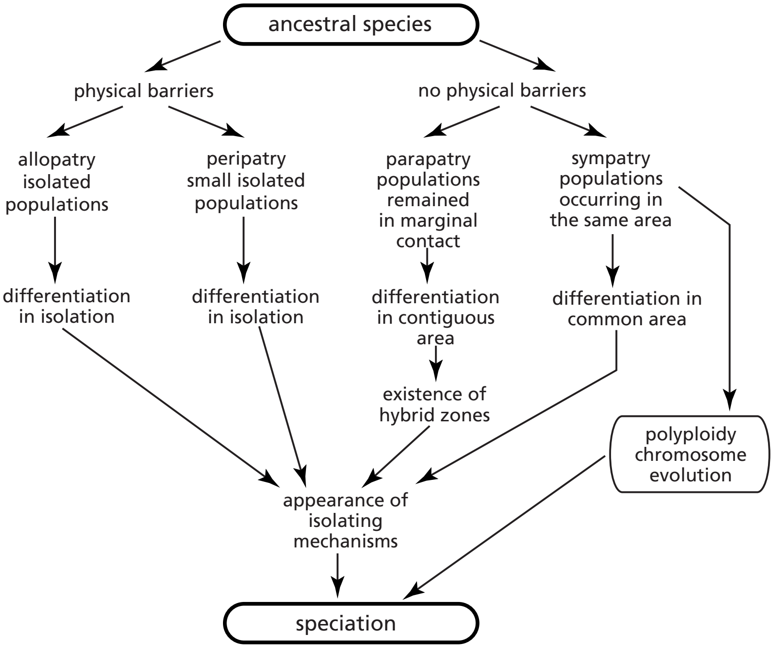


FIGURE 7.2.
Main pathways of speciation for African fishes (modified from Endler, 1977).

GENETIC DIFFERENTIATION OF *SAROTHERODON MELANOTHERON* POPULATIONS

Sarotherodon melanotheron is a tilapia that lives in the brackish waters of lagoons and estuaries on the coastal zone stretching from Senegal to the Congo.
While this species is always classified in the genus *Sarotherodon,* its genetic characters place it closer to the genus *Oreochromis.*
It may even form a distinct genus, as it displays rather marked differences compared with other *Tilapia s. l.* species (Pouyaud & Agnèse, 1995).
Moreover, it should be noted that it is the only known paternal incubator in the group.

The study of the enzymatic polymorphism of different *S. melanotheron* populations of the West African coast (Pouyaud & Agnèse, 1995), has also confirmed the existence of genetic differences between three sub-species described by Trewavas (1983) based on morphological characters:

- *S. m. heudeloti* from Senegal to Guinea;
- *S. m. melanotheron* from Côte d'Ivoire to Cameroon;
- *S. m. nigripinis* from Rio Muni to DRC.

These observations have been confirmed by mitochondrial DNA studies (Falk *et al*., 2003).

The presence from Sierra Leone to Liberia of another sub-species, *S. m. leonensis*, is also mentioned by Trewavas.

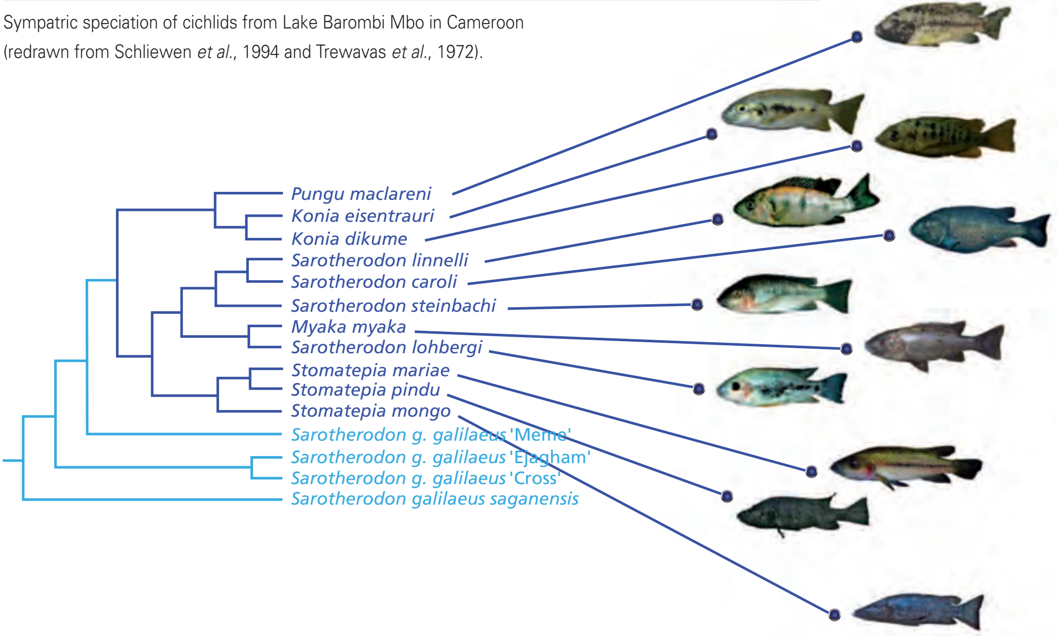
Sympatric speciation

Sympatric speciation occurs in a population that occupies the same geographic area and in which genetic exchange is theoretically possible. This type of speciation was very controversial and even rejected by some scientists. Based on the principle that the concept of biological species implies that each species is composed of populations that can interbreed, it was deemed that the flow and constant circulation of genes within a population was an obstacle to the emergence of new species. According to Mayr (1989), the sympatric theory leads to the following paradox: the coexistence of two forms is impossible without reproductive isolation. However, this isolation cannot occur unless the two forms coexist in a stable fashion. Nonetheless, a number of facts tend to show that isolation mechanisms can occur in sympatric conditions as an effect of natural selection, and the principle of sympatric speciation progressively gained ground (Gibbons, 1996). The processes involved can be described as follows: first, within a species' continuous area of distribution, natural selection promotes the appearance of two forms that may have different ethological behaviours (dietary preferences, habitat preferences, non-simultaneous reproductive seasons, etc.). If selection pressure is high enough, and if the process continues long enough, the two forms may end up diverging into two distinct species.

An example of sympatric speciation was proposed by Schliewen *et al.* (1994) for the Cichlidae of the crater lakes (Lakes Barombi Mbo and Bermin) in Cameroon (figure 7.3). Using mitochondrial DNA analysis, they showed that the nine species of Lake Bermin and the eleven found in Lake Barombi Mbo are monophyletic sets that each evolved in the lake itself from a single colonizing species. Given the size and shape of each lake, it is unlikely that geographic micro-barriers encouraged micro-allopatric speciation. The authors suggest, rather, that the

FIGURE 7.3.

Sympatric speciation of cichlids from Lake Barombi Mbo in Cameroon (redrawn from Schliewen *et al.*, 1994 and Trewavas *et al.*, 1972).



diversification of trophic behaviour (and the ecological behaviour resulting from it) was the main factor in the sympatric speciation for each of these lakes.

The *Labeobarbus* of Lake Tana (Ethiopia) also show remarkable morphologic diversity. They were initially described as species, then as morphotypes of the same species (Banister, 1973). Following a detailed investigation, Nagelkerk & Sibbing (2000) distinguished 16 morphotypes, of which 15 are endemic, and pointed out differences in the dietary habits of the morphotypes. It appears that the species differentiated because of their dietary niche and their preferences in terms of habitat (Nagelkerke *et al.*, 1994). They added that it was probably a sympatric speciation event and that the ancestral *Labeobarbus intermedius* species could have been at the origin of the flock present in Lake Tana. However, Mina *et al.* (1996) showed that morphologic diversification only took place at a late growth stage. Hence, while they support the hypothesis of sympatric speciation, they believe that it is an ongoing process rather than a completed one.

Given the aforementioned observations, it is quite possible that the process known as adaptive radiation, that is, the colonization of several niches of the same ecological system by populations or species descended from a common ancestor, is an illustration of sympatric speciation. This phenomenon does indeed encourage speciation, as colonizers develop morphological and behavioural adaptations that are specific to their new way of life.

A well-known example of adaptive radiation in fish can be seen in the Cichlidae of the East African Great Lakes. It appears that the Cichlidae of Lake Victoria are descended from a single species of fluvial origin that colonized the lake and spawned some 300 living species that occupy all the major ecological niches

SPECIES FLOCKS

"**S**pecies flock" (loosely translated in French as "essaim d'espèces" or "foule d'espèce") is the term used to designate groups of very closely-related species sharing a common ancestor (monophyletic) and endemic to the same physical system (Greenwood, 1984).
These species flocks contain an unusually high number of neighbouring species which are the product of especially rapid speciation (sometimes referred to as explosive speciation). This could correspond to the evolutionary response of a fauna that, after colonizing a new physical system, differentiates by specializing in the use of the various resources offered by this system.

While numerous Cichlidae genera of the East African Great Lakes meet the definition for a species flock, this phenomenon is also observed in other groups, such as the catfish of the genus *Bathyclarias* (10 species) of Lake Malawi, the *Chrysichthys* (6 species), *Mastacembelus* (8 species), *Lates* (4 species) of Lake Tanganyika, the *Labeobarbus* of Lake Tana (16 species), and the *Brienomyrus* of Gabon (only 6 species described among 38 Operational Taxonomic Units that constitute the *Brienomyrus* clade). This clade is the first freshwater fish species flock wholly within a riverine, as opposed to a lacustrine, environment.

available for freshwater fishes. For some adaptive functions related to diet, we can observe different stages of specialization, from the early stages of morphological change to very extreme body forms. For example, in molluscivorous fishes, some species only have a few enlarged pharyngeal teeth used to crush shells, while other species have a large number, and some even have pharyngeal bones mixed with the teeth (see chapter *Diets and food webs*).

Behavioural specialization is probably an important element in the success of adaptive radiation. In addition to trophic specialization, there is also specialization in reproductive behaviour, including mating rituals, sexual and specific colour, and territorial and parental behaviour. This brings together all the conditions that favour sympatric speciation.

Speciation of cichlids in the Great Lakes of East Africa: what processes are involved?

With their several hundred coexisting cichlid species, the African Great Lakes have been compared to natural laboratories for the study of speciation. Many scientists have puzzled over the origins of this high species diversity and the mode of speciation (allopatric or sympatric?) that allowed it. Strongly influenced by the idea that allopatric speciation was the dominant model, they wondered about the conditions that could have led to it, as fishes could in principle move freely throughout the lake and thus maintain gene flows across populations. (see boxes "Mechanisms involved in cichlid speciation" and "Cichlid palaeo-flock record").

To explain how such allopatric speciation could have taken place in these lakes, different but complementary mechanisms have been suggested (Martens *et al.*, 1994).

MECHANISMS INVOLVED IN CICHLID SPECIATION

When observing the cichlid species flocks in the Great Lakes of East Africa, what grabs one's attention is not just the extraordinary richness of shapes and colours that the fish come in, but also the great resemblance of forms from one lake to another.
This resemblance had led to the belief that these species flocks had a common origin. But Meyer *et al.* (1990) clearly showed that this was not the case and that each lake had developed its own species flock.
This raises the question of how, in such different lakes, evolution could have led to such similar forms.
What does the very deep (1,470 m) and very old (20 million years) Lake Tanganyika have in common with Lake Victoria, which is only some forty metres deep and had probably dried out, at least partially, around 15,000 years ago?
Why do identical phenomena occur repeatedly and independently in these lakes?

To understand this, one must first understand that in each lake, the species flock originated from a fluviatile species that colonized the lacustrine environment.

It then appears that evolution operated simultaneously on two main aspects: skull shape, particularly the jaw; and colour.
Once the fluviatile Cichlidae arrived in a lacustrine environment, it got the opportunity to colonize a large number of different biotopes, each with its own set of food resources: seaweeds to graze, molluscs and pelagic preys to capture, and so on.
Groups rapidly specialized in a type of diet, as shown by Alberston *et al.* (1999) in Lake Malawi, where species split into two groups early on: those that preferred rocky habitats, and those that preferred the sandy bottom.
This type of adaptation was possible owing to the extraordinary plasticity of the skull and jaw of these species.
Albertson *et al.* (2003a and b) also showed that only about a dozen genes would have been involved in the emergence of the different phenotypes observed (between grazers, filter feeders, predators, etc.).
These genes are for the most part grouped (or "linked") within the genome and often have multiple effects.
For example, some genes can affect both the height and the length of a jaw.
Albertson *et al.* (2003 b) also showed that selection phenomena were involved in leading to the shapes that we see today.

If we consider that the fluviatile species that led to these different species flocks had the same genetic potential for jaw evolution, it is no longer surprising that identical selective pressures in different lakes could have led to identical phenotypes.
In other words, in two different lakes, the selection pressures that would compel a species to specialize in, for instance, grazing seaweed, would lead to the same solution regardless of the lake.

Finally, colour variations are another form of diversification that involves sexual selection, which is particularly well studied in the Cichlidae of Lake Victoria.
Males are often brilliantly coloured while females are colourless.
Reproduction often depends on visual signals related to these colours.
Generally, the female selects the male based on colour criteria. Seehausen *et al.* (1997) have shown that water turbidity (for instance, due to eutrophication) can change colour perception in fishes and thus break the ethological barriers between species (thus leading to hybridizations.)
If we also add that the genes controlling skull morphology may be linked to those controlling partner choice (sexual selection), we can then predict a directional selection linking morphology and colour, and understand why the species flocks of the East African Great Lakes are so similar.

CICHLID PALAEO-FLOCK RECORD

ALISON MURRAY & OLGA OTERO

When did their ability to rapidly speciate and form species flocks evolve in cichlids? It may be that this ability arose early in the history of the family.

A major impediment to our understanding of the history of the family Cichlidae is not just a lack of fossils, but a lack of osteological characters that can be used to assign the fossil remains to a living group. Cichlids are conservative in their anatomy, with a diversity of external morphologies mainly associated with small changes in relative growth without major structural modification (Greenwood, 1974, 1984; Strauss, 1984; Stiassny, 1991). The large amount of convergent evolution and the extensive radiation of species make interpreting their interrelationships based on anatomical data very difficult. But anatomical or osteological characters are needed to determine cichlid interrelationships if fossil species are to be studied. Fortunately, there are a few skeletal characters that have been identified and found useful for interpreting cichlid relationships. Also, scales and squamation patterns have been studied and found useful for indicating cichlid relationships (Lippitsch, 1993, 1995, 1998).

Fossils cichlids are known from Africa, Saudi Arabia, the Levant, Europe, South America and Haiti. Their African fossil record starts in the Eocene (56Ma - 34Ma), with *Mahengechromis* in Tanzania (Murray, 2000) (figure 7.4) and a fish reported as being closely related to the modern genus *Tylochromis* found in the Fayum, Egypt (Murray, 2002). By the Oligocene (34Ma - 23Ma), there are a few records of fossil cichlids in Africa and Saudi Arabia. Conversely, during the Neogene (23Ma - Present), cichlids are known from a greater number of deposits throughout Africa.

So far, the African cichlid fossil record provides only one example of a potential flock. These are among the oldest known fossils of the family, about 45Myrs ago (Murray, 2001). These fossils, from the Mahenge site in northwestern Tanzania, were identified as belonging to a single genus, based on their scales and squamation pattern (Murray, 2000), and five different species within the genus are identified by differences in osteological features. Can we be sure they represent a species flock? In fact, we cannot. In order to qualify for species flock status, the members of the flock must all be each others' closest relatives, and be confined to a limited geographical area. Neither of these criteria can be determined for fossils. It may well be that some of these fish also lived outside the area in which they were found, or other species may have been more closely related to one or the other species. However, we have no fossil record for similar species outside of the small area of the lake deposit. So, although this group of Eocene species may well have been a flock, we have no method of determining this.

Instead of trying to find fossils to document the age of the flocking ability of cichlids, one group of scientists instead examined the diversity of living riverine cichlids in southern Africa to determine the time when they flock (Joyce *et al*. 2005). Molecular relationships and molecular clock dating of the extant cichlid flocks indicate that the flocking ability arose in these lineages millions of years ago. But conflicting results on divergence dates of different lineages prevent any agreement on how old these flocks may have been. This intriguing characteristic of cichlids may well have evolved millions of years ago, but we have yet to determine if this is the case.

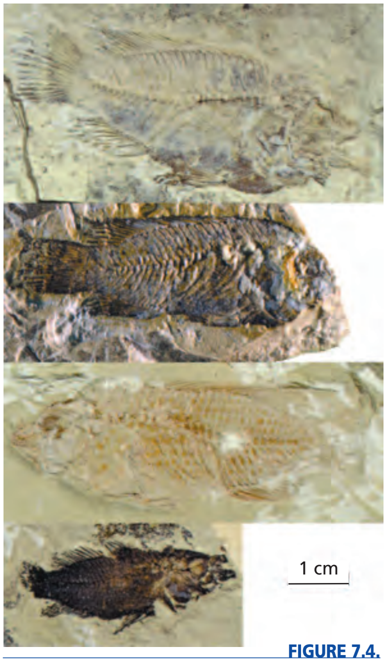


FIGURE 7.4.

Members of four species of *Mahengechromis* from the Eocene of Mahenge (Tanzania) (photos by Alison Murray).

Fragmentation of the lacustrine system in several smaller lakes

Proof now exists that the level of the African Great Lakes was not stable but fluctuated significantly even in the recent past. For instance, 15,000 years ago, the level of Lake Victoria was lower than its current one. The fluctuations of Lake Malawi's level reached 250 to 300 metres over the last 25,000 years (Owen *et al.*, 1990).

As for Lake Tanganyika, research has shown that its level 25,000 years ago was 600 metres lower than the current one (Tiercelin *et al.*, 1989). During the Pleistocene, Lake Tanganyika was fragmented into two or three separate basins as well as numerous small lakes occupying the graben.[1] This created conditions that favoured allopatric speciation (Martens *et al.*, 1994). The faunas could have mixed once again when the water level rose, but sexually isolated species continued to survive. If such a mechanism occurred repeatedly over a geological scale, this could explain the great wealth of species in the East African Great Lakes.

NOTE 1

In geology, a graben (graben is German for ditch or trench) is a depressed block of land bordered by parallel faults.

A great variety of diets

While the fluvial ancestors that populated the great lakes were apparently generalists, the Cichlidae, like Darwin's finches, developed a wide range of diets in the lacustrine physical system. This resulted in a number of morphological adaptations to the type of food and its capture, as well as ecological and behavioural adaptations such as a more systematic presence in certain habitats where food is present (see the aforementioned adaptive radiation).

Allopatric/sympatric speciation in the lake itself

Allopatric speciation can take place even without a fragmentation of the lacustrine physical system. Investigations on the population of the Great Lakes by fishes showed that many of the benthic Cichlidae species are only present at certain depths and certain bottom types from which they hardly move throughout their lifetime. This sedentary behaviour (also called stenotopy) is associated with reproductive behaviour that implies staying in a territory, as well as parental care, which does not promote dispersion either.

Numerous 'Mbuna' species, which are cichlids endemic to Lake Malawi, thus have very specific habitats and are likely to pass their entire lifetime, from fecundation to death, in the only habitat they are dependent on. It is therefore possible that in lakes covering a large area, the existence of heterogeneous islands and/or bottoms scattered in patches encourages the maintenance of isolated populations that, owing to their stenotopy, have little contact with each other. Such a situation favours the speciation of sympatric species following a model that can be compared, in a way, to allopatric speciation, as behavioural and ecological barriers within the same lacustrine system limit or prevent gene flows between sub-populations. Ribbink (1994) believes that the particularly marked stenotopy of the haplochromines would largely explain the extraordinary diversification observed in this group (nearly 1,000 species). It is accepted that the ancestors of the Cichlidae species flocks of the Great Lakes were eurytopic fluviatile species, and that their evolution went in the direction of greater specialization. The evolutionary potential of these eurytopic colonizers was probably poor, but could have become increasingly important as certain lineages specialized and became stenotopic (Ribbink, 1994).

Another hypothesis states that the variability of the riverine environment selects for eurytopic species to the detriment of stenotopic ones, which are unable to survive. This would explain why there are more Cichlidae species in African lakes compared with rivers. Moreover, tilapias, which are eurytopic – that is, less selective in terms of habitat – are only represented by about a dozen species in the Great Lakes. However, stenotopy is only possible in the lakes, where conditions remain relatively stable over the long term. The smaller number of Cichlidae in Lake Tanganyika could be related to the fact that demersal habitats are too unstable (upwelling of anoxic deep waters, in particular) to allow the evolution of specializations that would lead to stenotopy and the development of a large species flock (Eccles, 1986).

Similarly, the low number of Cichlidae (sixteen haplochromine species) observed in Lake Kivu could be due to geological instability since the Pleistocene which could have caused widespread species extinctions and inhibited the diversification of surviving species. The latter survived the unstable periods by seeking refuge in neighbouring rivers, whence they recolonized the lake during more favourable periods. Unlike most of the other haplochromines species in the Great Lakes, these species are generalists and eurytopic, which supports previous conclusions regarding the role of stenotopy.

The role of predation

African fish speciation, particularly that of the Great Lakes Cichlidae, has been much discussed. According to some hypotheses, because they patrol in areas that have shelter, predators play a role in fragmenting populations and keeping them in isolated patches, which encourages speciation (Lowe-Mc Connell, 1987). In pelagic populations, meanwhile, predation pressure appears to lead to uniformity and a reduction in diversity. This hypothesis is confirmed by Coulter (1991 a) for Lake Tanganyika species, where *Lates spp*. and the Cichlidae *Boulengerochromis microlepis* exert strong influence over juveniles and small fishes that are forced to either hide or adopt schooling behaviour. These predators also have a strong influence on the reproductive strategies, behaviour, and mortality rate of prey. Meanwhile, it appears that the role of predators is less significant in Lakes Victoria and Malawi, where the many predators are themselves limited to certain types of habitat. The consequences of the introduction of *Lates* in Lake Victoria show in retrospect that the many Cichlidae species that disappeared did not, in fact, possess the behavioural mechanisms or adequate shelter needed to evade predation.

How fast is speciation?

There is little data on the speciation rate of African fishes, but it obviously varies enormously depending on phylogenetic group and the environmental conditions (Coulter, 1994).

The speed at which speciation occurs is still under debate, and improbable figures have been put forward. There are five endemic species in Lake Nabugabo, a satellite of Lake Victoria, that has been isolated from the latter for a little over 5,000 years. Some scientists thus believe that in this lake, speciation could have occurred in this time frame. If we note today that these species are not present in the larger lake, this does not mean that they were not there at another period.

Geologists have shown that Lake Victoria probably dried up entirely between 15,600 and 14,700 years ago. For some scientists, the current fauna probably diversified after this period. Many ichthyologists thus raised the following question: how can we explain the appearance of so many species in so short a time? While some biologists accept this scenario, for the majority of specialists this time length is in contradiction to biological reality, and they believe it impossible for so many species (around 500) to have differentiated in such a short time period (around 15,000 years) from one or a few ancestor species. Specialists now consider that this is not possible indeed, and that the lineage must have diversified around 100,000 years ago. What explanation can therefore be proposed? Several hypotheses were made, including one that suggested that the lake did not dry out completely and that some small residual lakes subsisted. In these lakes, two strains more adapted to lacustrine conditions could have differentiated here, and are thus behind the two major lineages now found in Lake Victoria. While geophysicists acknowledge this possibility, they nonetheless believe that the physico-chemical conditions of the time were incompatible with the coexistence of numerous species (Stager *et al.*, 2004).

This debate between the adherents of the two scenarios is still ongoing. However, more recent investigations (Elmer *et al.*, 2009) suggest a new one: that Lake Victoria could have been recolonized by haplochromines from Lake Kivu after Lake Victoria was once again filled with water some 15,000 years ago (Verheyen *et al.*, 2003). Indeed, in the past, water flowed from Lake Kivu to the Victoria basin (2.6 Ma-12,000 BP) before the Virunga massif's volcanic activity blocked the Kivu outlet and isolated the two entities around 14,000 to 11,000 years (Pouclet, 1978) or 25,000 to 12,000 years (Beadle, 1981) ago.

According to the most accepted scenario, the complex evolutionary history of haplochromines in Lake Victoria began well before the dry period that affected the Victoria basin. Molecular studies all confirm that the genetic lineages, and thus the species, are at least 100,000 years old (Verheyen *et al.*, 2003 and 2004). At least part of this history could have taken place outside the basin of Lake Victoria, perhaps in Lake Kivu (figure 7.5).

Despite being the most popular scenario today, it still remains a hypothesis that simply reflects the current state of knowledge.

As for the haplochromines of Lake Malawi, Owen *et al.* (1990) believe that speciation was very rapid and proposed a period of 200 years, which seems to be extremely farfetched!

Evolution-wise, Vrba (1980) advanced the hypothesis that the differences observed for speciation rates within a "clade" were the result of a

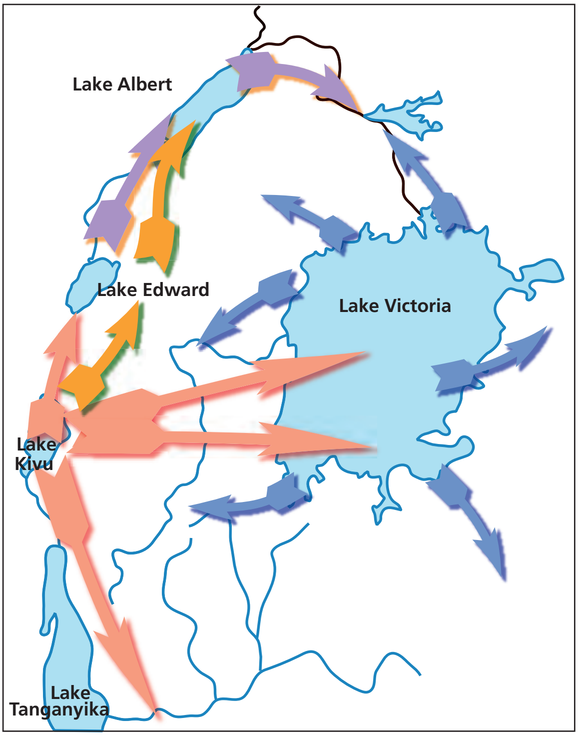


FIGURE 7.5.
Possible scenario of the pathways travelled by haplochromines to colonize the region of Lake Victoria from Lake Kivu (diagram adapted from Verheyen *et al.*, 2003).

eurytype/stenotype differentiation, that is, high speciation and extinction rates were associated with strong stenotopy. In other words, when stenotopy increases as a result of greater specialization, the speciation rate increases. This hypothesis appears to be verified in the Cichlidae of the African Great Lakes. Haplochromines, which are much more stenotopic than tilapias, also have many more species. Moreover, among the haplochromines, the species flocks with the most stenotopic members also have the greatest number of species (Ribbink, 1994).

Convergent evolution: chance or necessity?

Convergence occurs during evolution when similar characteristics appear in different species that may come from very distant lineages. Such convergences are often tied to the fact that the species are subjected to similar constraints when occupying comparable ecological niches found in different ecological systems.

Species from different taxonomic groups may display remarkable convergence in form. This is the case, for instance, of the African species *Hepsetus odoe* (Hepsetidae), which strongly resembles the northern pike *Esox lucius* and the South American genus *Boulengerella* (Ctenoluciidae) (figure 7.6).

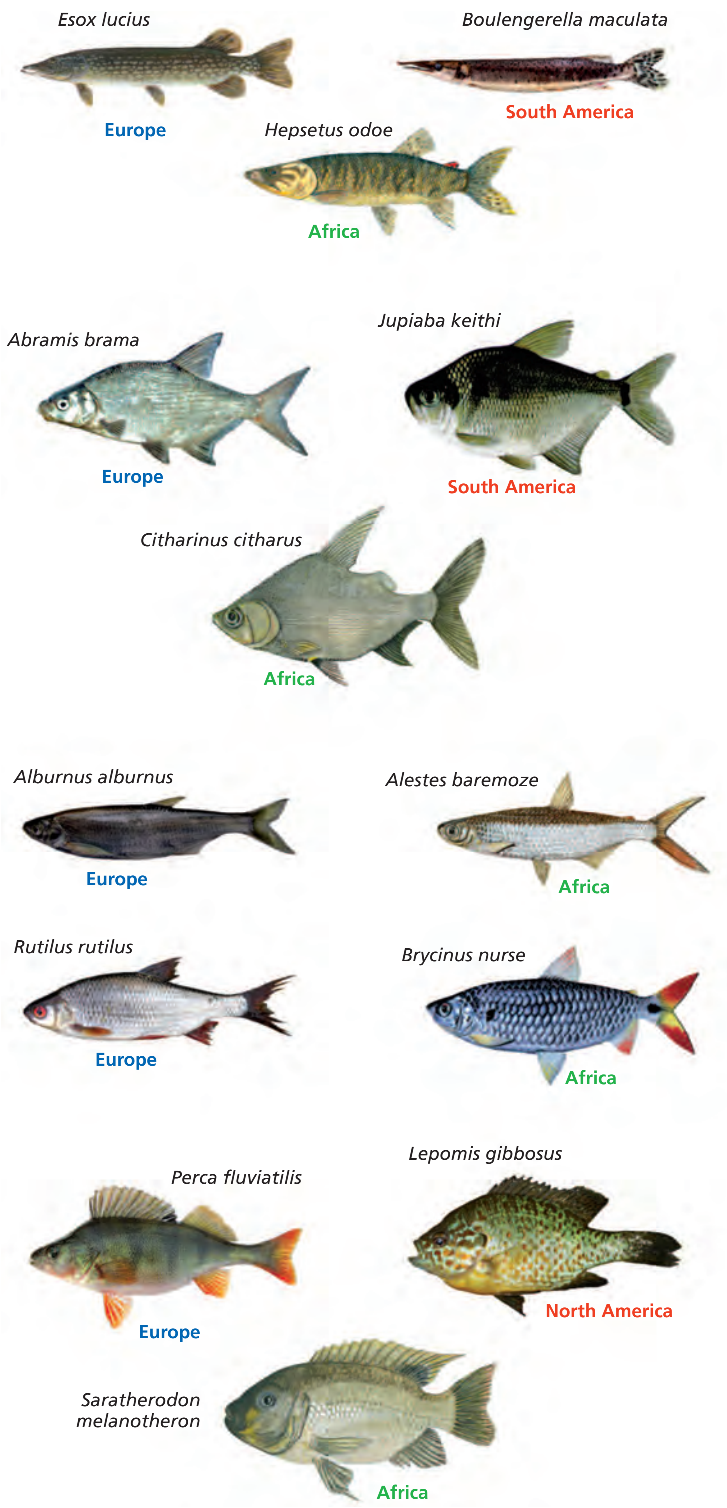


FIGURE 7.6.
Some examples of form convergence between species belonging to different families from Europe, America and Africa (sources: *Esox lucius* (Timothy Knepp); *Boulengerella maculata* (Clinton & Charles Robertson); *Jupiaba keithi* (Boujard *et al.*, 1997); *Abramis brama* (Iduns Kokbok); *Rutilus rutilus* (Algirdas); *Alburnus alburnus* (Kagor); *Perca fluviatilis* (Geshafish); *Lepomis gibbosus* (H. Krisp); *Hepsetus odoe*, *Citharinus citharus*, *Alestes baremoze*, *Sarotherodon melanotheron* (Cécile Paugy); *Brycinus nurse* (Pierre Opic).

Species of the African genera *Alestes* and *Brycinus* (Characidae) resemble, respectively, the Bleak *Alburnus,* the Roach *Rutilus*, or the Rudd *Scardinius* (Cyprinidae) in body shape, mouth, anal fins, and colouration (figure 7.6).

Citharinus (Citharinidae) of the Nilo-Sudanian basins or *Distichodus* (Distichodontidae) are also close to the Bream (*Abramis brama*) in terms of body and fin shape (figure 7.6).

Finally, the shape and some characteristics of Cichlidae recall those of some European Percidae and North American Centrarchidae (figure 7.6).

In the case of the East African Great Lakes, we also see examples of the convergent evolution of some anatomical or behavioural characters in Cichlidae. Specialization for the use of the same resources occurred simultaneously in several lakes, and often gave rise to comparable morphological changes in species that do not share an evolutionary lineage. These species have been referred to as "ecologically equivalent" (Fryer & Iles, 1972).

The study of small cichlids raises fundamental questions about the nature of evolution. Does it happen simply by "chance" or does it meet a deterministic pattern? In other words, is evolution contingent (something that may or may not happen) or does it address a "need"? The notion of "chance", as discussed by S.J. Gould,[2] does not mean the absence of a cause, but the impossibility of acquiring a precise knowledge of such a cause.

Chance or contingency probably play a central role in the phenomenon of species dispersion. Species may or may not seize opportunities to disperse that are offered by a series of geological or climatic phenomena. The colonization of new physical systems is thus a matter of chance, to a large extent. That said, adaptive radiations appear to be a form of determinism, as they involve diversifying diets or behaviours to maximize the use of available resources. As for ecological convergence, evolution appears to wear the mantle of "necessity", as it selected comparable shapes in the face of the same environmental constraints. This convergence thus reflects a type of adaptation.

This is how the genera *Bathybates* and *Rhamphochromis* that are endemic to Lakes Tanganyika and Malawi, respectively, are piscivorous open water fishes that share similar characters: elongated heads and bodies, and pointed teeth (Stiassny, 1981). These two genera are not phylogenetically close and evolved independently in each of the lakes (figure 7.7).

NOTE 2

Stephen Jay Gould was a champion of contingency, and thus of unforeseeable events ("chance"): "Wind back the tape of life to the origin of modern multicellular animals in the Cambrian explosion, let the tape play again from this identical starting point, and the replay will populate the earth (and generate a right tail of life) with a radically different set of creatures. The chance that this alternative set will contain anything remotely like a human being must be effectively nil, while the probability of any kind of creature endowed with self-consciousness must also be extremely small […].
At any of a hundred thousand steps in the particular sequence that actually led to modern humans, a tiny and perfectly plausible variation would have produced a different outcome, making history cascade down another pathway that could never have led to *Homo sapiens*, or to any self-conscious creature."
(Gould S.J., 2011 – *Full House. The spread of Excellence from Plato to Darwin*. Belknap Press, 256 p.).

FIGURE 7.7.
Example of endemic species that are "ecologically equivalent" and "phylogenetically distant". *Bathybates ferox* from Boulenger, 1898 and *Rhamphochromis macrophthalmus* from Regan, 1922.

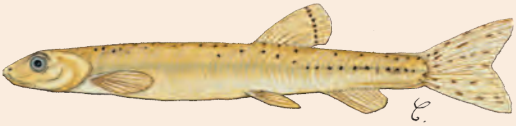
In molluscivorous cichlids, the development of thick pharyngeal bones to crush shells in the *Gaurochromis* of Lake Victoria as well as in Lake Malawi species such as *Mylochromis sphaerodon* or *Lethrinops mylodon* can be observed.

Other examples of morphological convergences (some authors prefer the term "parallelism") related to feeding behaviour have also been noted in paedophagous or lepidophagous fishes of the Great Lakes.

Taxonomy and systematics

DIDIER PAUGY

CHRISTIAN LÉVÊQUE



Taxonomy is the science of naming and describing organisms. It is a highly formalized science whose rules are established and revised regularly by an International Commission of Zoological Nomenclature created in 1895. The International Code of Zoological Nomenclature contains all the rules for designating animal species which are the same for all zoological groups.

One of its basic principles is that the first name given to a species has priority over the others. It is not uncommon for taxonomic revisions of a group to reveal that some species had been described under different names, because the authors did not have access to all available information or had made an error. In these conditions, the so-called priority rule must be applied. This sometimes leads to a change in the name used for the species up to that time. The situation may prove even more complex, as illustrated by the case of *Schilbe mystus* (see box "Who is *Schilbe mystus*?").

Another well-known case of ambiguity is that of the mounted holotype of *Synodontis xiphias* described in 1864 by Günther, which has a long and pointed snout similar to a swordfish. The species had never been recorded since then, for a perfectly good reason: an x-ray showed that the long snout was a fake nose, resulting from a metal frame used in mounting the animal (Poll, 1971) (figure 8.1). The holotype of *Synodontis labeo* Günther, 1865, described later, belongs to the same species, but the name *S. xiphias* remains valid in application of the principle of priority, and despite the deformity of the specimen retained as the type.

Systematics is the study of the diversity of organisms and the relationships between these organisms. Its goal is to classify species and detect phylogenies – a purpose that differs from the objectives of taxonomy. Classification consists of recognizing and defining groups or taxa (that is, a set of organisms that share a specific character) that taxonomists will then have to name. According to the hierarchical classification proposed by Linnaeus (1758), each level of the hierarchy corresponds to a taxon name. While ideas governing classification in particular have evolved significantly since the 18th century, the basic rules stated by Linnaeus remain solid. The discipline currently known as biosystematics is a modern approach to taxonomy and phylogeny that makes use of information from different sources: morphology, genetics, biology, parasite specificity, behaviour, and ecology. This type of approach is undoubtedly set to develop further.

WHO IS *SCHILBE MYSTUS?*

After examining the presumed holotype of *Schilbe mystus*, De Vos & Skelton (1990) showed that the specimen, described in 1758 by Linnaeus, actually belonged to the same species as the one named *S. (Eutropius) niloticus* described later in 1829 by Rüppell.
If the two species are synonyms, application of the International Code of Zoological Nomenclature means that the older name *S. mystus* takes priority over *S. niloticus*. In keeping with this, all fishes that had been identified as *S. niloticus* up to that time need to be renamed *S. mystus*.

While the holotype of *S. mystus* is a synonym of *S. niloticus*, this is not the case for all the other fishes identified up to then as *S. mystus* but different from *S. niloticus* and the *S. mystus* type. What species do they belong to?
Among the species erroneously considered a synonym of the *S. mystus* type, the oldest is *S. intermedius* described by Rüppell in 1832, and whose description matches that of the ex-*mystus*.
As a result, fishes described before 1990 under the name *S. mystus* must be renamed *S. intermedius*.

The application of perfectly reasonable taxonomic rules can therefore lead to a particularly confusing situation for non-specialists. The name *S. mystus* is now used for a species that was widely cited in literature under the name *S. niloticus*, and the former *S. mystus* take the name *S. intermedius*.
However, this change in nomenclature is not always rigorously applied by everyone everywhere, to the point that one often wonders if the name being used is the former or the post-revision name.
In this specific case, the legendary formal discipline of the taxonomist did not take into account the confusion that would result for ichthyologists, biologists and ecologists alike.

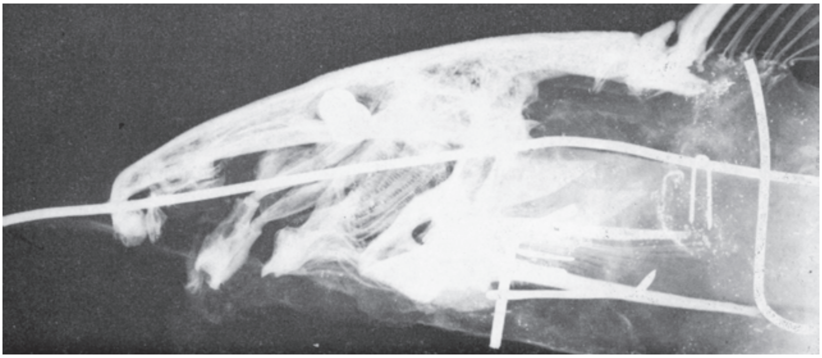


FIGURE 8.1.
Head radiography of the holotype of *Synodontis xiphias* (from Poll, 1971).

What is a species?

The binomial system originally proposed by Linnaeus (1758) is used by naturalists the world over to designate and identify species. But the concept itself of "species" has long been debated. To date, no definition is entirely satisfactory.

The typological species concept

Until the mid-19th century, systematists viewed species as fixed. They were as God had created them, immutable and limited in number. The purpose of taxonomy then was to draw up an inventory of all existing life forms and describe their specific characters. In the words of Linnaeus, "(…) there are as many species as the infinite being created diverse forms (…)", and he formalized this view by establishing the species through a type individual, the holotype (see box "International Code of Zoological Nomenclature"), to which a Latin binomial was assigned in order to identify and classify them.

EXTRACT OF THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE FOURTH EDITION

adopted by the
XXth General Assembly of the International Union of the Biological Sciences
December 1999

type, n. A term used alone, or forming part of a compound term, to denote a particular kind of specimen or taxon.

allotype, n. A term, not regulated by the Code, for a designated specimen of opposite sex to the holotype [Recommendation 72A].

cotype, n. A term not recognized by the Code, formerly used for either syntype or paratype, but that should not now be used in zoological nomenclature [Recommendation 73E].

genotype, n. A term not recognized by the Code, formerly used for type species, but that should not now be used in zoological nomenclature [Recommendation 67A].

hapantotype, n. One or more preparations consisting of directly related individuals representing distinct stages in the life cycle, which together form the name-bearing type in an extant species of protistan [Arts 72.5.4, 73.3]. A hapantotype, while a series of individuals, is a holotype that must not be restricted by lectotype selection; however, if a hapantotype is found to contain individuals of more than one species, components may be excluded until it contains individuals of only one species [Art. 73.3.2].

holotype, n. The single specimen (except in the case of a hapantotype, q.v.) designated or otherwise fixed as the name-bearing type of a nominal species or subspecies when the nominal taxon is established.

lectotype, n. A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies [Art. 74].

neotype, n. The single specimen designated as the name-bearing type of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no name-bearing type is believed to be extant.
If stability and universality are threatened, because an existing name-bearing type is either taxonomically inadequate or not in accord with the prevailing usage of a name, the Commission may use its plenary power to set aside that type and designate a neotype.

paralectotype, n. Each specimen of a former syntype series remaining after the designation of a lectotype [Art. 72.1.3, Recommendation 74F].

paratype, n. Each specimen of a type series other than the holotype [Recommendation 73D].

syntype, n. Each specimen of a type series (q.v.) from which neither a holotype nor a lectotype has been designated [Arts. 72.1.2, 73.2, 74]. The syntypes collectively constitute the name-bearing type.

topotype, n. (**topotypic**, a.). A term, not regulated by the Code, for a specimen originating from the type locality of the species or subspecies to which it is thought to belong, whether or not the specimen is part of the type series.

For practical reasons, the typological species concept is still used to this day: a species is a set of individuals that are identical to each other and to the "type" specimen, *i.e.,* the specimen used to describe and characterize the species in morphological terms. This type is deposited in a museum where it serves as a reference or a sort of standard for comparisons or future revisions.

The biological species concept

The typological species concept gradually gave way in the early 20th century to the concept of a biological species. In 1798, Cuvier had already used a biological criterion in defining a species as "the collection of all organized bodies, borne of each other or common parents, and of all those that resemble them as much as they resemble each other." The definition given by Mayr (1942) a century and a half later is not fundamentally different but emphasizes the biological aspect: species are groups of populations whose members can interbreed, and who are reproductively isolated from other groups. One of the major criteria for differentiating neighbouring species was the fact that any eventual hybrids were not viable or were sterile. "The origin of species is therefore simply the evolution of some difference – any difference at all – that prevents the production of fertile hybrids between populations under natural conditions" (Wilson, 1992).

On the genetic level, the concept of a biological species implies the existence of a gene pool that could recombine within the population during sexual reproduction, but that this gene pool is somehow "protected" from mixing with other pools by biological, physiological, or behavioural mechanisms.

While the concept of biological species is not debatable, it is nonetheless difficult to apply in fishes, in the sense that systematic cross-breeding trials in various natural populations are particularly difficult to carry out.

Concept of specific-mate recognition system

In reaction to the concept of reproductive isolation that undergirds that of the biological species, Paterson (1985) considers that there is no obvious reason for species evolving independently in isolated geographic areas to find it advantageous to develop mechanisms that lead to reproductive isolation.

The concept of a specific-mate recognition system, meanwhile, is based on the premise that conspecific sexual partners must share specific characters, such as a co-adapted set of signals and responses between males and females of the same species during their mating rituals, in order to meet and ensure fertilization of gametes (Ribbink, 1988). A species is thus made up of individuals possessing the same system of fertilization, that is, the set of adaptations that encourage and facilitate the encounter between sexual partners to ensure reproduction: visual, chemical, or sonic recognition signals; colouring; mating dances; synchronous reproductive periods; preference for the same types of habitat and laying sites; territoriality, etc.

This concept is an interesting alternative. The existence of selective recognition systems for conspecific partners, rather than barriers to hybridization, serves as an important criterion for speciation. In other words, we are in the realm of ethology.

Sister species

Sister species are biological species that have achieved reproductive isolation but are still difficult to discern based on morphology alone. These species probably result most frequently from recent speciation.

Here are two examples that provide a good illustration of how some recent techniques can help separate species with similar phenotypes and that probably thus result from fairly recent speciation.

- *Labeo* from Senegal and Niger. In the upper course of these two basins, we found numerous specimens that were intermediate between *L. senegalensis* and *L. coubie*, and initially thought they could be hybrids. While the shape is closer to *L. senegalensis* in terms of general morphology, the buccal anatomy was closer to *L. coubie*. Similarly, the number of gill rakers on the first gill arch was not conclusive and also suggested a hybrid form. Comparative analysis of gill parasite fauna (Monogeneans) of the three forms of *Labeo* made it possible to determine that the specimens were not hybrids but a separate valid species that had specific parasite fauna. Genetic analysis of the three forms using protein electrophoresis also lifted all doubt about the true specificity of the presumed hybrid. It was named *L. roseopunctatus* (Paugy *et al.*, 1990) (figure 8.2) for its distinctive colour.

FIGURE 8.2.
General morphology of three sympatric species of *Labeo* from Western Africa (from Paugy *et al.*, 1994).

Labeo senegalensis *Labeo roseopunctatus* *Labeo coubie*

- *Petrocephalus* from the Niger. Three *Petrocephalus* forms found in the upper Niger basin have identical metric and meristic characteristics and only differ in their colour pattern:
  - Form A: uniformly silver colouring.
  - Form B: first dorsal fin rays strongly black; black spot under and touching the base of the dorsal fin.
  - Form C: grey spot under and not touching the dorsal fin.

Form A, long known to science, corresponds to *P. bovei*, a widely-distributed species but whose morphology – aside from colouring – does not differ from the other two forms. To draw a conclusion on the possible specificity of the three forms, the characteristics of the electrical discharges of these Mormyridae were studied. While forms A and C could not be distinguished, individuals of group B showed different characteristics. Also, while the type of discharge could

FIGURE 8.3.
General morphology of three sympatric species of *Petrocephalus* from Western Africa (from Paugy *et al.*, 1994).

Petrocephalus bovei *Petrocephalus soudanensis* *Petrocephalus pallidomaculatus* not distinguish A and C, genetic separations confirmed the specific level of these three forms (Agnèse & Bigorne, 1992). In addition to the already identified *P. bovei*, two new species, *P. soudanensis* and *P. pallidomaculatus* were described with the help of new techniques that allowed recognition of the specific validity of these two other forms (Bigorne & Paugy, 1991) (figure 8.3).

Polytypic species

In a species' area of distribution, environmental factors are generally not uniform. Populations can react locally to changes in these factors through morphological changes. The concept of a polytypic species refers to a species that can present several forms and/or which is composed of several subspecies that may show differences on the morphological, physiological, ecological or behavioural level.

Recognizing variability within a population can lead to two positions between which ichthylogists have long hesitated. Either "varieties" are local adaptations of the same species, or they are truly different species. Thus, for the species *Brycinus nurse* common in the Sahelian zone, there are two known lacustrine dwarf populations, each sympatric with riverine populations: *B. nurse dageti* in Lake Chad and *B. nurse nana* in Lake Turkana. The first subspecies was initially described as a different species, *B. dageti* (see Paugy, 1986). There are also numerous examples of polytypic species among the Cyprinidae (Lévêque, 1989a and b) and Mormyridae (Bigorne, 1987 and 1989; Bigorne & Paugy, 1991). In reality, given that hydrographic basins currently act as geographic islands, a species is most often split in several isolated populations with little or no contact among them (figure 8.4). In such conditions, it is unsurprising

FIGURE 8.4.
Distribution of *B. imberi*, *B. abeli*, *B. carolinae* and *B. nigricauda*.

for isolated populations to begin developing certain adaptations in response to their environmental conditions, which would explain the variability observed.

In tropical zones, several studies have shown the influence of food habits on the morphological variations of fishes (see chapter *Diets and food webs*).

Geographical clines

In a terrestrial physical system, we have observed that when environmental factors vary gradually, there may also be gradual changes in certain morphological or morphometric characteristics in the populations of a species. These geographic variations result from the response of organisms to environmental conditions and/or the limitation of gene exchanges between isolated populations.

Endler (1977) defined cline as follows: "a geographic gradient in a measurable character, or gradient in gene, genotype, or phenotype frequency." Thus, phenotype variability or variability in morphological or meristic characters observed in a species can be considered a cline.

Regional scale

In the upper Niger basin, the number of soft rays in the anal and dorsal fins of *Petrocephalus bovei* (Bigorne *et al.*, unpublished) changes along an upstream-downstream gradient (figure 8.5). There is an average difference of two rays between extreme populations. No solid explanation has been given for this phenomenon.

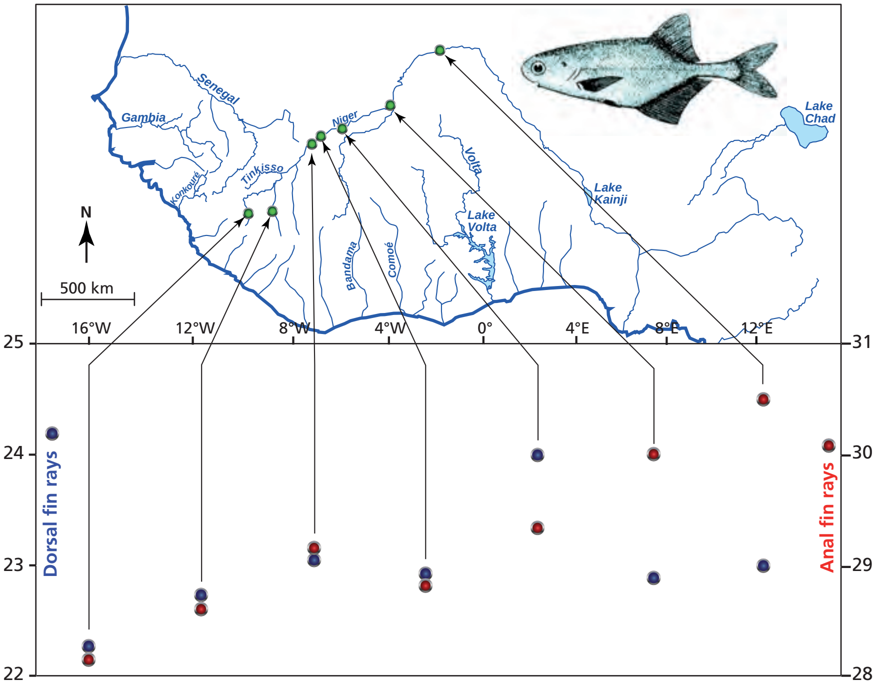


FIGURE 8.5.
Petrocephalus bovei: clinal changes in two meristic characters (average) along an upstream-downstream gradient (Upper Niger).

West African scale: *Schilbe mandibularis*

Schilbe mandibularis (Schilbeidae) is found in the Atlantic basins of Upper Guinea, from eastern Liberia to western Ghana (Lévêque & Paugy, 1999). The number of anal fin rays and vertebrae in this species increases from west to east, as is also the case for body size, size at first maturity, and maximum size (figure 8.6) (Lévêque & Herbinet, 1982). From an ecological viewpoint, the west-east gradient corresponds to the transition from forest rivers (Cess, Cavally) to savannah rivers (Comoé) with intermediate situations (Sassandra and Bandama). In this example, there is also a correlation between the maximum size of individuals and the number of vertebrae.

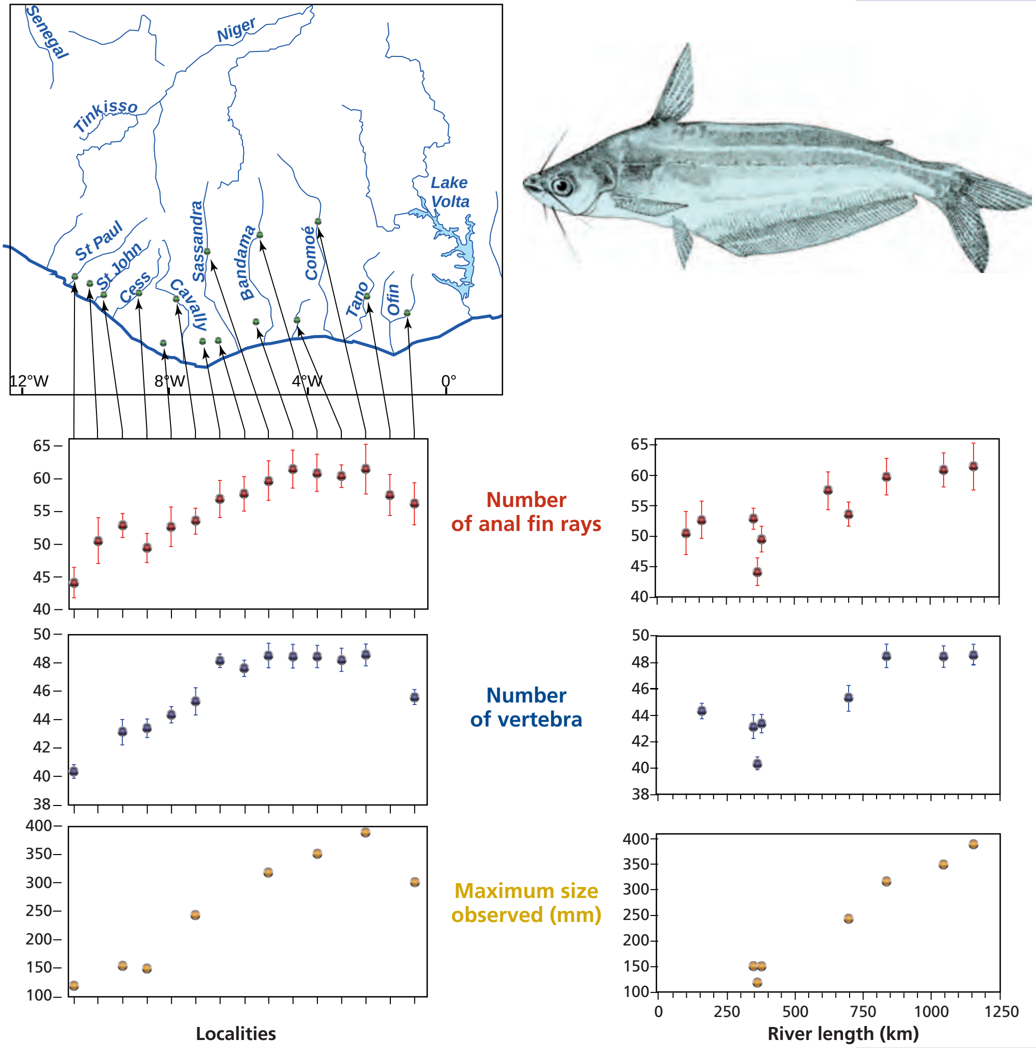


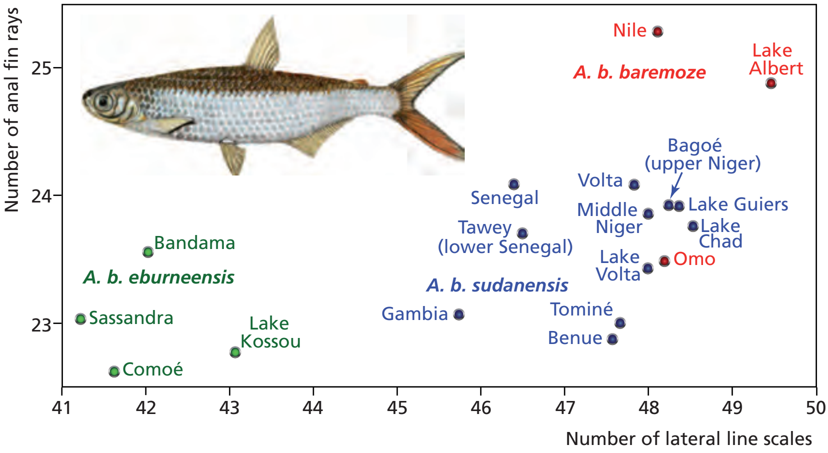
FIGURE 8.6.
Schilbe mandibularis: clinal changes in two meristic characters (average) and maximum size observed along an east-west gradient in river catchments of Côte d'Ivoire.

Subcontinental scale: *Alestes baremoze, Brycinus macrolepidotus* and *Barbus bynni*

Alestes baremoze (Alestidae) is found in all the basins of the Nilo-Sudanian zone (Paugy *et al.*, 1994; Lévêque & Paugy, 1999). Populations are not identical and, depending on the sub-regions, there are geographic variations in some meristic characters such as the number of scales along the lateral line, the number of vertebrae, and the number of soft rays of the anal fin (figure 8.7). The values of these three characters decrease along the cline from the Nile to the Côte d'Ivoire with intermediate values for the Sudanian basins. Three subspecies were described on the basis of the variations of these meristic characters. No detailed explanation has been given to explain this trend.

FIGURE 8.7.

Alestes baremoze: clinal changes in two meristic characters (average).



Prior to the morphometric analysis of *B. macroplepidotus,* two species had been identified throughout its area of distribution in tropical north Africa: *Brycinus rutilus* in the forest sector and *B. macrolepidotus* in the savannah zone. On the basis of two main morphometric characteristics (body height and position of the dorsal fin in relation to the pelvic fin), we were able to highlight the existence of a geographic cline (figure 8.8), and only *B. macrolepidotus* is now considered a valid species (Paugy, 1982a). There are in fact two extreme morphs and several intermediate forms. A look at the forest-savanna gradient shows that the bodies of individuals lengthen and become more slender, and that the position of the anal fin retreats in relation to the insertion of the pelvic fins.

Within the *Barbus bynni* complex, three allopatric species have been identified: *B. bynni* (Nile basin), *B. occidentalis* (Sahelian zone: Chad, Niger, Ouémé, Volta, and Senegal basins) and *B. waldroni* (coastal basins of Côte d'Ivoire and Ghana). In fact, a parasitology study (fauna of gill parasites, Monogenean) (Lévêque & Guégan, 1990) show that the two West African species *B. waldroni* and *B. occidentalis* had the same Monogenean fauna as *B. bynni*. The strict specificity of this type of parasite thus proves that these three forms belong to the same species and must each be considered a subspecies of that group. The

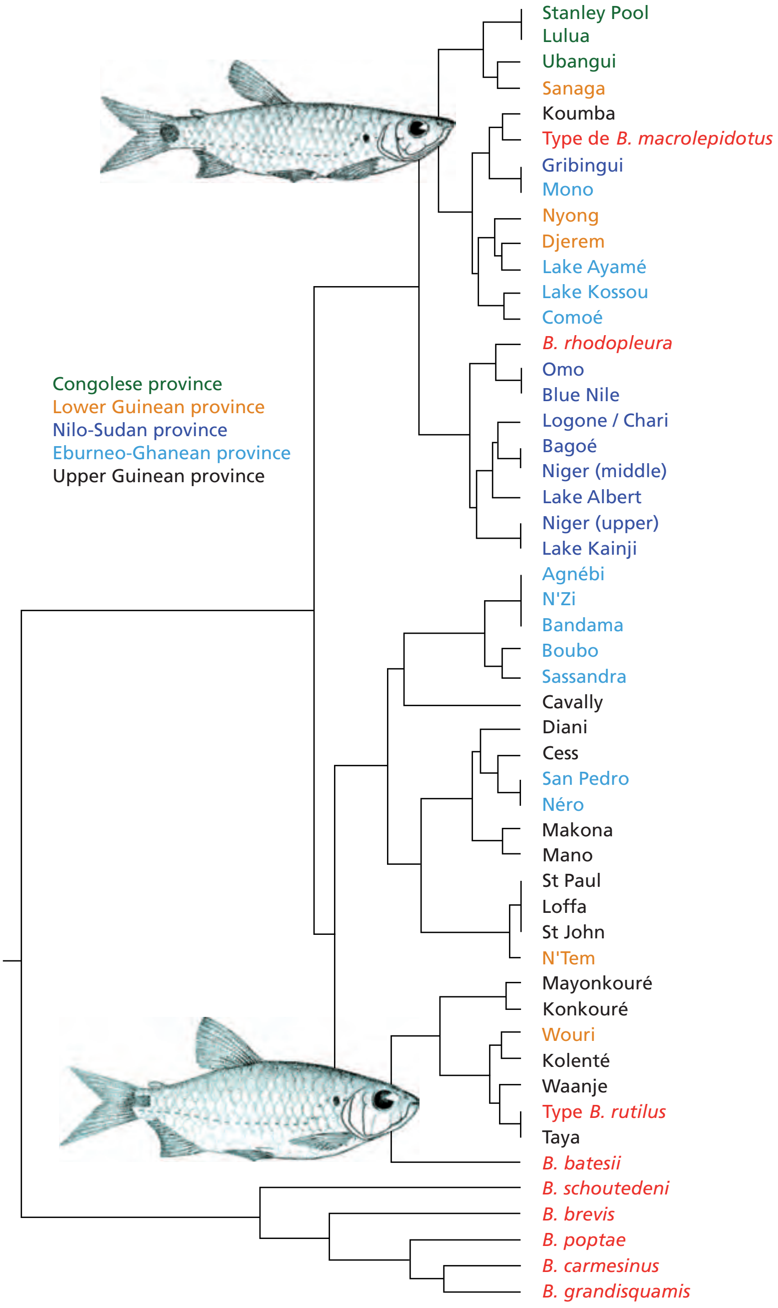
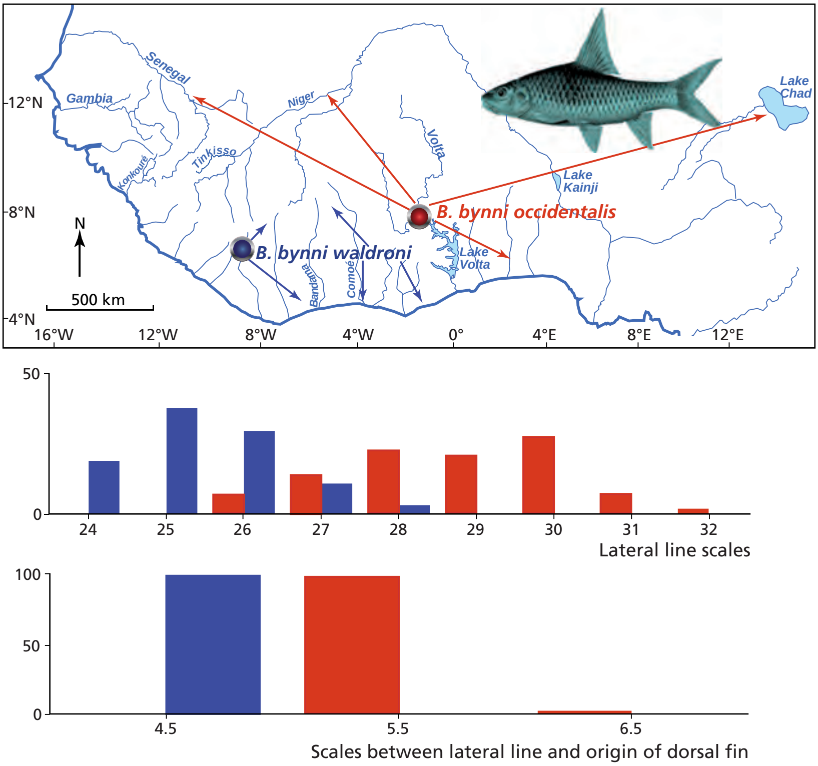


FIGURE 8.8.
Brycinus macrolepidotus: clinal changes in two morphological characters (average) across the whole distribution area of the species.

parasitology study showed that there was but one species whose meristic characters change according to a geographic cline. In West Africa, the two subspecies (respectively *B. b. occidentalis* and *B. b. waldroni*) are distinguishable through the number of scales (figure 8.9).

FIGURE 8.9.
Barbus bynni: clinal changes in two meristic characters (average).



Question of hybrids

Natural or artificial hybridization is a way of testing the concept of biological species. Hybridization in the natural world has been observed, but it remains a rare phenomenon to the extent that there has been little systematic research in the matter and that hybrids are not always identifiable to an untrained eye. Daget (1963) was able to identify young specimens from the Benue as hybrids of *Citharidium ansorgii* and *Citharinus distichodoides*. In Lake Itasy in Madagascar, *Oreochromis macrochir* and *O. niloticus* that were introduced in the 1960s hybridized to produce a form called tilapia 3/4 which co-existed for many years with the parental species (Daget & Moreau, 1981). A similar phenomenon was observed in Lake Naivasha in Kenya between the introduced species *Oreochromis spilurus niger* and *O. leucostictus* (Elder *et al.*, 1971).

More recently, natural hybridization between *Coptodon zillii* and *Tilapia guineensis* was observed in the lake of the Ayamé dam (Côte d'Ivoire). These two species are usually parapatric, with *C. zillii* found exclusively in fresh water and *T. guineensis* in brackish water. It is probable that with the building of the dam in 1958, populations of the two species were trapped, forcing them to cohabit (Pouyaud, 1994). Another example of hybridization that involved three Cichlidae species (*Coptodon zillii*, *T. guineensis* and *T. dageti*) was also found in the Comoé River in Côte d'Ivoire and confirmed by protein analysis, as was the previous case (Pouyaud, 1994).

The last two cases are probably an illustration of what is called a hybrid zone, that is, a contact zone where parapatric populations may hybridize. It is likely that the phenomenon was underestimated up to now owing to limited technical means and a lack of interest.

Generally speaking, hybridizations in the natural environment among Cichlidae occur when environmental changes remove the barriers that ensure reproductive isolation between species, or when a species colonizes or is introduced to a physical system where similar species already exist.

Another example is the case of an Alestidae hybrid between *Alestes baremoze* and a *Brycinus* which was observed in Côte d'Ivoire with the closure of the Kossou storage lake. Finally, there is the case of a *Hydrocynus somonorum* species described in the Niger River by Daget (1954) which was then found to be a hybrid of *H. forskalii* and *H. brevis*. In all these cases, we see the rather elusive nature of the appearance of a hybrid form.

Artificial hybridization was much used by aquariologists studying Cyprinodontiformes in an attempt to identify the biological species among the numerous, sometimes highly similar forms, some of which possess different karyotypes (Scheel, 1968).

Genetics and species concept

Given the difficulty of recognizing the existence of species using morphology alone, ichthyologists sought to use other data, notably from genetics (see box "Genetic differentiation of *Sarotherodon melanotheron* populations" in chapter *Diversity of African fish: heritage of evolution*).

Number and shape of chromosomes

Each living cell contains several chromosome pairs. Each pair contains one chromosome from the mother's egg cell and another from the father's sperm. The number of chromosomes is constant in a given species, and 2n (n being a set of chromosomes, either paternal or maternal) is used to define the number of chromosomes in somatic cells, which are diploid. Gametes or sex cells (eggs, sperm) contain only one set of chromosomes (n) and are called haploid. After fertilization, the gametes fuse and yield diploid cells. In some cases when the number of chromosomes in a cell is higher than 2n, such cells are called polyploid.

The number, shape, and size of chromosomes vary from one species to another. These characters can be useful for taxonomic or phylogenetic research, and are increasingly used given the advances in karyotype preparation techniques (Ozouf-Costaz & Foresti, 1992). In particular, we can expect significant progress to be made in chromosome marking techniques which would make them easier to identify.

The number of chromosomes for several African fish species has been determined (table 8.I). For many of them, this number ranges between 2n = 48 and 2n = 52, but in some cases the number is different owing to diverse reasons:

- In some Cyprinidae species, 2n can be as high as 148-150. In this case it is a hexaploid number resulting from a polyploid phenomenon that consists of a mutation that leads to an increase in the number of chromosomes within a population. This number may be double (tetraploid individuals), triple (hexaploid individuals), or any other multiple of the number of chromosomes usually observed. The recent discovery of large hexaploid *Barbus* in South, East, and West Africa suggests that the origin of Cyprinidae should be reconsidered.
- In the Siluriformes, 2n is between 70 and 72 in species of the genera *Clarotes* and *Chrysichthys*. This higher number, compared for instance with the genera *Bagrus* and *Auchenoglanis*, could trace its origin to centromere fissions in some chromosomes (Agnèse, 1989).
- The highly variable karyotype of Cyprinodontiformes (2n between 9 and 24) appears to be unique among fish, if not in the animal world altogether. The mechanism behind the reduction in the number of chromosomes apparently results from the fusion of centromeres in some ancestral chromosomes (referred to as Robertsonian fusion).

Genetic distances and morphological differences: two separate phenomena

Speciation and morphological evolution are two independent phenomena. In particular, there is not necessarily a correlation between the genetic distance between species and the morphological divergence observed. Thus, Cichlidae in the Great Lakes that evolved rapidly through adaptive radiation are close from a genetic perspective, even though many of the species are well-differentiated morphologically (figure 8.10). For ten *Haplochromis* species in Lake Victoria, for instance, there is little divergence in terms of protein analysis but the same species show significant anatomical divergence (Sage *et al.*, 1984).

FIGURE 8.10.

Genetics as marker of phylogeny: example of Cichlidae (from Meyer, 1993).

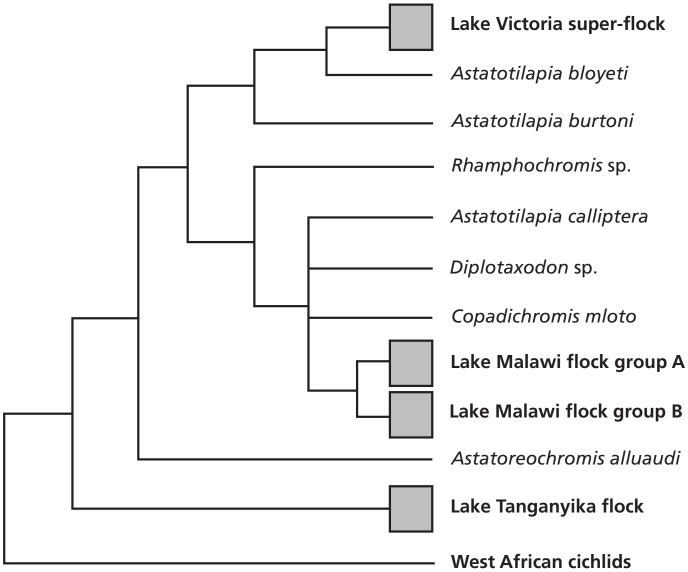


TABLE 8.I

Number of chromosomes for different African species (2n: diploid number of chromosomes).

Families / species	2n	Authors
Protopteridae		
Protopterus annectens	34	Wickbom, 1945
Polypteridae		
Erpetoichthys calabaricus	36	Denton &Howell, 1973
Polypterus palmas	36	Denton & Howell, 1973
Polypterus senegalensis	36	Urishido *et al.*, 1977
Phractolaemidae		
Phractolaemus ansorgii	28	Vervoort, 1979
Pantodontidae		
Pantodon buchholzi	48	Uyeno, 1973
Notopteridae		
Notpterus afer	34	Uyeno, 1973
Cyprinidae		
Barbus bynni	150	Golub. & Krys., 1993
Barbus bynni occidentalis	148	Guégan *et al.*, 1995
Barbus capensis	150	Oellerm. & Skelt., 1990
Barbus ethiopicus	150	Golub. & Krys., 1993
Barbus intermedius	150	Golub. & Krys., 1993
Barbus natalensis	150	Oellerm. & Skelt., 1990
Barbus petitjeani	150	Guégan *et al.*, 1995
Barbus wurtzi	148	Guégan *et al.*, 1995
Barbus ablabes	48	Rab *et al.*, 1996
Barbus anema	50	Golub. & Krys., 1993
Barbus bigornei	50	Rab *et al.*, 1996
Barbus holotaenia	50	Rab, 1981
Barbus macrops	50	Rab *et al.*, 1996
Garra dembeensis	50	Krys. & Golub., 1993
Garra quadrimacukata	50	Krys. & Golub., 1993
Labeo senegalensis	50	Paugy *et al.*, 1990
Labeo coubie	50	Paugy *et al.*, 1990
Labeo roseopunctatus	50	Paugy *et al.*, 1990
Raiamas steindachneri	58	Rab *et al.*, 2000
Bagridae/Claroteidae		
Auchenoglanis occidentalis	56	Agnèse, 1989
Bagrus docmak	54	Agnèse, 1989
Chrysichthys auratus	72	Agnèse, 1989
Chrysichthys maurus	70	Agnèse, 1989
Clarotes laticeps	70	Agnèse, 1989
Clariidae		
Clarias anguillaris	56	Agnèse, 1989
Clarias gariepinus	56	Teugels *et al.*, 1992
Heterobranchus longifilis	52	Teugels *et al.*, 1992
hybrid C. gariepinus x H. longifilis	54	Teugels *et al.*, 1992
Mochokidae		
Synodontis bastiani	54	Agnèse *et al.*, 1990
Synodontis budgetti	54	Agnèse *et al.*, 1990
Synodontis courteti	54	Agnèse *et al.*, 1990
Synodontis filamentosus	56	Agnèse *et al.*, 1990
Synodontis membranaceus	54	Agnèse *et al.*, 1990
Synodontis ocellifer	54	Agnèse *et al.*, 1990
Synodontis schall	54	Agnèse *et al.*, 1990
Synodontis sorex	54	Agnèse *et al.*, 1990
Synodontis violaceus	54	Agnèse *et al.*, 1990
Cyprinodontiformes		
Aphyosemion ahli	36	Scheel, 1968
Aphyosemion arnoldi	38	Scheel, 1968
Aphyosemion bivittatum	40	Scheel, 1968
Aphyosemion, bualanum	40	Scheel, 1968
Aphyosemion calliurum	26	Scheel, 1972
Aphyosemion cameronense	34	Scheel, 1972
Cyprinodontiformes (cont.)		
Aphyosemion christyi	18	Scheel, 1968
Aphyosemion exiguum	36	Scheel, 1968
Aphyosemion filamentosum	36	Scheel, 1968
Aphyosemion franzwerneri	22	Scheel, 1972
Aphyosemion gardneri	40	Scheel, 1968
Aphyosemion guineense	38	Scheel, 1968
Aphyosemion gulare	32	Scheel, 1968
Aphyosemion labarrei	28	Scheel, 1972
Aphyosemion louessense	20	Scheel, 1972
Aphyosemion lujae	40	Scheel, 1968
Aphyosemion mirabile	32	Scheel, 1972
Aphyosemion obscurum	34	Scheel, 1968
Aphyosemion roloffi	42	Scheel, 1968
Aphyosemion scheeli	40	Scheel, 1972
Aphyosemion sjoestedti	40	Scheel, 1968
Aphyosemion walkeri	36	Scheel, 1968
Poropanchax luxophthalmus	48	Scheel, 1972
Poropanchax normani	48	Scheel, 1972
Epiplatys annulatus	50	Scheel, 1972
Epiplatys barmoiensis	34	Scheel, 1972
Epipltys bifasciatus	40	Scheel, 1968
Epiplatys chaperi	50	Scheel, 1972
Epiplatys dageti	50	Scheel, 1968
Epiplatys duboisi	48	Scheel, 1968
Epiplatys fasciolatus	38	Scheel, 1968
Epiplatys sexfasciatus	48	Scheel, 1968
Epiplatys spilargyreius	34	Scheel, 1968
Nothobranchius guentheri	35	Scheel, 1981;
Nothobranchius guentheri	36	Ewulonu *et al.*, 1985
Nothobranchius kirki	36	Scheel, 1972
Nothobranchius melanospilus	36	Ewulonu *et al.*, 1985
Nothobranchius palmquisti	34	Scheel, 1968
Nothobranchius palmquisti	36	Ewulonu *et al.*, 1985
Nothobranchius patrizii	36	Ewulonu *et al.*, 1985
Nothobranchius rachovii	18	Scheel, 1981
Nothobranchius rachovii	16	Ewulonu *et al.*, 1985
Cichlidae		
Astatotilapia burtoni	40	Thompson, 1981
Aulonocara kornelia	44	Foerster & Schartl, 1987
Aulonocara huesheri	44	Foerster & Schartl, 1987
Aulonocara stuartgranti	44	Foerster & Schartl, 1987
Hemichromis bimaculatus	44	Zahner, 1977
Heterotilapia multispinosa	48	Zahner, 1977
Melanochromis auratus	46	Thompson, 1981
Alcolapia alcalica	48	Park, 1974
Oreochromis aureus	44	Kornfield *et al.*, 1979
Oreochromis karongae	38	Harvey *et al.*, 2002
Oreochromis macrochir	44	Jalabert *et al.*, 1971
Oreochromis mossambicus	44	Fukoka & Muram., 1975
Oreochromis niloticus	44	Jalabert *et al.*, 1971
Sarotherodon galilaeus	44	Kornfield *et al.*, 1979
Tilapia guineensis	44	Vervoort, 1980
Oreochromis macrochir	44	Vervoort, 1980
Tilapia mariae	40	Vervoort, 1980
Coptodon rendalli	44	Michele & Takah., 1977
Tilapia sparmanni	42	Vervoort, 1980
Coptodon zillii	44	Kornfield *et al.*, 1979
Channidae		
Parachanna obscura	34	Nayyar, 1966

Meanwhile, significant genetic differences have been observed for populations of the genus *Tropheus*, a group of Cichlidae in Lake Tanganyika that dates back around 1.25 million years, whereas these populations are only distinguishable through minor morphological variations and some marked differences in colouring. In Mormyridae, genetic distances measured using enzymatic polymorphism are greater between *Petrocephalus* populations from different West African basins than between the genera *Mormyrops*, *Pollimyrus* and *Marcusenius* which are very well-differentiated morphologically (Agnèse & Bigorne, 1992) (figure 8.11). This result shows that there is no correlation between genetic distance and morphological similarity in fish.

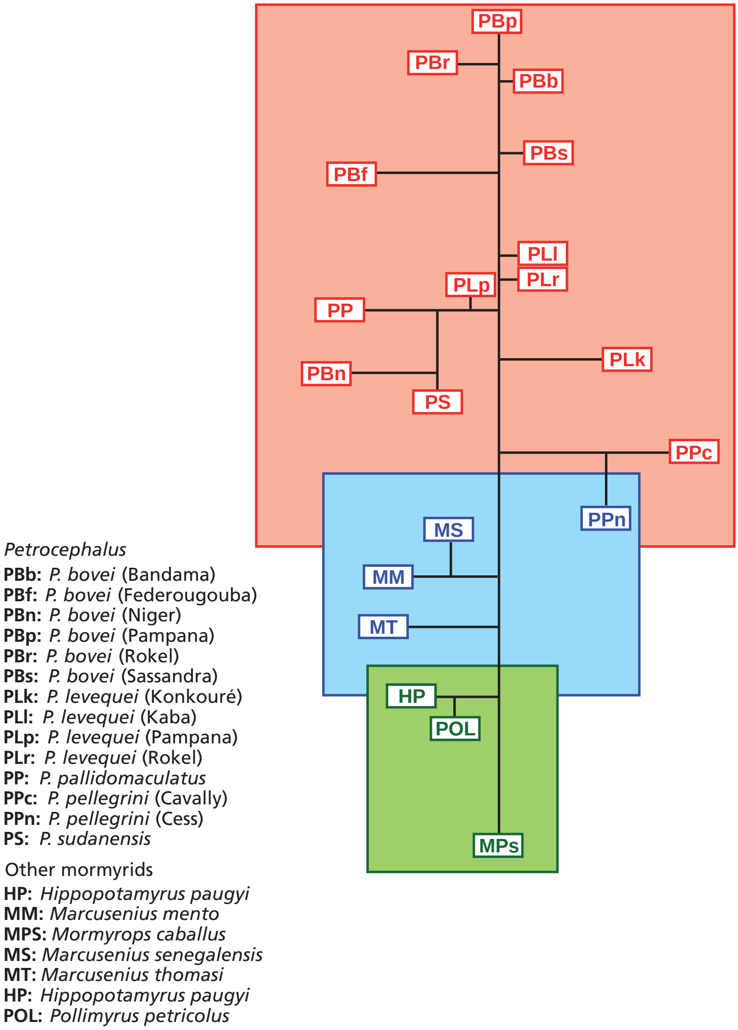


FIGURE 8.11.
Phylogenetic network of some West African mormyrids (from Agnèse & Bigorne, 1992).

Petrocephalus
PBb: *P. bovei* (Bandama)
PBf: *P. bovei* (Federougouba)
PBn: *P. bovei* (Niger)
PBp: *P. bovei* (Pampana)
PBr: *P. bovei* (Rokel)
PBs: *P. bovei* (Sassandra)
PLk: *P. levequei* (Konkouré)
PLl: *P. levequei* (Kaba)
PLp: *P. levequei* (Pampana)
PLr: *P. levequei* (Rokel)
PP: *P. pallidomaculatus*
PPc: *P. pellegrini* (Cavally)
PPn: *P. pellegrini* (Cess)
PS: *P. sudanensis*

Other mormyrids
HP: *Hippopotamyrus paugyi*
MM: *Marcusenius mento*
MPS: *Mormyrops caballus*
MS: *Marcusenius senegalensis*
MT: *Marcusenius thomasi*
HP: *Hippopotamyrus paugyi*
POL: *Pollimyrus petricolus*

Some Cyprinodontiformes species are also similar in appearance while having very different karyotypes.

The rules of classification

Classification of the living world is hierarchical, with groups included in larger sets that do not overlap. But this hierarchy can be based on different principles. Phenetic hierarchy is based on the similarity of appearance of the classified groups: number and position of fins, presence or absence of barbels, number of fin rays, etc. Phylogenetic hierarchy, meanwhile, is based on evolutionary relationship: groups are defined according to the closeness of their relationships and the age of their common ancestors. These two classification systems, which gave rise to different schools of thought, can provide concordant results but may also differ in their conclusions. The numerical taxonomy school fosters phenetic classification, whereas phylogenetic classification is supported by the so-called cladistic school.

Supporters of numerical taxonomy believe that organisms sharing common characteristics have a similar evolutionary history, but do not make hypotheses on genealogy. By using a large number of characters in a large number of individuals, and assigning them equal weights, statistical methods are expected to identify homogeneous sets. However, morphological convergences during evolution occasionally led to artificial groupings, and the biases that could be generated by statistical methods were also criticized (Ridley, 1989). This school peaked in the 1960s but lost much of its relevance since. An example of its application in African fishes was proposed by Daget (1966); he was able to establish a phenogram of Citharinidae (figure 8.12) that confirmed the empirical classification used up to that time.

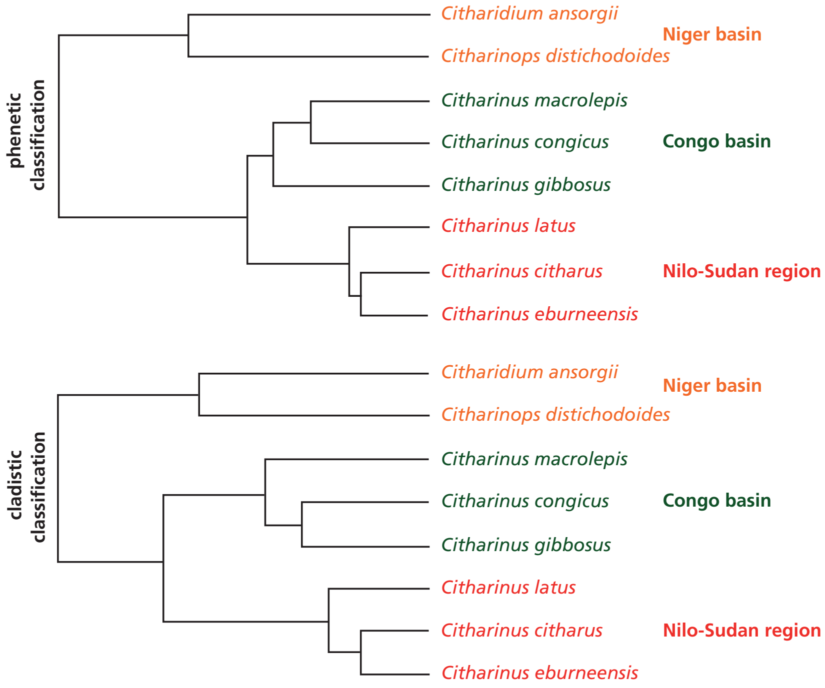


FIGURE 8.12.
Phenetic and cladistic classifications of the citharinids (from Daget, 1966 and 1980).

Cladistic classification (sometimes called Hennigean classification) is based on the principle that during evolution, an ancestral species gave rise to two daughter species. For each species, it is therefore necessary to determine with which other species it shares the most recent common ancestor, because this will form the basis for the first group. A monophyletic group is derived from a single common ancestor, whereas a polyphyletic group includes species that have similarities but are not direct descendants of a common ancestor.

Unlike phenetic relationships, phylogenetic relationships cannot be observed directly. How, then, can they be identified? The method proposed by Hennig (1950) consists of looking for characters that can be qualified as evolutionary innovations. We can thus distinguish evolved or apomorph characters in opposition to ancestral characters, referred to as primitive or plesiomorph. This method, which often used comparisons with distant groups to determine if characters were evolved or primitive, also shows a bias – it considers that evolution always proceeds from a plesiomorph state to an apomorph state, and never the reverse (Daget, 1980).

This method was also applied to the Citharinidae (Daget, 1980). We see (figure 8.12) that it would be possible to include the species *C. distichodoides* and *C. ansorgii* in the genus *Citharidium*, a sister group of the genus *Citharinus* comprising six species. A conservation measure would be to consider that the species *C. distichodoides* is perhaps not the sister species of *C. ansorgii*, and create a genus *Citharinops*. We would then have two monotypic genera which are also sister groups, and this set would be a sister group of the genus *Citharinus*. The phylogenetic proximity between *Citharidium* and *Citharinops* does not contradict the possibility of hybridization of these two species in a natural physical system as signalled by Daget (1963). Among the *Citharinus*, the group of three Nilotic species is a sister group of three other Congolese species. Phenetic and cladistic classifications lead to similar conclusions on the systematic level, which means that in the present case, the morphological similarity reflects the phylogenetic relationship. The only difference with regard to the phenetic analysis is that *C. congicus* is closer to *C. gibbosus* than to *C. macrolepis*.

Using 15 anatomical and morphological characters, Daget & Desoutter (1983) also proposed a phylogenetic classification of Polypteridae from a common ancestor. The group *Polypterus bichir-endlicheri* probably diverged very early on, whereas the monospecific genus *Calamoichthys*, with a distinct morphology compared to the others, is curiously classified with the other *Polypterus*, which could indicate that it is of recent origin (figure 8.13).

Using her own work as well as results obtained by other ichthyologists, Stiassny (1991) proposed a cladogram summarizing the current state of knowledge on phylogenetic relationships within the Cichlidae family. In Africa and South America, this family forms two sister groups. There are nonetheless indications that the genus *Tylochromis* could be the sister group of other African Cichlidae, whereas the Congolese genus *Heterochromis*, phylogenetically different from the other African species, could be a sister group of Asian Cichlidae (Etroplines). Malagasy Cichlidae (Ptychochromines) form the sister group of all other Cichlidae (figure 8.14).

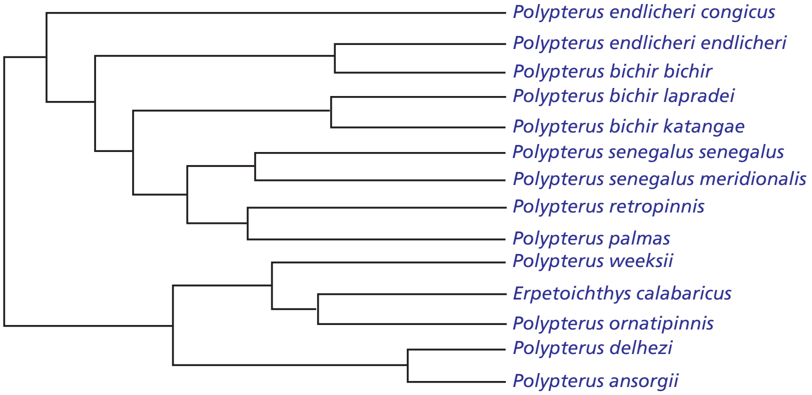


FIGURE 8.13.
Cladogram illustrating the phylogenetic relationships between the African Polypteridae (from Daget & Desoutter, 1983).

For many scientists, phylogenetic classification is currently preferred to phenetic classification, even if methods are not quite perfected. While anatomical studies have revealed both their relevance and their limitations, molecular tools currently in development are hoped to yield spectacular technical progress in coming years, thereby allowing a better understanding of the relationships between species.

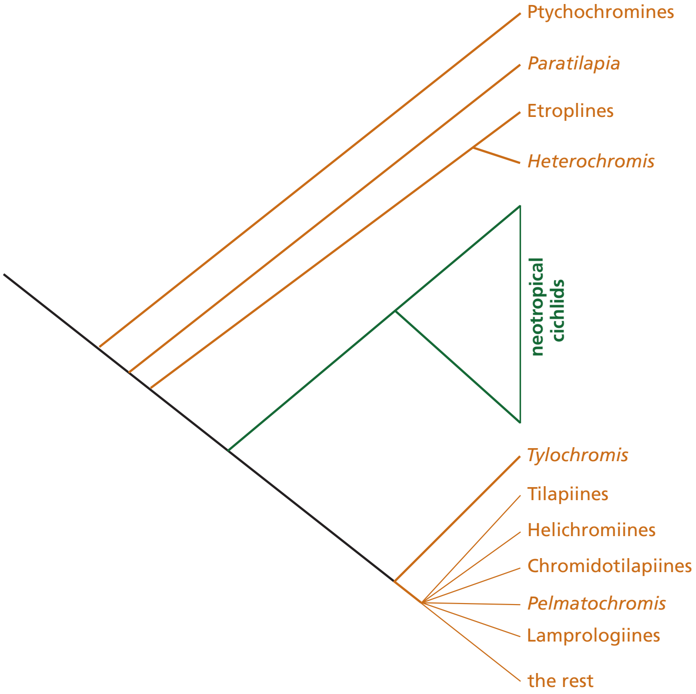


FIGURE 8.14.
Summary cladogram of cichlid intrafamily relationships (from Stiassny, 1991).

Thus, based on enzymatic polymorphism and chromosome studies, a phylogeny of West African Bagridae was proposed by Agnèse (1989) (figure 8.15). For the eight species investigated, two sister groups can be distinguished: on one hand *Bagrus* and perhaps *Auchenoglanis* which possess 54 and 56 chromosomes, and *Chrysichthys-Clarotes* on the other hand with 70-72 chromosomes. Within

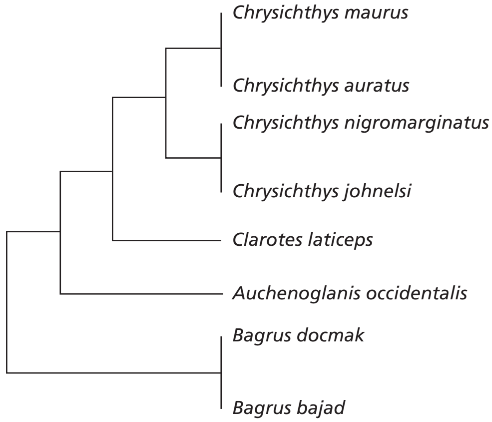


FIGURE 8.15.
Phylogenetic relationships among West African Bagridae and Claroteidae (from Agnèse, 1989).

Chrysichthys we can also observe two sister groups, the sub-genera *Chrysichthys* (*C. maurus*, *C. auratus*) and *Melanodactylus* (*C. nigrodigitatus* and *C. johnelsi*) as Risch (1986) proposed on the basis of anatomical and morphological studies. *Clarotes* is a sister group of the *Chrysichthys* and they were both separated, along with *Auchenoglanis*, in the Claroteidae family by Mo (1991).

The use of genetic markers such as mitochondrial DNA, which are more precise than protein markers, is also becoming more widespread. Kornfield (1991) managed to propose a phylogenetic classification of *Oreochromis niloticus* subspecies in East Africa, and the phylogeny of Tanganyika Cichlidae of the genus *Tropheus* was established by Sturmbauer & Meyer (1992). For other groups, phylogeny was determined thanks to molecular biology techniques. This is the case for the Mormyridae whose familial phylogeny was defined (Lavoué, 2001), and for the Alestidae, for which group monophyly was underscored, confirming the clearly individualized status of this strictly African family (Calcagnotto *et al.*, 2005; Hubert *et al.*, 2005a and 2005b). In the same way, some families with an indeterminate status could be grouped together afterwards. For instance, within the Gonorynchiformes, the monophyly of the Cromeriidae, Grasseichthyidae, and Kneriidae has been proven (Lavoué *et al.*, 2005).

A fairly recent study on the phylogeny of the Protopteriformes highlights the monophyly of the African forms of the genus *Protopterus* (Tokita *et al.*, 2005). Within this genus, three clades are identified: *P. amphibius* (Eastern province), *P. dolloi* (Congolese and Lower Guinea provinces) and *P. aethiopicus*/*P. annectens* (*P. aethiopicus*: lakes Victoria, Edouard, Tanganyika and Albert; *P. annectens*: Nilo-Sudanian province). However, the differentiation of each of these three units does not enjoy strong support.

It has long been thought that the divergence of the three Protopteriforme genera followed the fragmentation of Gondwana (see chapter *General characteristics of ichthyological fauna*). *Protopterus* and *Lepidosiren* (Amazon) have always been considered sister groups, and analysis of all the species in this study confirms it. The authors' hypothesis on the closeness of relationships among the species is based on the more or less sustained presence of a neotenic character, the external gills. According to them, this character is not generated during the ontogeny of *Neoceratodus* (Australia), disappears rapidly in the juveniles of *P. dolloi* and *P. aethiopicus*, but can persist longer in *P. annectens* and even remain in the adult *P. amphibius*.

THE CLARIIDAE: AN EXAMPLE WHERE MORPHOLOGICAL DIFFERENTIATION DOES NOT NECESSARILY REFLECT EVOLUTIONARY HISTORY

JEAN-FRANÇOIS AGNÈSE

The genus *Clarias* Scopoli 1777 is an interesting example of a fairly well-defined group in terms of appearance based on a set of morphological criteria, whereas they actually represent a discontinuous evolutionary unit. Günther (1864) defined the genus *Clarias* based on about ten characters including the shape of the gill accessory organ, the presence of a spine in the pectoral fin, and the absence of an adipose fin.

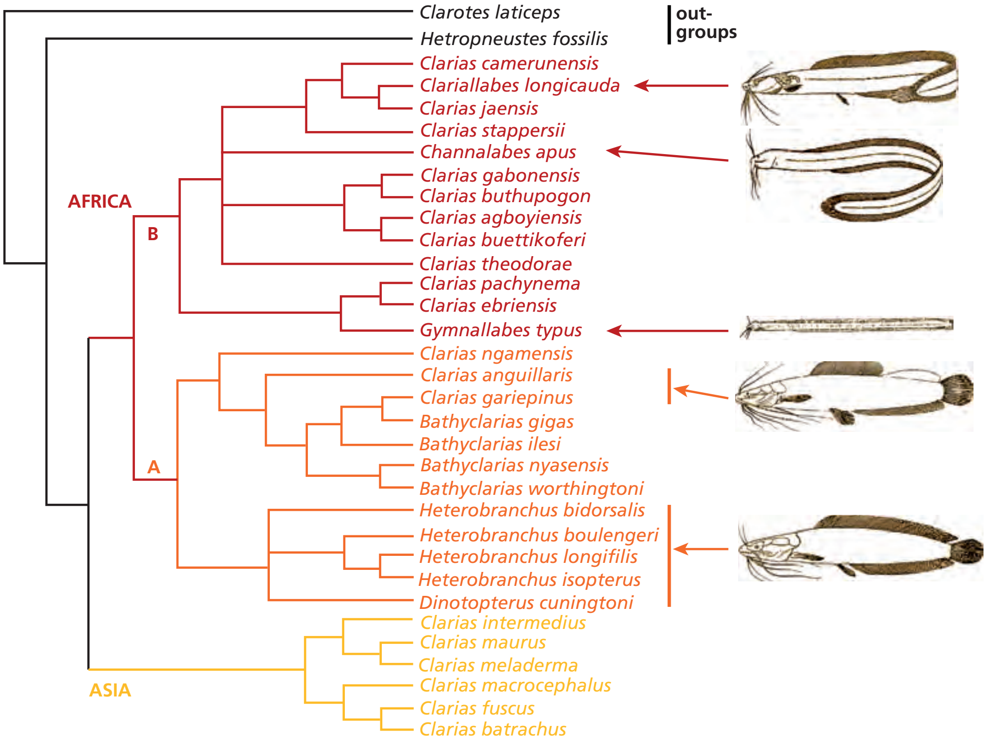
Although Teugels (1986) had recognized six sub-genera within *Clarias*, this genus appeared to be composed of a set of closely-related species from an evolutionary viewpoint.

Recently, a number of phylogenetic reconstitutions carried out using mitochondrial markers clearly showed that the genus *Clarias* was in fact extremely paraphyletic (Agnèse & Teugels, 2000, 2001, 2005) (figure 8.16). Some species that are currently classified in other genera of the Clariidae family (because they are highly differentiated morphologically), are in fact very closely related genetically to species of the genus *Clarias*. Among the Clariidae, it thus seems that there is no link between morphological differentiation and genetic differentiation.

As a result, morphological criteria are inadequate for classifying species in one genus or another, and a revision of the family that takes genetic affinities into account is now needed.

FIGURE 8.16.

Phylogenetic relationships among Clariidae species.
Morphological and osteological evolution (in this example "anguilliform body") in Clariidae did not follow an orthogenetic series (from Agnèse & Teugels, 2005).
Group A represent the "big head and numerous fins" species, eel-like species are only found in group B.
Sketches of species with particular body shapes are represented on the right side, arrows indicated their position in the tree.



Moreover, genetic differentiation is not necessarily linked to morphological differentiation, as seen in the Clariidae (Agnèse & Teugels, 2005). In this case, it was shown that the 'anguilliform' criterion of some species was a character independent of the phyletic groups to which they belong. It clearly seems to be an adaptive response that appeared independently in several groups (see box "The Clariidae: an example where morphological differentiation does not necessarily reflect evolutionary history").

The genus concept

While the notion of the species concept is relatively clear, despite some difficulties related to the concept's implementation, how about higher taxonomic levels? Are they conventional sets, or can they be defined on a similar basis as that used to distinguish species?

According to the principles of taxonomy, each species must belong to a genus, which is a category comprising at least one species or according to the principles of phylogenetic classification, a monophyletic group of species. Obviously, the principle of interbreeding cannot be used to define higher taxonomic levels.

On the other hand, we can distinguish morphologic sets, with the attendant uncertainties (bias resulting from convergences, for instance) regarding their affiliation to the same evolutionary line.

The improvement of ideas about classification and the lack of standardization in defining taxa higher than species gave rise to a certain anarchy, and led to many nomenclature changes as a result of advances in knowledge of phylogenetic relationships. It was suggested (Dubois, 1988) that the genus should constitute a discontinuous evolutionary unit that could be defined through a set of genetic, phylogenetic, and ecological characters.

An interesting example is that of the genus *Tilapia sensu lato* that Trewavas (1983) split into three genera based on their reproductive behaviour:

- *Tilapia sensu stricto* which lays eggs on substrate;
- *Sarotherodon*, which includes paternal and biparental mouth breeders;
- *Oreochromis* which includes only maternal mouth breeders.

This classification, based on behavioural aspects, sets itself apart from the conventional approach based on morphology and anatomy. It aroused many reactions, and Thys van den Audenaerde (see Teugels & Thys van den Audenaerde, 1992) long argued that it was preferable to not split the genus *Tilapia* according to these criteria. This debate attracted the interest of molecular biologists, and results of genetic studies showed on the whole that Trewavas' division was quite right from the phylogenetic viewpoint, with a few exceptions for species such as *Sarotherodon galilaeus* that is close to *Oreochromis* (Sodsuk & McAndrew, 1991; Pouyaud & Agnèse, 1995) and *S. melanotheron*, the sole paternal incubator among the *Tilapia* (Seyoum, 1990; Pouyaud, 1994) and whose position is indeterminate.

Higher classification of African fishes

In this chapter, the classification schema above genus level is limited to the ranks of class, order and family. This has the advantage of simplicity, but ignores some important groups in fish phylogeny such as Chondrichthyes, Teleostei, Acanthomorpha, and Percomorpha.

In general, it follows Nelson's "Fishes of the World" (2006) with the notable exception of Elasmobranchii and Holocephali being elevated to class rank. But at family level, we may follow Eschmeyer's "Catalog of Fishes", as it is updated more frequently to integrate new stable groupings.

Wiley & Johnson published a new classification for Teleostei (2010). They proposed the stabilization of several recent or (much) older published hypotheses by listing known evidence (synapomorphies). We will follow this new arrangement as soon as the ichthyological community endorses it, e.g., through publication in a subsequent edition of Fishes of the World. In the meantime, to avoid confusion for non-specialists, we shall continue to use the current one.

We adopted the rules followed by FishBase, as it is currently the better updated database.

Note that the numbers of species given below do not take subspecies into account.

For the world as a whole, total count of genera is 5,056 and total count of species is 33,148

The origin and evolution of species could be reconstituted through the study of fossils. Like all palaeontological investigations, conclusions from such studies can be called into question upon the discovery of new deposits and new fossils. Current hypotheses must thus be viewed as conclusions based on the current state of knowledge rather than statements of fact.

We have also seen that for existing fishes, systematics has far from resolved all issues, and the introduction of new molecular techniques in phylogenetic classifications will probably lead to changes in these classifications, most of which were established using anatomical and morphological criteria. Moreover, ichthyologists are not always in agreement regarding the proposed novel phylogenies, which complicate the situation. There is nevertheless a sort of consensus for the broad lines of the fish classification that we present here.

The oldest known fish remains date to the Cambrian (over 500 million years ago). A form of lamprey, *Hardistiella montanensis*, from the Upper Carboniferous was found in Montana, USA (-325 M.A.), but a fossil that may have been related to lampreys, *Haikouichthys ercaicunensis,* was found in Lower Cambrian layers in Yunan, China (-530 M.A.) (Lecointre & Leguyader, 2001). Jawless fishes (Agnatha, still represented today by lampreys) and Placodermi initially dominated but gave way to bony and cartilaginous fishes in the late Devonian and Carboniferous (-400 to -350 million years) eras, during which they diversified greatly in seas and freshwaters. New groups, the holostei, then radiated during the Triassic (-250 to -210 million years) and Jurassic (-210 to -150 million years), followed by teleosts during the Jurassic and Cretaceous. The radiation of teleosts is behind most of the marine and freshwater species that we know today.

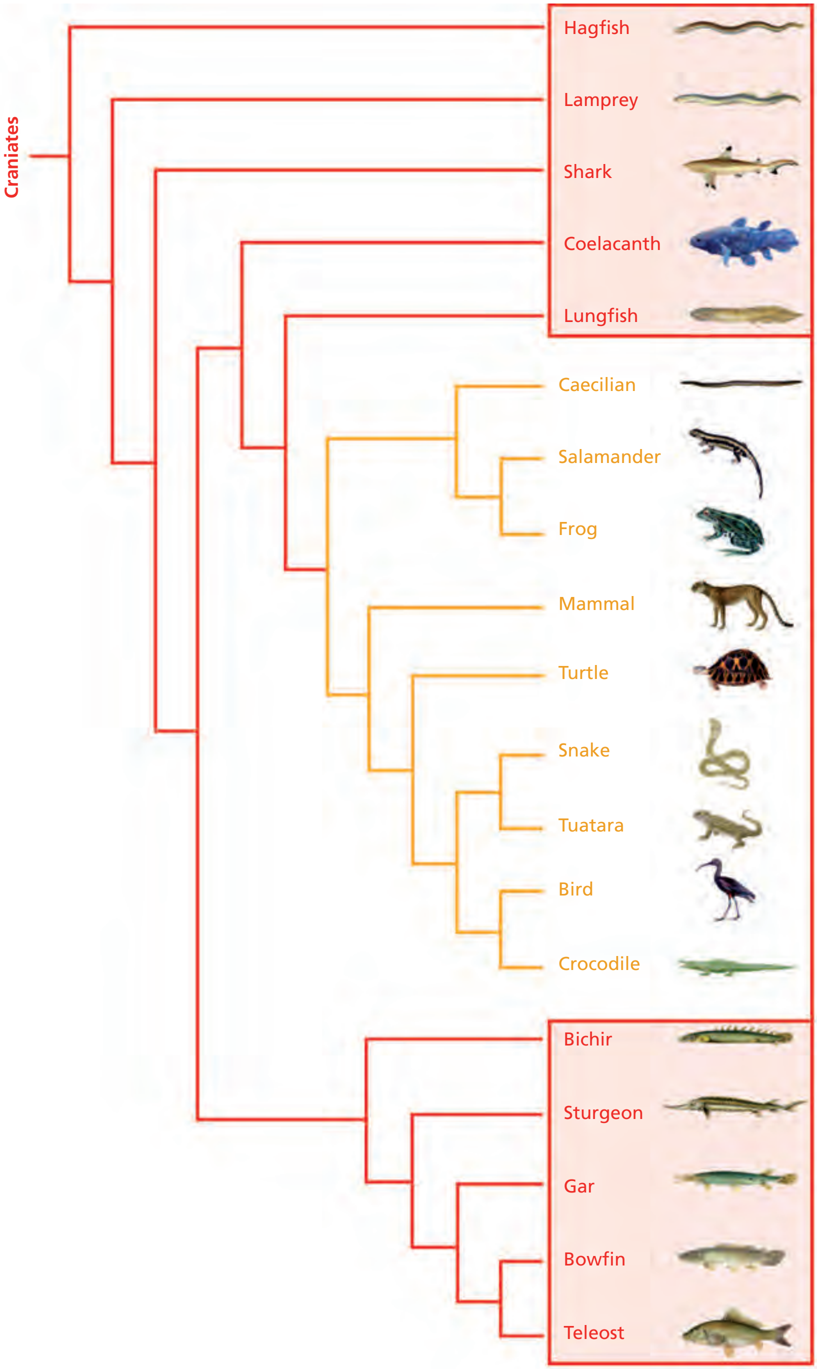


FIGURE 8.17.
Cladogram representing the phylogeny of the major living group of current craniata (from Lecointre & Le Guyader, 2001).

We shall only mention the Myxini (hagfish: 1 family, 6 genera, 78 species) and the Cephalaspidomorphi (lampreys: 3 families, 10 genera, 47 species), two jawless Craniata that do not exist in the inter-tropical zone. Forms likely to be encountered in Africa belong to the Gnathostomata, that is, jawed vertebrates.

The **Elasmobranchii** contain the craniata with cartilaginous skeletons, commonly known as rays or sharks. From a phylogenetic viewpoint, these "fishes" are very distant from the bony fishes (see box "Systematic ichthyology"; figure 8.17).

The **Osteichthyes** include other vertebrates including bony fishes that are unevenly distributed in two groups: the Sarcopterygii (lungfish and cœlacanth, but also mammals, birds, squamata, etc.) and the Actinopterygii (or ray-finned fishes).

LIVING FOSSILS

Groups of archaic fish can still be found on the African continent. The best-known of these is certainly the **cœlacanth** which, in the sixties, was the star of a media frenzy. We shall not devote much space to this species, which remains oceanic and therefore distant from our continental concerns. It is worth noting that this very ancient group, which appeared in the Devonian (400-350 10^6 BP) and disappeared at the same time as the dinosaurs (around 70 10^6 BP), was once found throughout the planet and thought to have lived in fresh waters.

Polypterus or bichir: this group is endemic in Africa. The only known fossils were also found in Africa (135-65 10^6 BP) in the same area of distribution as modern species. These fishes have a swim bladder whose highly vascularized wall serves as a "lung" that allows the animal to survive in oxygen-poor waters.

Note as well that juveniles have external gills (see box "Polypterids", chapter *Geographical distribution and affinities of African freshwater fishes*).

Lungfishes currently exist in the Amazon (*Lepidosiren*), Australia (*Neoceratodus*), and Africa (*Protopterus*).

African *Protopterus* can survive during dry periods by entering a state of aestivation.

To do so, *P. annectens* burrows a tunnel into the mud when the water level begins to go down but before the water dries out completely.

Once the water goes below the level of the tunnel opening, the animal blocks the entrance with mud then goes to the end of the tunnel, where it covers itself with a layer of integumentary mucus that hardens and forms a cocoon to keep itself moist. Thus protected, the lungfishes can live for up to four years in the cocoon, using their own muscle fibres as food.

Like their South American cousins, African lungfish larvae have external gills whose level of development depends on the water's oxygen content.

As the juveniles age, the external gills are generally resorbed and the fish breathe using their lungs and internal gills.

Among the **Sarcopterygii**, the **lungfishes** or **Dipnoi** are the oldest freshwater bony fishes, and their origins can be traced to the Devonian (Rosen *et al.*, 1981) (see box "Living fossils"). The swim bladder is connected to the oesophagus and can serve as a lung. They were represented by many forms in the primitive era, but only a few species survive, including those belonging to the genus *Protopterus* in Africa.

Recent studies have shown that the mitochondrial DNA of Protopteridae is closer to an amphibian's DNA than to a coelacanth's, which tends to support the hypothesis that terrestrial vertebrates could come from a split in a line that gave rise to lungfishes (Meyer & Wilson, 1990). Dipnoi would thus be the sister group of tetrapods (figure 8.17).

The Polypteridae are currently considered to be the earliest line of **Actinopterygii**. Their bodies are covered with bony scales. The swim bladder can serve as an accessory respiratory organ. Juveniles possess arborescent external gills that disappear in adults, and which are perhaps morphological characteristics of primitive Actinopterygii. In the past, this primitive character misled zoologists into classifying them away from Actinopterygii, and even placing them among Sarcopterygii.

In continental Africa, the Actinopterygii comprise the majority of other families and species grouped among the teleosts, whose most ancient known fossil, *Pholidophorus*, dates to the lower Triassic (-195 Myrs). This extremely diverse

SYSTEMATIC ICHTHYOLOGY

The term "fishes" is not scientific and in any case refers to a grade, that is, a group without its own history. In fact, the relationship is not stronger between a teleost and a shark (figure 8.17) than between birds and bats, or even some flying or gliding reptiles or fishes. We could even note that they are in truth more distant. In concrete terms, "fishes" comprise a vast heterogeneous set traditionally defined as legless craniata.
This definition is fitting, if, like Nelson (1994) or more recently Lecointre & Le Guyader (2001), we agree that this current fauna includes:

- Myxini or hagfish (without vertebrae or jaws)
- Cephalaspidomorphi = lampreys (jawless)
- Elasmobranchii = cartilaginous fishes (sharks, rays)
- Actinopterygii = ray-finned fishes
- Sarcopterygii = vertebrates with fleshy members (cœlacanth and lungfishes, closer to tetrapods than to the other "fishes")

Until around the 1960s, this "fishes superclass" was considered a valid taxon, owing to lack of recognition or use of phylogenetic criteria.
The shift from a purely utilitarian classification to a phylogenetic one only took place later, even though the Darwinian theory of evolution (Darwin, 1859) had already been long accepted.
It appears that the situation only moved forward after the translation of Hennig's method (1966).
Cladistics – which is what we are discussing now – has the advantage "(…) of highlighting the feasibility – or refutability – of a theory of phylogenetic relationships" (Janvier, 1986).
Following the palaeontologists, palaeoichthyologists and ichthyologists rapidly began using cladistics and, in doing so, gained an advantage over other disciplines involving vertebrates.
The classification of "fishes", by becoming phylogenetic, was obviously going to be overthrown. As such, compared with previous classifications (Bertin & Arambourg, 1958) that still served as the reference until recently, things changed considerably, particularly under the initial impetus of Greenwood *et al.* (1966) which was a sort of pre-cladistics classification that was not informed by the works of Hennig.
Even if the classifications can be debated, it is mentally easier to arrange taxa in categories that include groups or species that have the most similarities.
As such, the notions of species, genus, family, or even order are still generally accepted or tolerated by the cladistic school.
We have summarized data on current forms following the structure orders/families/genera/species in table 8.II which is necessarily incomplete, as not everything is known, and reflects only the specific interest focused on the different taxa.
Thus, we have cause to believe that the number of mammal and bird species is close to being accurate, which is certainly not the case for amphibians and fishes, for which the number of species is by all indications underestimated.

TABLE 8.II.
Number of Craniata known at the present time.

Craniata	Common name	Order	Families	Genus	Species
Hyperotreti	hagfishes	1	1	6	78
Claspidomorphi	lampreys	1	3	10	47
Elasmobranchii	sharks, rays	12	51	190	1164
Holocephali	chimera	1	3	6	50
Aves	birds	28	163	1 975	9 672
Crocodylomorpha	crocodiles	1	3	8	23
Squamata	lizards, snakes	1	31	821	6 850
Sphenodontida	tuatara	1	1	1	1
Testudines	turtles	1	13	75	290
Synapsida	mammals	20	133	1 041	4 496
Amphibia	frogs,newts	3	34	398	4 975
Dipnoi	lungfishes	2	3	3	6
Actinistia	coelacanth	1	1	1	1
Polypteriformes	bichirs	1	1	2	14
Acipenseriformes	sturgeons	1	2	6	27
Lepisosteiformes	gars	1	1	2	7
Amiiformes	bowfin	1	1	1	1
Teleostei	teleosts	42	482	4 829	31 752
total		**119**	**927**	**9 375**	**59 454**

group in fact represents the overwhelming majority of modern fishes. There are several major subdivisions, some of which are represented in continental Africa (Wiley & Johnson, 2010):

- **Osteoglossomorpha** (bony-tongued fishes) including the most primitive of modern teleosts. They have been known since the late Jurassic and are currently represented by five families in Africa (figure 8.18);
- **Elopomorpha** comprises different families and species that are almost exclusively marine, but which can occasionally penetrate into freshwater. Eels belong to this group;
- **Otomorpha** is composed of 4 large monophyletic groups:

– **Clupeiformes**, which appeared in the lower Cretaceous. They include primarily marine species, but some have adapted to freshwater;

– the order **Gonorynchiformes** which has 3 families in Africa, including the Kneriidae (which now covers the former Cromeriidae and Grasseichthyidae families) and two other families represented by a single species (Phractolemidae and Chanidae);

– the order **Cypriniformes** whose origin is under debate;

– the order **Characiformes** represented by numerous species. The origin of the Characiformes and the Cypriniformes could date back to the end of the Cretaceous or the Palaeocene (Cavender, 1991);

– the order **Siluriformes** (catfishes) forms a highly characteristic group of fishes with scale-free bodies and bony spines in their dorsal and pectoral fins.

- the **Euteleosteomorpha** including the majority of species, in particular:

– the **Osmeriformes** represented by a single family (Galaxiidae) in Africa;

– the **Cyprinodontiformes** including numerous fresh and brackish water species.

– the **Synbranchiformes** represented by two families: the Synbranchidae of marine origin, and the Mastacembelidae (spiny eels) that were formerly classified among the Perciformes (Travers, 1984).

– the **Perciformes** which is poorly defined and whose classification is unclear and problematic, as it is probably not a monophyletic grouping. In total it includes 150 mostly marine families, some of which have adapted to continental waters. This is the case in particular for the Cichlidae, Latidae, Nandidae, and Anabantidae. The Cichlidae probably appeared very early in the Cretaceous and their evolution was already well on its way prior to the separation of Gondwana (Stiassny, 1987; 1991).

– the **Pleuronectiformes** and the **Tetraodontiformes** including families of marine origin of which certain species have adapted to freshwater. The Tetraodontiformes and Pleuronectiformes appeared in the lower Eocene and mostly include marine forms.

Advances in African freshwater ichthyology

Currently 3,360 species of fresh and brackish water fish have been described from Africa, belonging to 95 families (Lévêque *et al.*, 2008). Numerous other species collected in the East African lakes are awaiting description.

The knowledge of the ichthyological brackish and freshwater fauna in Africa is a very long story (Paugy, 2010a). From the time of the Ancient Egyptians to the present, more than 3,300 species (95 families and 542 genera) have been discovered, drawn and described. Michel Adanson (mid-18th century) initiated the first material collections during the eighteenth century. During the 19th century, the work of travelling scientists (Étienne Geoffroy Saint-Hilaire, Andrew Smith) and explorers (including Mungo Park, Pierre Savorgnan de Brazza and Henry Morton Stanley) added substantially to developing zoological collections from their field trips. At that time, many species descriptions were based on fish preserved in these collections. Towards the end of the 19th and into the early part of the 20th century, knowledge of African fishes was greatly enhanced, especially through the work of Georges A. Boulenger, Albert C.L.G. Günther and Franz Steindachner who, respectively, described 640, 119 and 53 species. Boulenger did visit Africa once during his life, in 1905 when he went to Cape Town for a conference. With this one exception, none of these scientists ever travelled to Africa themselves. In contrast to those of the previous century, the majority of naturalists of the 20th century who were interested in African fishes took part in collecting expeditions. The majority of the naturalists working in Africa during the middle and later parts of the 20th century tended to specialize in particular groups.

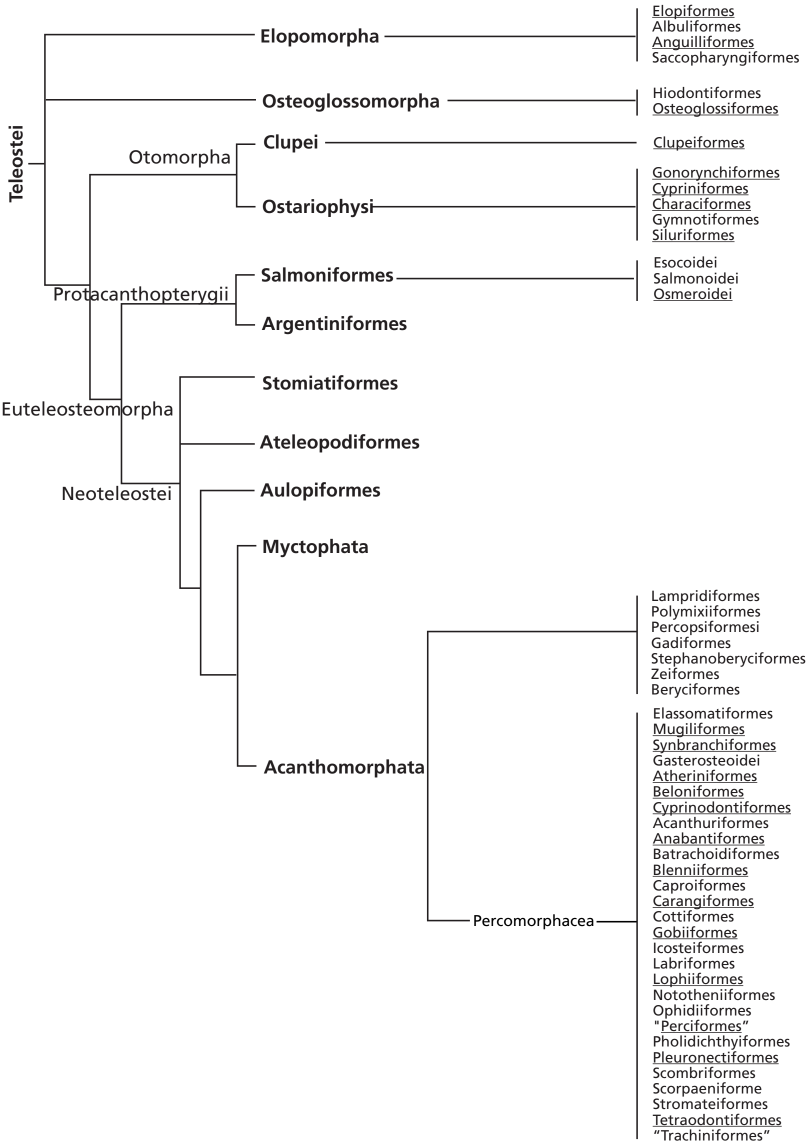
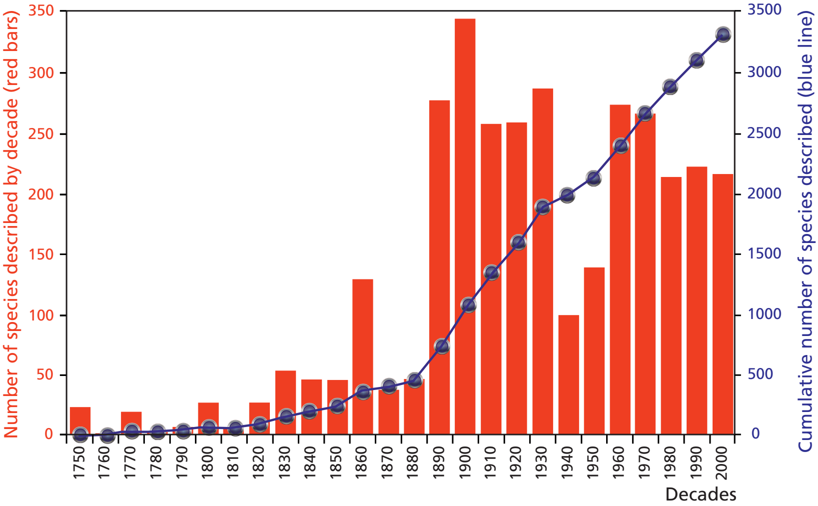


FIGURE 8.18.
Cladogram representing the phylogeny of the major living group of teleosts (adapted from Wiley & Johnson, 2010). In the right column, taxa existing in inland Africa (fresh and brackish waters) are underlined.

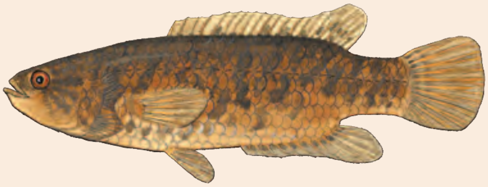
Thanks to these naturalists the number of known African freshwater fish species reached 1,900 before the Second World War, 2,150 at the end of the 1950s and finally more than 3,300 at present (figure 8.19). In addition to conventional systematic studies, there was a steady rise in the number of contributions dealing with genetics, specific parasites, and electrophysiology, amplifying fish identification using criteria other than morphology. These methods have proved helpful in finding explanations for the radiation of cichlids in the Rift Valley Lakes of East Africa. Blending all these methods, descriptions of hitherto unknown species continue to be published (see also chapter *General characteristics of ichthyological fauna*).

FIGURE 8.19.
Number of African freshwater fish species currently described (updated from Paugy, 2010a).



Most of the African continent has remained above sea level since more than 600 Myrs ago (Precambrian). Such a long period of land emergence may explain the diversity of the freshwater fish fauna and its unparalleled assemblage of so-called archaic families of which most are endemic.

Life-history strategies



Didier Paugy

Christian Lévêque

Fabrice Duponchelle

The biological and demographic profile of a population is defined by a set of biological traits such as age or size at first reproduction, fecundity rate, lifespan, mortality rate of each age group, etc. This demographic profile represents a certain adaptation of a population to its environment. The theory of adaptive strategies is based on the assumption that demographic, ecological, ethological and physiological features of a population are co-adapted and modelled by natural selection.

Since environmental changes are continuous, each state of adaptation is only provisional, and the sustainability of a species depends on its aptitude for adapting its demographic strategy to new environmental conditions in order to maintain large populations.

Over the last forty years, several studies have tried to explain the origin of variability of characters among organisms. The various methods of reproduction and their degrees of success in various environments thus formed a basis for theoretical and empirical research referred to as "life history".

Life history studies attempt to explain the trade-off between reproductive and demographic parameters (Stearns, 1983a; Reznick, 1985; Pease & Bull, 1988) in relation to various environmental conditions (Whittaker & Goodman, 1979; Winnemiller & Rose, 1992).

Resource allocation: constraints and compromises

One of the principal ideas of the concept of demographic strategy is that various biological features are interdependent. A fundamental point is the comprehension of how and to what point an organism is willing to invest into each bio-demographic option in order to optimize the use of the resources and their distribution among its various fundamental needs. In other words, each organism has limited time and energy to survive and reproduce. What is thus the ideal resource partition in regards to time and energy for growth, maintenance and reproduction? This allocation of energy among these requirements must be equitable in order to enable the species to optimize the success of its reproduction.

The current theories consider that the evolution of biological features generally involve compromise. An increase in the time (or energy) devoted to an activity will be done at other activities' expense. Thus, for a similar availability of resources, an increase in the investment in gamete production is characterized by reduced growth and accumulation of reserves, which certainly induces a lower survival probability. Conversely, by minimizing the necessary energy for searching and capturing prey, fish will have more energy to devote to growth and metabolism (Hart, 1986). This concept of compromise is particularly important in current theories of evolution concerning biological factors. In such an ecological context, an organism may carry out various possible compromises. The theory makes the assumption that an organism will choose the optimal solution, *i.e.*, that which will provide the best possible adaptation to the conditions of the environment in which it evolves.

The main goal of studying bio-demographic strategies has been to understand the adaptive value of biological factors such as fecundity, age at first reproduction, survival and mortality rates in relation to the conditions of the environment inhabited by these populations. In other words, the selective pressure of the environment moulds the demographic structure of a population and the morphological and physiological characteristics of the individuals. The gamble therefore is to identify the factors and the mechanisms responsible for selecting various combinations of biological or demographic features (Barbault, 1981).

This gives rise to the need to understand the processes behind selection and biological responses in the context of dynamic relationships between populations and environments. It is assumed that biological systems contain sufficiently flexible mechanisms to respond to the fluctuations of the environment. Slobodkin & Rapoport (1974) illustrated the scenario of an organism confronted with an environment in the course of its evolution as a game it plays against nature, where its success is measured by the duration of time it remains in the game. In other words, an individual loses the game when it can no longer reproduce and a population loses the game when it becomes extinct.

At what point are biological characteristics such as fecundity or mortality rates of different ages likely to be modified by the changes in the environment inhabited by an individual? The nature of the adaptive response depends on the scale of time considered compared to the generation time. However there are limits within which adaptations are possible due to constraints that an organism cannot entirely transcend. These constraints may be consequences of the phylogenetic history of the species which resulted in limitations on possible options. Others are of a genetic nature because any evolution requires a certain degree of variability related to the genome. They may also be of a physiological, mechanical, ecological or behavioural nature, enabling organisms to withstand short-term changes in the environment, or of physiological or biochemical nature if these changes persist. In general, fish respond to changes in the environment in two ways:

- by phenotypical plasticity of behavioural and/or physiological nature enabling it to counteract the changes of the environment;
- on a population level, where selection of more competitive genotypes occur vis-a-vis the new environmental conditions.

During successive generations their descendants form a larger proportion in the population whose genetic pool thus becomes modified by natural selection.

A priority: assurance of descent

The reproductive success of individuals is determined by the manner in which they reallocate time and energy investments as a response to changes occurring in the environment, due to their effects on survival and reproduction. This search for compromise between various biological requirements is aimed at optimizing the selective value ("fitness"), *i.e.*, the relative contribution of an individual to future generations. Individuals that possess the highest fitness are those that produce the greatest number of descendants compared to less adapted individuals within the population. The individuals that provide the greatest proportion of descendants are also those that have the greatest influence on hereditary characters in this population (Begon *et al.*, 1996). Survival, fecundity and the generation time are the principal components of "fitness" (Winemiller & Rose, 1992).

Major types of demographic strategies: theory and empiricism

Theoretical studies and their predictions

The majority of theoretical studies are based on the postulate that natural selection tends to optimize reproductive effort of each age so that fitness (*i.e.*, "selective value, reproductive success and/or sustainability of descent") of individuals and the population at large is optimized. In order for this to happen, natural selection would act by adjusting certain parameters (fecundity, age and size at first maturation, etc.) depending on prevailing ecological conditions, thus constituting a "vital strategy".

Theoretical studies are based on mathematical models which analyse methods by which fitness is maximized. Most of these mathematical models use "r", which is the "Malthusian parameter" as a measure of fitness, and apply the assumption that age distribution is stable.

Cole (1954) commended the use of mathematical models in the study of the evolution of life strategies. He also asserted the need for a simple demographic procedure which consists of varying one parameter and considering the others to be fixed in order to evaluate the consequences of a variation of this parameter.

One of the basic hypotheses shared by all theorists relates to the cost of reproduction (the most recent include Reznick, 1985; Winkler & Wallin, 1987; Stearns, 1992; and Blondel, 1995).

Every organism had a fixed quantity of a limited resource at its disposal which it must distribute between reproduction, growth and maintenance. This theory is very important for species that have an indefinite growth.

The question lies in understanding what would be, for different organisms, the optimal investment in reproduction in a given environmental condition. Two major approaches have been applied to life history studies (Stearns, 1977):

- "deterministic models" (Cole, 1954; Mc Arthur & Wilson, 1967; Southwood *et al.*, 1974), which predict that organisms exposed to high mortalities regardless of their initial density experience large fluctuations in population density or repeated episodes of colonization, evolving towards earlier maturation, larger ranges, increased reproductive effort and a shorter life-span than organisms exposed to a density-dependent mortality or a constant population density.
- "stochastic models" (Murphy, 1968; Schaffer, 1974b) which predict the evolution of the same combination of traits, although for different reasons. When environmental variability involves a highly variable juvenile mortality, the following combination of traits would emerge: late maturation, decreased reproductive effort and increased longevity.

Fitness and variation of reproductive effort with age

Increase of reproductive effort with age leads in theory to better reproductive performance for each age (Gadgil & Bossert, 1970). This effort however also leads to a reduction in survival and growth, and thus to a consequent reduction in the contribution to reproduction in successive ages. That said, many authors (review by Giesel, 1976) consider that, except for animals with unlimited growth such as fish, the reproductive effort increases to a peak then decreases with age.

Fitness and parental investment in offspring

How much energy should be invested in caring for young? If the energy allocated per offspring increases:

- the number of offspring produced decreases;
- the size of offspring at birth increases;
- the individual fitness of offspring increases.

Fitness and iteroparity/semelparity

Semelparity is the reproductive strategy where individuals reproduce only once during their lifetime, while iteroparity refers to several reproductions during one lifetime.

The existence of organisms presenting such varied reproductive strategies aroused the curiosity of scientists studying the evolution of vital cycles such as Cole (1954), who tried to determine why iteroparity, although apparently advantageous, is not common in organisms. In a relatively stable environment, iteroparity would be the least effective manner to increase the intrinsic growth rate of a population (and thus its fitness), but in a variable and unstable environment, where chances of reproductive success are weak, iteroparity supports fitness. Iteroparity is also more advantageous for species which attain their first sexual maturity later than others and which produce small offspring.

Structures of mortality per age group were incorporated thereafter in the theory. A invariable environment or high juvenile mortality would generate an evolutionary pressure for multiple reproduction (iteroparity) whereas a variable or high adult mortality would imply few reproductions or even only one reproduction (semelparity) (Murphy, 1968).

Fitness and age at first sexual maturity

The ascent to sexual maturity represents a critical phase in the life of an individual. Initially, resource and time are allocated uniquely to survival and growth and are thereafter subjected to trade-offs between reproduction, growth and survival (Wootton, 1979).

The age of first spawning is one of the most important life history traits because it constitutes one of the main evolutionary adjustments imposed by natural selection (Cole, 1954; Roff, 1984). A decrease in the age at first maturity can significantly increase fitness by maximizing the number of offspring produced at early ages. In fact, the age of first spawning is the parameter that has the greatest impact on fitness (Noakes & Balon, 1982). If there is juvenile survival due to environment variability, reproductive performance decreases and first maturity is delayed. Conversely, if environment variability acts against adult survival, the reproductive effort increases and the first breeding occurs earlier (Schaffer, 1974b).

Fitness and resource availability

In theory, for a population limited by resource, a resource increase must lead to an increase of reproductive effort at all ages for iteroparous organisms and a decrease in the age of first maturity for semelparous organisms (Gadgil & Bossert, 1970).

Boyce (1979) presents a model that analyses the effects of seasonal changes in resource availability on the evolution of life histories. In a constant environment, natural selection favours the population whose individuals have a high growth rate (r) if the resource is abundant, and a low need of food if the resource is limited. In a seasonal (*i.e.,* variable) environment, the population that has the best fitness maximizes the ratio between benefits (growth) during favourable periods and loss (decrease) during unfavourable conditions. The model shows that, whatever the life cycle, the growth rate of the population (r) and carrying capacity (K) decrease when the environmental variability increases. Thus, when seasonality tends to decrease the chances of reproductive success, natural selection favours individuals that present a low reproductive effort and allocate a more significant part of their resource to other functions (e.g. growth). In return, this scenario increases survival chances for future reproduction (Schaffer, 1974a and b; Boyce, 1979).

Fitness and fecundity

With regard to the reproductive strategies, most mathematical models use "r" as the fitness index. Thus, they are based on the hypothesis of a stable age distribution, which is never the case in the field. If we consider the effects of the interaction between age and fertility on fitness, it is observed that populations with closer age and fertility distributions will have the largest rate of increase and the largest reproductive success in the long term (Giesel, 1976). Thus, populations with a majority of old individuals should breed later and should have a late fertility. Conversely, those with a "young" age distribution should have an early fertility distribution.

Phenotypical plasticity in the life history theory

Although very few theories take phenotypic plasticity (the ability to respond quickly) to environmental variability into account, a majority of authors agree that it is one of the determinants of life histories and that it contributes to increase fitness. Whether the conditions are favourable or not, it allows organisms to maximize reproduction. Thus progeny will be perpetuated against environmental heterogeneity.

A single genotype may show several potential phenotypes if it is exposed to environmental conditions included in its reaction range (Stearns & Koella, 1986; Blondel, 1995). Although geneticists and ecologists recognize the importance played by ranges of reactions in their theories, there are only very few predictions on the shape and position of reaction ranges. Stearns & Koella (1986) propose a model in which ranges of reaction for the age and size of first maturity have been calculated. Thus, they vary the growth rate and calculate an optimal age of first maturity for each growth rate (the fitness estimator). This model distinguishes the genetic and phenotypic components of the variation of age and maturity size:

- shape and position of the curve in the size/age space reflects the evolutionary response (genetic) to selection;
- location of the point (representing maturation) on the curve reflects the phenotypic response of an individual to a growth variation.

Discussion about the "r-K" selection

The terms 'r' and 'K' refer to the parameters of the logistic growth curve of a population, where 'r' is the slope (population growth rate) and 'K' the upper asymptote (carrying capacity of the environment for the population).

Species possessing short lifespans and high rates of reproduction are said to have evolved in "density-independent" conditions which would support a high growth rate (r), this is referred to as "r" selection. Conversely, species that have a long lifespan and a low rate of reproduction have evolved in "density-dependent" conditions which support the carrying capacity of high densities of individuals, *i.e.,* "K" selection.

The characteristics of "r" selection are: early maturation, high individual growth rate, high relative fecundity, small size offspring, increased effort on reproduction and short lifespan. Organisms in this selection evolve in variable environments with abundant resources.

"K" selection is characterized by: late maturation, low individual growth rate, low relative fecundity, decreased effort in reproduction, large sized offspring and long life expectancy. This occurs for organisms occupying environments dominated by trophic and spatial competition (figure 9.1).

The theory of "demographic strategies" was initially highly successful because it was simple, practical and accorded a good explanation for regulation of populations. According to Southwood *et al.* (1974), the habitat as a unit is the framework in which evolutionary pressures are exerted. The ecological strategy for "r strategists" is to be small sized and opportunistic. They possess an enormous capacity for adaptation and a very low level of extinction and thus have a high potential for selection. The "K strategists" on the other hand tend to be extremely adapted to their habitat, acquire large sizes and thus lose their plasticity for selection. If their habitat changes because of environmental variations on a large temporal scale, their population is threatened with extinction.

FIGURE 9.1.
Responses of species to global environmental conditions: comparison between equatorial and tropical African fishes

ZONE	Equatorial	Tropical
SEASONAL VARIATIONS	Weak	Well-defined
HYDROLOGICAL CYCLE	Weak fluctuations	High fluctuations

SPAWNING	*Several in the year*	*Once a year*
FECUNDITY	*Small or medium*	*High*
DIET	*Generally specialized*	*Rarely specialized*
SELECTION/ STRATEGY	*Mainly "K" strategy*	*Mainly "r" strategy*

However, various authors consider the r-K continuum of Pianka (1970), on which most of the theories on life histories is based, to be very limited and inadequate in accounting for the diversity of the life histories observed (review by Stearns, 1992 and Blondel, 1995). In most cases, the carrying capacity of the environment (K) and the mode of regulation of the concerned population (limited by resource or predation) are unknown, which makes the parameters observed compatible with several hypotheses (Wilbur *et al.,* 1974; Stearns, 1992).

Even when it is used as a simple classification method for life histories, the r-K dichotomy is unable to justify over 50% of the case studies (Wilbur *et al.*, 1974; Stearns, 1977; Stearns, 1992). As a result of the focus on the effects of "density-dependence" of r and K selections, other important biological constraints of life cycles are masked. These include: environmental variability, predator-prey relationships, factors of mortality per age group (Wilbur *et al.*, 1974; Michod, 1979), and also fecundity per age group (Stearns, 1983b). In spite of this, the r-K selection concept has made it possible to draw the attention of researchers to certain aspects of life histories and to formulate considerations in terms of evolution (Noakes & Balon, 1982).

Due to the drawbacks of the r-K continuum in dealing with evolutionary diversity of life histories, various authors such as Southwood (1977), Whittaker & Goodman (1979) and Winnemiller (1992) have proposed additional themes to the Pianka (1970) model.

In place of "r" and "K" strategies, Balon (1985, 1990) distinguishes two major types of ontogenetic models. First is the indirect development model, which involves generally small eggs produced in large number that give rise to young, partially developed larvae of small size, with a low volume of vitellus, which is insufficient to produce the final phenotype. The second is the direct development ("precocial") model in which fish produce a restricted number of eggs of large size with a great quantity of vitellus, enabling embryonic development up to an advanced stage.

This presents two major types of strategies: indirect development, which consists of producing a great number of eggs which will be subjected to a high mortality, but which frees the parents for other activities after spawning; and direct development, which consists of investing in the survival of a small number of individuals, an activity that requires a prolonged energy investment by the parents.

Empirical models

The multiplicity of selective forces which act on life histories and the diversity of responses by organisms have made it impossible for any demographic strategy to account for the diversity of the life histories (Southwood, 1988; Stearns, 1992; Blondel, 1995).

Due to this difficulty, scientists have turned to single or multi-dimensional empirical models. The Winemiller & Rose (1992) model of reproductive strategies, for example, identifies three strategies of reproduction along a three-dimensional continuum (table 9.I). These strategies form a triangular

Periodic	Opportunistic	Equilibrium
Optimizations of fecundity at the expense of the juveniles' survival	Optimization of the growth rate of the population by the generation time reduction	Optimization of the survival of eggs and young by parental care practice
Late maturity at a medium or large size Small and numerous eggs Single seasonal breeding	Early maturity at a small size Small or medium eggs Numerous breeding	Late maturity at a small or medium size Few large eggs Multiple breeding
Reproduction synchronized with most favourable periods for survival of the young	Fish living in little predictable environments or pioneer species able to repopulate quickly after disturbance	Fish living in relatively stable environments; highly developed parental care
Alestidae (*Alestes*) Mormyridae (*Mormyrus*) Siluriformes Cyprinidae	Cyprinodontiformes Small Alestidae Small Cichlidae	Cichlidae Mormyridae Anabantidae
Females generally larger than males, without significant differences in colouration	Males more coloured than females	Males generally larger and more coloured than females.

TABLE 9.I.
Biological characteristics of species belonging to the three major categories of demographic strategies (see figure 9.2).

continuum (figure 9.2) whose tips are characterized by the optimization of one demographic component at the expense of the other two.

Equilibrium strategies correspond to the "K" strategies of MacArthur and Wilson. These species optimize juvenile survival by a larger investment during egg (vitellus) production and practice parental care. These strategies are often developed by sedentary populations living in stable environments such as the Cichlids of the large East African Lakes. Others include Ariidae and Arapaimidae;

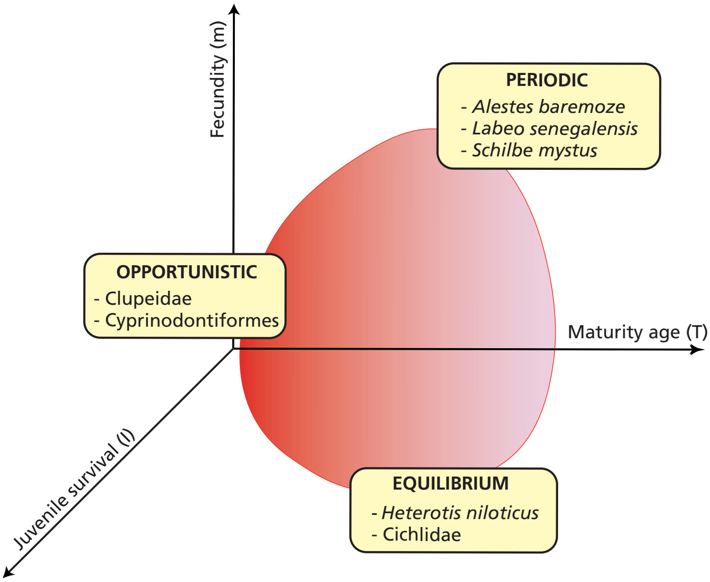


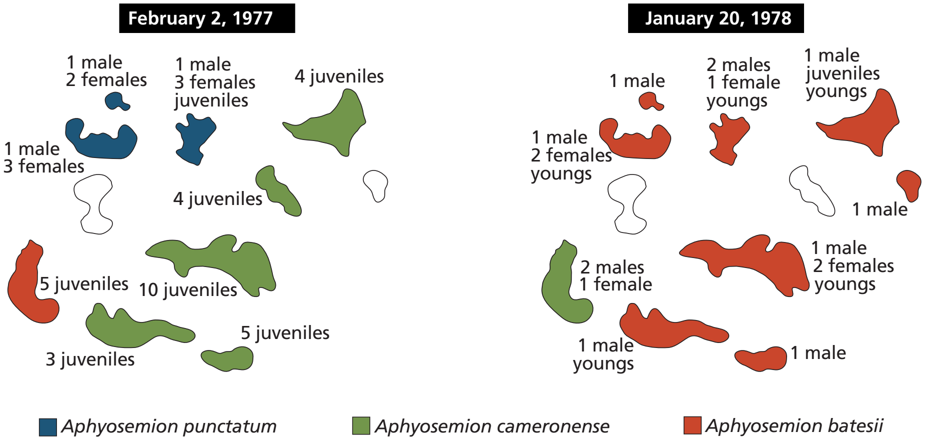
FIGURE 9.2.
Major types of demographic strategies in fish (modified from Winemiller & Rose, 1992).

APLOCHEILIDAE OF THE IVINDO BASIN

Eight species belonging to five genera appear to use the same niche. All are sympatric and diurnal, occupy the same habitat, and feed mainly on small insects that fall from surrounding trees. Many of these species can lay drought-resistant eggs[1], which allow them to colonize temporary environments. These low-fecundity species are characterized by their ability to release specific pheromones that inhibit the reproduction of other species. Thus, the first species to colonize a new environment also prevents other species from establishing themselves there. Coexistence, theoretically impossible, can only take place when disturbances sweep the entire system clean, forcing a redistribution of species. This occurs, for instance, following floods or the passage of an elephant herd (Brosset, 1982). The first species to reach a new pool of water will occupy the space and prevent other species from developing there (figure 9.3). Disturbances occur frequently enough that each of the species manages to be the first in a given space at one time or another; otherwise extinction would occur. This example shows how essential the temporal dimension is, as system diversity and the survival of the different species depend on the high frequency of disturbances.

FIGURE 9.3.

Aplocheilidae from Gabon: sharing space by mutual exclusion of the different species in confined spaces (elephant track) (redrawn from Brosset, 1982).



NOTE 1

[1] This diapause, of variable duration [a period of five years has been reported (Munro *et al.*, 1990)], may be occasional and have no effect on egg survival. For some species, however, egg desiccation is a necessary step for future development. This drought resistance is well-known to aquarium enthusiasts, who take advantage of it to swap material by post.

Periodic types of strategies are implemented in environments where seasonal and spatial variability are relatively predictable, and in which selection supports individuals who reproduce when the conditions of the environment are most favourable to the survival of the juveniles. The eggs are numerous and of small size, and maturation is delayed to a time when abundant egg production is maximized. Moreover, the large size of the adults enables them to survive during unfavourable periods for reproduction, and to store energy necessary for gonad development. This type of strategy is often associated with species that undertake long distance migrations for reproduction as it enables them to spawn for instance in seasonally flooded zones. Alestidae (*Alestes baremoze*) has developed this type of strategy which corresponds to type-"r" strategy

Finally, opportunist type strategies are implemented by species that favour the reduction of generation time in order to colonize environments much faster and to maximize population growth rate. Early maturation, small size, several but small spawns (which in the final analysis correspond to increased fecundity) characterize this type of strategy. It also corresponds partly to the "r"-type strategy or the abovementioned indirect mode of development. Some species, especially within Cypriniformes, Alestidae and certain Cyprinidae, are adapted to diapause or dormancy which enables them to survive highly unfavourable conditions during a particular stage of development in their life (see box "Aplocheilidae of the Ivindo basin (Gabon)").

The identification of these three major types of strategies does not imply that all species can be classified in one or the other. Many fish have developed several intermediate strategies between these extremes. However, there are compromises between certain biological features which are not viable and which are eliminated by natural selection. Therefore, late maturation, low fecundity and low parental investment are a poor combination and such populations would be eliminated rapidly because they are not highly apt to compete. In the same way, physical and physiological constraints are such that it is not possible to consider that compromises between the biological characteristics would lead to "super-fish" that would reproduce early, possess high fecundity and a long lifespan (figure 9.4).

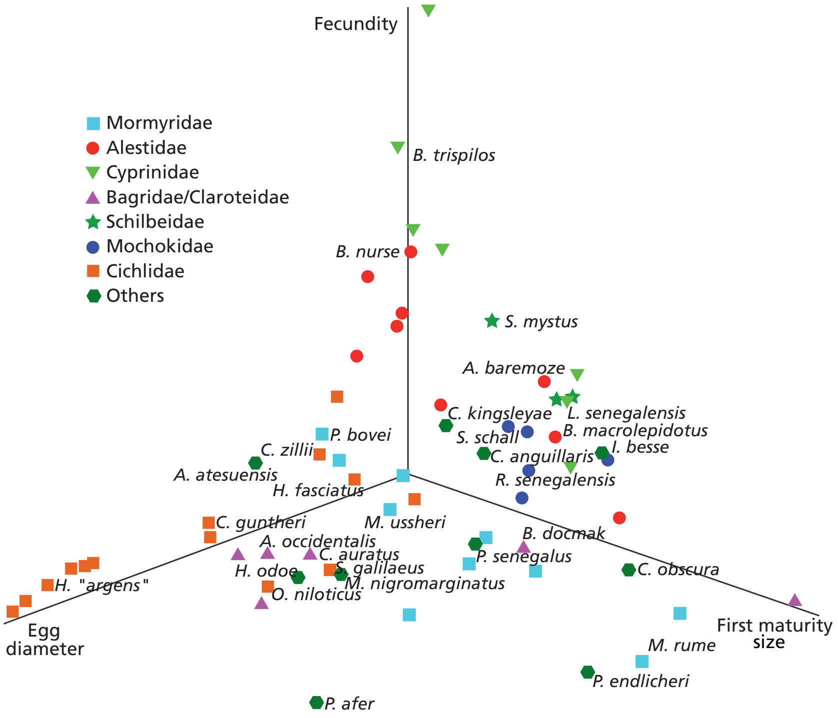


FIGURE 9.4.
Demographic strategies of some African fish species.

Reproduction

DIDIER PAUGY

CHRISTIAN LÉVÊQUE

FABRICE DUPONCHELLE

The reproductive cycle of a species implies a set of physiological and behavioural processes influenced by various factors in the abiotic and biotic environment. Traditionally a distinction is made between gametogenesis and spawning. Gametogenesis is the physiological process involved in gonad development that leads to the formation of gametes (oocytes and spermatozoa). In tropical regions, gametogenesis is controlled by tiny changes in environmental factors, and its duration varies according to species (Munro, 1990). Spawning is the critical moment of the reproductive cycle, which includes the sequence of events that leads to laying of the gametes (maturation of oocytes, ovulation, spermiogenesis), under the influence of specific stimuli (Billard & Breton, 1978).

Gametogenesis is the longest of these processes. It generally lasts several months, but reproductive success depends to a large extent on the success of a set of behavioural activities. These include the search for partners, parental care before and after spawning, whether or not migration is required to find suitable sites for eggs and larvae, synchronization of spawning with changes in environmental factors, synchronization of the genital products laying, etc. These activities may be accompanied by a set of phenological adaptations, such as the development of secondary sexual characters with regard to morphology or colouring.

The study of the fish reproductive cycle thus requires a multidisciplinary approach that involves ecologists, physiologists, ethologists, and geneticists. Coordinating all these disciplines is not always a straightforward affair, and explains why data is often fragmentary. Yet we need studies that include them if we want to understand the cause-and-effect relationships between environmental factors, physiological processes, and reproductive behaviour of species.

Gonad maturation and fecundity

Reproductive effort is the fraction of absorbed energy that an organism devotes to its reproductive activities. This investment can be partially measured through the amount of material or energy stored in the gonads, keeping in mind that it would also need to add all the energy spent on eggs or larvae care, or on mating displays.

Gonado-somatic index

To describe the growth of gonads in relation to body mass, scientists frequently use the gonado-somatic index (GSI) which is the ratio of gonad weight to body weight excluding gonads:

$$GSI = \frac{GW}{TW - GW}$$

where GW is the weight of the gonads and TW the total weight.

The growth of ovaries during the gonad maturation cycle reflects the growth of oocytes through yolk accumulation. The GSI of mature females varies widely from one species to another. It can reach 20 to 30% prior to spawning in some species, but only remain at a few % in others (tables 10.I and 10.II).

In many tropical species, testes develop much less than ovaries, and for African species, the GSI of mature males rarely exceeds 2% (table 10.I; see also box "Gonado-Somatic Index (GSI)"). While the reasons for such a difference are unknown, males generally reach maturity before females and remain mature longer.

TABLE 10.I.
Comparison of female and male gonado-somatic index for different species in the Baoulé River, Upper Senegal in Mali. Maximum observed values quoted for different species (from Paugy, 2002).

Species	Females	Males
Polypterus bichir	23.4	0.2
Hyperopisus bebe	8.0	0.2
Mormyrus rume	11.8	0.2
Mormyrops anguilloides	7.5	
Marcusenius senegalensis	18.7	0.5
Petrocephalus bovei	21.4	0.4
Hydrocynus forskalii	9.4	2.1
Alestes baremoze	13.4	1.3
Brycinus nurse	26.1	2.0
Brycinus leuciscus	17.0	1.2
Brycinus macrolepidotus	19.8	6.7
Labeo senegalensis	17.2	2.0
Labeo coubie	12.0	0.8
Chrysichthys auratus	27.5	0.7
Schilbe intermedius	23.4	1.1
Schilbe mystus	16.2	
Clarias anguillaris	14.4	
Synodontis schall	16.7	2.1
Synodontis ocellifer	26.3	1.5
Sarotherodon galilaeus	4.8	

The gonado-somatic index is a simple but rough estimate of sexual activity. A more refined assessment of gonad development requires a histological study, such as an investigation into the frequency distribution of oocyte size, provided that the relationship between oocyte size and the physiological state of gonads has been predetermined. The GSI is a good tool for estimating reproductive seasons of species that spawn only once per year or per reproductive season. However, it becomes inexact for species with multiple spawning events, because a low GSI (for instance between 0.5 and 1.5% for *Oreochromis niloticus*)

GONADO-SOMATIC INDEX (GSI)

In the African inter-tropical zone, testes weight is always lesser than that of ovaries (table 10.I). This is also often the case in temperate zone. Thus, in *Gasterosteus aculeatus* (Gasterosteidae), while the GSI of the female reaches or even exceeds 20%, the fully mature male's GSI is below 2% (Wootton, 1984). Nonetheless, in some brackish water species, higher values can be observed. In very favourable conditions, the GSI of male *Fundulus heteroclitus* (Cyprinodontidae) can reach 4.7% (Taylor, 1990). Even higher values can be found in some marine species. The male Arctic cod *Boreogadus saida* (Gadidae) can have testes weighing 10 to 27% of the body weight (Craig *et al.*, 1982).

Theory suggests that testes size (and thus weight) could be linked to the mode of fertilization used by the species. Thus, in the case of "coupling" with partners, the amount of sperm needed is less than in the case of dissemination in the physical system without an actual meeting of the progenitors, as with numerous marine species. In the latter, the chances of an encounter are greater if more sperm is released.

Other "solutions" can be found, such as variations in the sex ratio. When a species lays all its eggs in one instance and leaves them to sink to the bottom, where they become attached on submerged surfaces, a large number of spermatozoa is needed to increase chances of fecundation. Consequently, testes are as developed as ovaries in these species, and males must be at least as numerous as females (high sex ratio). In other cases, meanwhile, spawning is spaced out and eggs float, so spermatozoa found in the same waters can be less abundant. As a result, testes are less developed then ovaries and there can be fewer males than females (low sex ratio). As the reproductive behaviour of tropical species is still poorly known, we cannot yet state if this strategy has been verified in this zone.

In any case, the energy allocated for the constitution of genital products appears to be lower in males than in females.

can characterize very different stages of ovarian maturity, such as a gonad in early maturation (stage 2 according to the scale by Legendre & Écoutin, 1989) or a post-spawning gonad (stage 6). The resulting loss of information can be detrimental, particularly in attempts to correlate the reproductive season with environmental factors involved in the regulation of sexual cycles, and it is advisable to use a gonad maturity scale rather than the GSI for species that spawn several times during a reproductive season (Duponchelle *et al.*, 1999).

Maturity scales allow rapid characterisation of the different developmental states of ovaries and testes. In particular, they take into account the macroscopic appearance of gonads (shape, colour, vascularization, transparency) and the GSI. Such scales have been established for *Alestes baremoze* (Durand & Loubens, 1970), *Schilbe mystus*, *S. uranoscopus* (Mok, 1975) and *Sarotherodon melanotheron* (Legendre & Écoutin, 1989). The maturity scale proposed for the last species has been applied successfully to *Oreochromis niloticus* (Duponchelle & Panfili, 1998, Duponchelle *et al.*, 1998, 1999, 2000a; Duponchelle & Legendre, 2000, 2001) and to numerous *Haplochromis* species (Duponchelle *et al.*, 2000b). It appears to be suitable for the majority of Cichlidae.

Fecundity

The ovaries contain oocytes of different sizes corresponding to the different stages of development. A unimodal distribution suggests single spawning, while polymodal structures suggest that the species under study has multiple spawning events (Albaret, 1982) (figure 10.1). In all cases, absolute fecundity (F) corresponds to the number of mature oocytes found in the ovary immediately prior to spawning. For species with only one annual spawning, F equals total annual fecundity. In species that spawn several times, F is the number of oocytes that will be released in the next spawning event (these oocytes are the largest in size), and annual fecundity is the sum of all oocytes released over the year in successive spawning events.

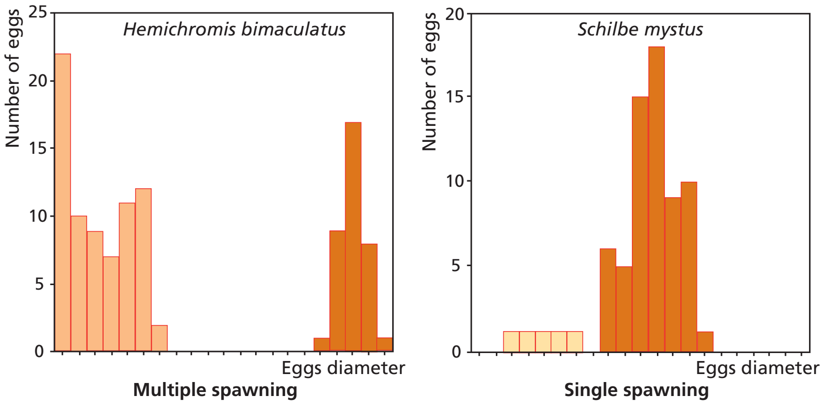


FIGURE 10.1.
Distribution in oocyte diameters of two species from Côte d'Ivoire (from Albaret, 1982).

Brosset (1982) calculated the annual fecundity for three species of Cyprinodontiformes found in the Ivindo River (Gabon). The number of eggs released annually by a female is the same, that is, 200 to 300, regardless of the strategy adopted during the reproductive season: one egg a day in *Diapteron sp.*, 8 to 15 eggs every 8-10 days in *Aphyosemion hertzogi*, 30-75 eggs a month in *Aphyosemion cameronense* and *A. punctatum*.

In the Nothobranchiidae species *Nothobranchius guentheri*, a mature female weighing 1 g produces 20 eggs a day, which represents a reproductive effort equivalent to 27% of its weight in a month. In this case, in a 4-5 month period, the total egg production can be equivalent to the female's weight. This is much higher than the energy investment usually made by species that have single spawning (table 10.II).

To compare the fecundity of fishes of different sizes or from different physical systems, we often calculate the *relative fecundity* which is the number of eggs per unit of body weight, expressed in g or in kg. However, in some species including a lot of Cichlidae, a correlation (generally negative) exists between relative fecundity and female weight (*Sarotherodon melanotheron*, Legendre 1992; *Oreochromis niloticus*, Duponchelle, 1997; Duponchelle *et al.*, 2000a), and we must thus proceed by comparing lines of regression between fecundity and female body weight.

TABLE 10.II.

Selected data on mean female size at first sexual maturity (mm), egg diameter (mm), relative fecundity expressed as number of eggs per kilogram of female body weight, maximum gonado-somatic index (GSI in %) and maximum size observed (MSO in mm) for different African fish species.

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Polypteridae							
Polypterus bichir	Mali/Senegal				23.4		Paugy (unpublished)
Polypterus endlicheri	Côte d'Ivoire	320	2.45	15 000	9.2	750	Albaret,1982
Polypterus senegalus	Côte d'Ivoire	185	1.75	50 000	15	505	Albaret,1982
Clupeidae							
Pellonula leonensis	Lake Kainji	30	0.3-0.5		10.5	75	Otobo, 1978a
Sierrathrissa leonensis	Lake Kainji	19	0.1-0.3		12.5		Otobo, 1978a
Notopteridae							
Papyrocranus afer	Côte d'Ivoire	431	3.6	531	2	590	Albaret,1982
Mormyridae							
Brevimyrus niger	Chad	110	1.3-1.5	80 000			Lek, 1979
Gnathonemus longibarbis	Lake Ihema				15		Plisnier *et al.*, 1988
Hyperopisus bebe	Mali	320	1.8	50 000	9	510	Bénech & Dansoko, 1994
Hyperopisus bebe	Nile	300	1.72				Nawar, 1960
Hyperopisus bebe	Mali/Senegal		1.64		8		Paugy (unpublished)
Hippopotamyrus psittacus	Ogun	166	1.48	15 010		240	Adebisi, 1987
Mormyrops anguilloides	Ogun	397	2.4	15 550			Adebisi, 1987
Mormyrops anguilloides	Côte d'Ivoire	210	2.65	11 300	11	1500	Albaret, 1982
Marcusenius furcidens	Côte d'Ivoire	228	1.8	39 250	14.4	286	Albaret,1982
Mormyrus hasselquistii	Côte d'Ivoire	190	1.85	24 300	12	480	Albaret, 1982
Mormyrus kannume	Lake Victoria	183	2.14			1000	Okedi, 1970
Mormyrus rume	Ogun	350	2.16	15 820			Adebisi, 1987
Mormyrus rume	Mali	330	2.2	20 000	8	870	Bénech & Dansoko, 1994
Mormyrus rume	Mali/Senegal		1.57		11.8		Paugy (unpublished)
Marcusenius senegalensis	Ogun	190	1.35	14 670		321	Adebisi, 1987
Marcusenius senegalensis	Mali/Senegal		1.31		18.7		Paugy (unpublished)
Marcusenius ussheri	Côte d'Ivoire	130	1.75	51 800	15.3	305	Albaret, 1982
Petrocephalus bane	Chad	110	1.0-1.2	46 000			Lek, 1979
Petrocephalus bovei	Côte d'Ivoire	67	1.55	91 230	20.4	100	Albaret,1982
Petrocephalus bovei	Chad	70	1.0-1.1	133 000			Lek, 1979
Petrocephalus bovei	Côte d'Ivoire	65		105 900		100	Mérona, 1980
Pollimyrus isidori	Chad	65	1.2	141 000			Lek, 1979
Petrocephalus soudanensis	Côte d'Ivoire	83	1.6	76 440	16.3		Albaret,1982
Hepsetidae							
Hepsetus odoe	Côte d'Ivoire	140	2.3	18 250	8.4	700	Albaret,1982
Hepsetus odoe	Okavango	150	2.7	12 100		279	Merron *et al.*, 1990
Alestidae							
Alestes baremoze	Côte d'Ivoire	175	1.1	224 100	11.5	284	Albaret,1982
Alestes baremoze	Chad	205		231 000		326	Durand, 1978
Alestes baremoze	Côte d'Ivoire	170	1.1	236 000		284	Paugy, 1978
Brycinus imberi	Côte d'Ivoire	65	1	251 000	14.6		Albaret,1982
Brycinus imberi	Zambezi	120		284 000		189	Marshal & van der Heiden, 1977
Brycinus imberi	Côte d'Ivoire	65	0.89	191 000			Paugy, 1980a
Brycinus leuciscus	Mali	30	0.8	250 000	16		Bénech & Dansoko, 1994
Brycinus leuciscus	Mali/Senegal	65	0.9		18.9		Paugy (unpublished)
Brycinus longipinnis	Côte d'Ivoire	46	1.95	166 000	13.5		Albaret,1982
Brycinus longipinnis	Bandama	74		156 000	12.35		Paugy, 1982b
Brycinus longipinnis	Cavally	68		97 000	11.6		Paugy, 1982b
Brycinus macrolepidotus	Ogun	269	1.26	148 650			Adebisi, 1987
Brycinus macrolepidotus	Côte d'Ivoire	180	1.2	182 400	13.8		Albaret,1982
Brycinus macrolepidotus	Côte d'Ivoire	180	1.33	180 000		330	Paugy, 1982a
Brycinus nurse	Côte d'Ivoire	80	1.05	339 000	19.5	218	Albaret,1982
Brycinus nurse	Côte d'Ivoire	80		368 000		218	Paugy, 1980b
Hydrocynus forskalii	Côte d'Ivoire	150	1.05	127 300	6.9	780	Albaret,1982
Micralestes acutidens	Chad	35	0.6	183 000			Lek & Lek, 1977

TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Distichodontidae							
Ichthyborus besse	Chad	183	0.85	111 500		208	Lek & Lek, 1978a
Cyprinidae							
Barbus spurelli	Côte d'Ivoire	47	0.85	320 000	11.8	87	Albaret,1982
Barbus sublineatus	Côte d'Ivoire	55	0.85	677 000	21.6	100	Albaret,1982
Barbus trispilos	Côte d'Ivoire	50	0.9	449 000	20.2	95	Albaret,1982
Labeo capensis	Vaal River	310		303 000		500	Mulder, 1973
Labeo coubie	Côte d'Ivoire	200	1.25	122 000	8.6		Albaret,1982
Labeo ogunensis	Ogun	185	1.04	233 940		120 ?	Adebisi, 1987
Labeo parvus	Côte d'Ivoire	100	0.95	347 000	19	350	Albaret,1982
Labeo senegalensis	Côte d'Ivoire	175	1	181 500	14.3	550	Albaret,1982
Labeo umbratus	Vaal River	300		410 000		420	Mulder, 1973
Raiamas senegalensis	Côte d'Ivoire	100	1.35	47 700	8.3		Albaret,1982
Bagridae							
Bagrus bajad	Mali	330	1.1	30 000	2.5	720	Bénech & Dansoko, 1994
Bagrus docmak	Nile	200	1.2	36 000		1110	El Sedfy & El Bolock, 1987
Claroteidae							
Auchenoglanis occidentalis	Côte d'Ivoire		2.6	4 150	4		Albaret,1982
Auchenoglanis occidentalis	Mali	100	2	3 000	2.1	480	Bénech & Dansoko, 1994
Chrysichthys auratus	Côte d'Ivoire	140	2.2	11 980	13.2	250	Albaret,1982
Chrysichthys auratus	Mali/Senegal	70	2.3	19 000	27.5		Paugy (unpublished)
Chrysichthys maurus	Côte d'Ivoire	140	2.55	19 700	16.7		Albaret,1982
Chrysichthys maurus	Lekki Lagoon	100	2.2	19 100		510	Ikusemiju, 1976
Chrysichthys nigrodigitatus	Côte d'Ivoire	195	2.9	16 990	19.5	650	Albaret,1982
Chrysichthys nigrodigitatus	Côte d'Ivoire			24 000			Kouassi, 1973
Schilbeidae							
Schilbe mandibularis	Bandama	154	0.95	217 000	9.6	450	Albaret,1982
Schilbe mandibularis	Bandama	175		175 800		389	Lévêque & Herbinet, 1982
Schilbe mystus	Ogun	246	0.87	437 190			Adebisi, 1987
Schilbe mystus	Côte d'Ivoire	100	0.85	253 700	8		Albaret,1982
Schilbe mystus	Côte d'Ivoire	110		228 200		267	Lévêque & Herbinet, 1980
Schilbe mystus	Chad	120		207 000		330	Mok, 1975
Schilbe mystus	Nile			255 000		340	Nawar & Yoakim, 1964
Schilbe niloticus	Mali/Senegal				16.2		Paugy (unpublished)
Schilbe uranoscopus	Chad	180		207 000		360	Mok, 1975
Amphiliidae							
Amphilius atesuensis	Côte d'Ivoire	38	1.7	41 400	11.2	63	Albaret,1982
Clariidae							
Clarias anguillaris	Côte d'Ivoire	235	1.3	62 000	9.6		Albaret,1982
Clarias anguillaris	Mali	150	1.4	180 000	16	1500	Bénech & Dansoko, 1994
Clarias gariepinus	Lake Sibaya	280		36 400		1500	Bruton, 1979a
Clarias gariepinus	Lake Ihema				17		Plisnier *et al.*, 1988
Heterobranchus isopetrus	Côte d'Ivoire	255	1.5	122 000	13.8	900	Albaret,1982
Mochokidae							
Synodontis membranaceus	Mali	210	1.1	150 000	10.5	460	Bénech & Dansoko, 1994
Synodontis afrofisheri	Lake Ihema				26		Plisnier *et al.*, 1988
Synodontis eupterus	Volta Lake			28 000		160	Ofori-Danson, 1992
Synodontis ocellifer	Volta Lake			126 000		200	Ofori-Danson, 1992
Synodontis ocellifer	Mali/Senegal		0.81		26.3		Paugy (unpublished)
Synodontis schall	Ogun	291	1.12	96 880			Adebisi, 1987
Synodontis schall	Côte d'Ivoire	150	1.2	156 600	13.6	380	Albaret,1982
Synodontis schall	Volta Lake	200	1.1	179 000		400	Ofori-Danson, 1992
Synodontis velifer	Volta Lake			70 300		290	Ofori-Danson, 1992
Channidae							
Parachanna obscura	Ogun	245	1.33	19 460		400	Adebisi, 1987
Latidae							
Lates niloticus	Chad	520	0.7	86 000	4.5		Loubens, 1974
Cichlidae							
Alticorpus 'geoffreyi'	Lake Malawi	90	2202	4,3	3.9	165	Duponchelle *et al.*, 2000b
Alticorpus macrocleithrum	Lake Malawi	97	3682	5,4	3.6	136	Duponchelle *et al.*, 2000b
Alticorpus mentale	Lake Malawi	160	1330	3,7	4.2	246	Duponchelle *et al.*, 2000b
Alticorpus pectinatum	Lake Malawi	70	3677	5	3.7	136	Duponchelle *et al.*, 2000b
Astatoreochromis alluaudi	Lake Victoria	98	2.9				Goldschmidt & Goudswaard, 1989

TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Aulonocara 'blue orange'	Lake Malawi	48	5548	3,3	3.1	78	Duponchelle *et al.*, 2000b
Aulonocara 'cf. macrochir'	Lake Malawi		2285	1,5	3.2	134	Duponchelle *et al.*, 2000b
Aulonocara 'minutus'	Lake Malawi	42	7525	3,2	3.1	72	Duponchelle *et al.*, 2000b
Aulonocara 'rostratum deep'	Lake Malawi	75	2467			139	Duponchelle *et al.*, 2000b
Buccochromis lepturus	Lake Malawi	160	970	2,7	4	327	Duponchelle *et al.*, 2000b
Buccochromis nototaenia	Lake Malawi	115	2308	2,5	3.5	300	Duponchelle *et al.*, 2000b
Chromidotilapia guntheri	Côte d'Ivoire	60	2.25	8 100	3.4		Albaret,1982
Copadichromis quadrimaculatus	Lake Malawi	100	692	3,4	5.2	149	Duponchelle *et al.*, 2000b
Copadichromis virginalis	Lake Malawi	75	1343	3,5	3.9	123	Duponchelle *et al.*, 2000b
Cynotilapia afra	Lake Malawi	50	2896	5,5	3.8	75	Duponchelle *et al.* (unpublished)
Diplotaxodon apogon	Lake Malawi	88	632	3,6	5.4	129	Duponchelle *et al.*, 2000b
Diplotaxodon argenteus	Lake Malawi	140	360	4	6.9	206	Duponchelle *et al.*, 2000b
Diplotaxodon limnothrissa	Lake Malawi	105	454	3,7	6.3	175	Duponchelle *et al.*, 2000b
Diplotaxodon macrops	Lake Malawi	98	498	3,7	6	134	Duponchelle *et al.*, 2000b
Genyochromis mento	Lake Malawi		2323	3,8	3.7	97	Duponchelle *et al.* (unpublished)
Haplochromis "argens"	Lake Victoria	61	3.4	3 850	4.4	78	Goldschmidt & Witte, 1990
Haplochromis "reginus"	Lake Victoria			6 500		72	Goldschmidt & Witte, 1990
Haplochromis anastodon	Lake Kivu	68	3.5	3 400			Losseau-Hoebeke, 1992
Haplochromis heusinkveldi	Lake Victoria	63	3.6	3 490	5.1	80	Goldschmidt & Witte, 1990
Haplochromis laparogramma	Lake Victoria	55	3.4	3 230	3.9	79	Goldschmidt & Witte, 1990
Haplochromis olivaceus	Lake Kivu	67	3.7	3 100			Losseau-Hoebeke, 1992
Haplochromis paucidens	Lake Kivu	70	3.6	2 500			Losseau-Hoebeke, 1992
Haplochromis piceatus	Lake Victoria	62	3.2	7 210	5.7	74	Goldschmidt & Witte, 1990
Haplochromis pyrrhocephalus	Lake Victoria	59	3.1	5 290	4.4	76	Goldschmidt & Witte, 1990
Hemichromis bimaculatus	Côte d'Ivoire	45	1.2	111 700	7.1	92	Albaret,1982
Hemichromis fasciatus	Ogun	104	1.26	28 740		204	Adebisi, 1987
Hemichromis fasciatus	Côte d'Ivoire	80	1.65	30 000	4.5	204	Albaret,1982
Labeotropheus fuelleborni	Lake Malawi	74	5	1 900			Marsh *et al.*, 1986
Labeotropheus fuelleborni	Lake Malawi	64	1670	4,5	4.4	100	Duponchelle *et al.* (unpublished)
Labeotropheus trewavasae	Lake Malawi		1967	3,4	4	90	Duponchelle *et al.* (unpublished)
Lethrinops argenteus	Lake Malawi	108	2162	5	4	166	Duponchelle *et al.*, 2000b
Lethrinops 'deep water albus'	Lake Malawi	82	3642	4,8	3.5	161	Duponchelle *et al.*, 2000b
Lethrinops 'dw altus'	Lake Malawi	60	4086	4,1	3.3	130	Duponchelle *et al.*, 2000b
Lethrinops gossei	Lake Malawi	92	2087	5,2	4.1	170	Duponchelle *et al.*, 2000b
Lethrinops longimanus	Lake Malawi		1839	4,6	3.7	168	Duponchelle *et al.*, 2000b
Lethrinops macrochir	Lake Malawi		3107	4,2	3.5	150	Duponchelle *et al.*, 2000b
Lethrinops 'minutus'	Lake Malawi		5272				Duponchelle *et al.*, 2000b
Lethrinops 'oliveri'	Lake Malawi	60	4931	4,3	3.3	98	Duponchelle *et al.*, 2000b
Lethrinops polli	Lake Malawi	65	2775	3,9	3.6	120	Duponchelle *et al.*, 2000b
Melanochromis auratus	Lake Malawi	62	4	3 900			Marsh *et al.*, 1986
Melanochromis auratus	Lake Malawi	55	2861	5,3	3.5	76	Duponchelle *et al.* (unpublished)
Melanochromis vermivorus	Lake Malawi	55	2774	5,3	3.8	73	Duponchelle *et al.* (unpublished)
Mylochromis anaphyrmus	Lake Malawi	105	2430	3,3	3.5	164	Duponchelle *et al.*, 2000b
Nyassachromis 'argyrosoma'	Lake Malawi	57	4901	3,9	3.3	97	Duponchelle *et al.*, 2000b
Alcolapia alcalica	Lake Magadi	59	2.8				Coe, 1969
Oreochromis niloticus	Côte d'Ivoire	160	2.55	3 720	2.6		Albaret,1982
Oreochromis niloticus	Mali	135	2.8	4 000	2.8		Bénech & Dansoko, 1994
Oreochromis niloticus	Lake Ihema	187	2		5.2	530	Plisnier *et al.*, 1988
Oreochromis niloticus	Lake Kossou/ Côte d'Ivoire	140	4526	3,3	2.3	252	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Ayamé/ Côte d'Ivoire	125	4367	3,5	2.5	198	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Buyo/ Côte d'Ivoire		4806	3,2	2.2	225	Duponchelle, 1997
Oreochromis niloticus	Lake Sambakaha/ Côte d'Ivoire Duponchelle *et al.*, 2000a	106	4738	3,4	2.4	233	Duponchelle & Panfili, 1998;
Oreochromis niloticus	Lake Tine/ Côte d'Ivoire	115	4380	3,4	2.3	357	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Lokpoho/ Côte d'Ivoire	129	3734	3,4	2.5	250	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Solomougou/ Côte d'Ivoire	115	4610	3,8	2.3	255	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a

TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Oreochromis niloticus	Lake Korokara-T/ Côte d'Ivoire	105	6324	5	2.3	194	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Korokara-S/ Côte d'Ivoire	123	5133	3,8	2.3	252	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Otopharynx 'productus'	Lake Malawi		2287				Duponchelle *et al.*, 2000b
Otopharynx speciosus	Lake Malawi		853				Duponchelle *et al.*, 2000b
Pallidochromis tokolosh	Lake Malawi	135	489	3,6	6.8	214	Duponchelle *et al.*, 2000b
Petrochromis polyodon	Lake Tanganyika	134	7.1				Kuwamura, 1986
Petrotilapia 'fuscous'	Lake Malawi	80	1867	4,1	4.1	103	Duponchelle *et al.* (unpublished)
Petrotilapia nigra	Lake Malawi	80	1466	4,1	4.3	104	Duponchelle *et al.* (unpublished)
Placidochromis 'long'	Lake Malawi		4602	2,4	3.1		Duponchelle *et al.*, 2000b
Placidochromis 'platyrhynchos'	Lake Malawi		2662	4,7	3.6	115	Duponchelle *et al.*, 2000b
Protomelas taeniolatus	Lake Malawi	72	3.9	3 000			Marsh *et al.*, 1986
Pseudotropheus 'ag. grey head'	Lake Malawi	55	2914	4,6	3.7	79	Duponchelle *et al.* (unpublished)
Pseudotropheus 'aggressive blue'	Lake Malawi		2213	6,3	4.1	90	Duponchelle *et al.* (unpublished)
Pseudotropheus aurora	Lake Malawi	60	2859	5,5	3.7	80	Duponchelle *et al.* (unpublished)
Pseudotropheus barlowi	Lake Malawi		3162	4,7	3.6	83	Duponchelle *et al.* (unpublished)
Pseudotropheus callainos	Lake Malawi	57	1735	5,3	4.4	83	Duponchelle *et al.* (unpublished)
Pseudotropheus heteropictus	Lake Malawi		2953	4,5	3.6	83	Duponchelle *et al.* (unpublished)
Pseudotropheus livingstonii	Lake Malawi	37	6740	3,9	3.2	63	Duponchelle *et al.*, 2000b
Pseudotropheus tr. 'lilac'	Lake Malawi		2099	4,6	3.8	90	Unpublished)
Pseudotroph. tr. 'orange chest'	Lake Malawi	65	2264	5,1	3.9	88	Unpublished)
Pseudotropheus tr. 'red cheek'	Lake Malawi	65	1677	3,8	3.9	88	Unpublished)
Pseudotropheus tropheops 'blue'	Lake Malawi		2264	4,2	3.7	83	Unpublished)
Pseudotropheus williamsi	Lake Malawi	65	2619	5,4	3.9	87	Unpublished)
Pseudotropheus zebra	Lake Malawi	72	4.2	2 600			Marsh *et al.*, 1986
Pseudotropheus zebra	Lake Malawi	55	2572	5,1	3.9	84	Unpublished)
Pseudotroph. z. 'black dorsal'	Lake Malawi	62	2503	5,4	3.9	86	Unpublished)
Pseudotroph. zebra 'red dorsal'	Lake Malawi	52	2926	5	3.6	89	Unpublished)
Pseudotroh. zebra 'yellow throat'	Lake Malawi		2239	5,1	3.9	86	Unpublished)
Sarotherodon galilaeus	Ogun	284	2.01	3 740			Adebisi, 1987
Sarotherodon galilaeus	Côte d'Ivoire	145	2.3	3 940	2.1		Albaret,1982
Sarotherodon galilaeus	Mali	140	2.6	4 000	4.2	410	Bénech & Dansoko, 1994
Sarotherodon melanotheron	Ebrié Lagoon/ Côte d'Ivoire			1 700	8		Legendre & Écoutin, 1989
Sarotherodon melanotheron	Ebrié Lagoon/ Côte d'Ivoire	176	1757	5,8	4.1	334	Legendre & Écoutin, 1989
Sarotherodon melanotheron	Gambia/Senegal	170	4395	4,9	2.8	220	Panfili *et al.*, 2004a
Sarotherodon melanotheron	Saloum/Senegal	131	5091	8,2	2.8	200	Panfili *et al.*, 2004a
Sciaenochromis alhi	Lake Malawi		2006	4,2	3.9	124	Duponchelle *et al.*, 2000b
Sciaenochromis benthicola	Lake Malawi	100	1271	4,2	4.4	167	Duponchelle *et al.*, 2000b
Simochromis diagramma	Lake Tanganyika	75	5.2		5.5		Kuwamura, 1986
Stigmatochromis 'guttatus'	Lake Malawi	100	1220	3,9	4.5	147	Duponchelle *et al.*, 2000b
Taeniolethrinop. praeorbitalis	Lake Malawi	130	1450	4	4.3	200	Duponchelle *et al.*, 2000b
Taeniolethrinops furcicauda	Lake Malawi	130	1911	1,9	3.4	178	Duponchelle *et al.*, 2000b
Tilapia guineensis	Ebrié Lagoon/ Côte d'Ivoire			20 600	11		Legendre & Écoutin, 1989
Oreochromis macrochir	Lake Ihema	185	2		4	402	Plisnier *et al.*, 1988
Tilapia mariae	Ogun	116	1.41	9 270			Adebisi, 1987
Tilapia moorei	Lake Tanganyika	70	5.7		4.6		Kuwamura, 1986
Tilapia nigra	East Africa	75	2.4	10 400			Cridland, 1961
Coptodon rendalli	Lake Ihema				6		Plisnier *et al.*, 1988
Tilapia tholloni				85 000	14		Peters, 1963c
Coptodon zillii	Côte d'Ivoire	70	1.65	38 600	4		Albaret,1982
Coptodon zillii	Mali	100	1.5	100 000	6.5	285	Bénech & Dansoko, 1994
Coptodon zillii	East Africa	110	1.5	65 500		250	Cridland, 1961
Trematocranus brevirostris	Lake Malawi	50	4577	3,9	3.3	85	Duponchelle *et al.*, 2000b
Trematocranus placodon	Lake Malawi	105	2043	3	3.6	159	Duponchelle *et al.*, 2000b
Xenotilapia longispinnis	Lake Tanganyika	69	3.2				Kuwamura, 1986
Anabantidae							
Ctenopoma kingsleyae	Côte d'Ivoire	115	1.05	103 000	8.7	215	Albaret,1982
Mastacembelidae							
Mastacembelus nigromarginatus	Côte d'Ivoire	150	2.35	19 800	12.5	340	Albaret, 1982

There is an inverse relationship between the number of eggs released at each spawning event and the size of the oocytes. Very prolific species that produce small eggs mostly belong to the Cyprinidae, Alestidae, and Schilbeidae families. Most are pelagic species, and are often migratory. Species producing a few large eggs mainly belong to the Bagridae, Mormyridae (which only possess the left gonad), and Cichlidae families. For the latter, substrate layers (*H. bimaculatus, H. fasciatus,C. zillii*) have smaller and more numerous eggs than mouth brooding species (*S. galilaeus, O. niloticus*).

Mouth brooders generally have a limited number of large eggs, as shown in the results obtained for various Cichlidae species of the African great lakes (table 10.II).

Relationships between fecundity and length or weight of females

The fecundity of a species is most often a function of the size of the females. The larger they are, the more eggs they lay. It is customary to determine the relationship between fecundity and size of females, expressed either by length (often the standard length) or weight (table 10.III).

The relationship is generally $F = a\ SL^b$.

Reproductive strategies

Each individual possesses a set of biological characteristics related to reproduction that are the heritage of evolution and phylogeny. The reproductive strategy of a fish species in a given environment is indeed a set of biological traits such as age and size at first reproduction, fecundity, gonad development and gamete size, reproductive behaviour including the existence of parental care, reproductive season, etc.

But an individual can also develop tactics, which are in fact variations on the typical reproductive schema of the species, to adapt to changes in environmental factors. This adaptive behaviour to special ecological conditions is intended to ensure the survival of the species, as we have already seen. This is the case for instance of *Oreochromis niloticus* in artificial reservoirs in Côte d'Ivoire, whose reproductive characteristics (reproductive season, size at first sexual maturity, fecundity, egg size, etc.) vary from one year to another depending on environmental conditions (Duponchelle & Panfili, 1998; Duponchelle *et al.*, 1998, 1999 et 2000a).

Main modes of reproduction

Most fishes are oviparous. Oocytes and sperm are released into the water and fecundation takes place immediately. There are also cases of intra-buccal fecundation, particularly in Cichlidae.

Depending on the demographic strategies implemented by fishes and the ecological adaptations to certain physical systems, we can distinguish different

TABLE 10.III.

Relationships between fecundity (F) and standard length (SL in mm) or weight (W in g) for different African fish species.

Species	F *vs* SL	F *vs* W	Source
Mormyridae			
Marcusenius ussheri	F = 80 SL - 9742	F = 45 W + 592	Albaret, 1982
Petrocephalus bovei	F = 55 SL - 3335	F = 105 W - 180	Albaret, 1982
Hepsetidae			
Hepsetus odoe	F = 172 SL - 41581	F = 59 W - 14250	Albaret, 1982
Hepsetus odoe	F = 10.8 SL - 803.0		Merron *et al.*, 1990
Alestidae			
Alestes baremoze	F = 657.4 SL - 117813.5	F = 323 W - 19122	Durand, 1978
Alestes baremoze		F = 288 W - 7078	Paugy, 1978
Alestes baremoze	F = 391 SL - 51456	F = 253 W - 1884	Albaret, 1982
Brycinus imberi	F = 6994.6 SL - 73028.3		Marshall & van.der Heiden, 1977
Brycinus imberi	F = 176.7 SL - 11768.6	F = 186 W + 140	Paugy, 1980a
Brycinus imberi	F = 328 SL - 24686	F = 356 W - 2800	Albaret, 1982
Brycinus longipinnis	F = 119 SL - 6633	F = 224 W - 540	Albaret, 1982
Brycinus longipinnis (Bandama)	F = 124.3 SL - 6834.6	F = 323 W - 1295	Paugy, 1982b
Brycinus longipinnis (Cavally)	F = 70 SL - 3818.9	F = 108 W - 151	Paugy, 1982b
Brycinus macrolepidotus	F = 814 SL - 137900	F = 195 W - 1980	Albaret, 1982
Brycinus macrolepidotus	F = 812.8 SL - 138120	F = 187 W - 1460	Paugy, 1982a
Brycinus nurse	F = 448.6 SL - 34638	F = 423 W - 2406	Paugy, 1980b
Brycinus nurse	F = 491 SL - 39871	F = 450 W - 3967	Albaret, 1982
Hydrocynus forskalii	F = 1325 SL - 319084	F = 187 W - 25065	Albaret, 1982
Micralestes acutidens	F = 19.93 SL - 539	F = 0.23 W - 70.3	Lek, 1978
Cyprinidae			
Barbus ablabes	F = 122 SL - 5266	F = 258 W + 413	Albaret, 1982
Barbus kimberleyensis	F = 0.222 SL^3 - 495.2		Gaigher, 1976
Barbus sublineatus	F = 534 SL - 27819	F = 958 W - 1849	Albaret, 1982
Barbus trispilos	F = 150 SL - 6325	F = 439 W + 87	Albaret, 1982
Labeo capensis	F = 1220 SL - 367774	F = 518 W - 214717	Mulder, 1973
Labeo parvus	F = 721 SL - 69461	F = 424 W - 5933	Albaret, 1982
Labeo umbratus	F = 1324 SL - 381914	F = 625 W - 215164	Mulder, 1973
Bagridae			
Bagrus docmak	F = 617 SL - 278389	F = 43 W - 16827	El Sedfy & El Bolock, 1987
Claroteidae			
Chrysichthys maurus	F = 45 SL - 5265	F = 18 W + 138	Albaret, 1982
Schilbeidae			
Schilbe mandibularis	F = 353 SL - 44425	F = 157 W + 5970	Albaret, 1982
Schilbe mystus	F = 1.5 SL - 185.1	F = 207 W - 1292	Lévêque & Herbinet, 1980
Schilbe uranoscupus	F = 528 SL - 98770	F = 250 W - 7475	Mok, 1975
Amphiliidae			
Amphilius atesuensis	F = 3.8 SL - 104	F = 40 W + 2	Albaret, 1982
Mochokidae			
Synodontis schall		F = 201 W - 7841	Albaret, 1982
Synodontis schall		F = 174.9 W + 5784	Ofori-Danson, 1992
Cichlidae			
Alticorpus 'geoffreyi'	F = 2.4365 SL - 171.76	F = 1.7836 W + 28.037	Duponchelle *et al.*, 2000b
Alticorpus macrocleithrum	F = 3.6323 SL - 259.3	F = 3.3229 W + 14.744	Duponchelle *et al.*, 2000b
Alticorpus mentale	F = 2.4897 SL - 211.7	F = 0.9359 W + 63.115	Duponchelle *et al.*, 2000b
Alticorpus pectinatum	F = 2.2238 SL - 114.87	F = 3.2395 W + 12.796	Duponchelle *et al.*, 2000b
Aulonocara 'blue orange'	F = 1.0608 SL - 33.755	F = 3.3845 W + 9.6689	Duponchelle *et al.*, 2000b
Aulonocara 'cf. macrochir'	F = 1.5397 SL - 87.623	F = 1.6714 W + 18.2	Duponchelle *et al.*, 2000b
Aulonocara 'rostratum deep'	F = 2.6948 SL - 191.6	F = 2.3872 W + 1.3981	Duponchelle *et al.*, 2000b
Buccochromis lepturus	F = 4.7556 SL - 768.67	F = 0.9143 W + 22.481	Duponchelle *et al.*, 2000b
Buccochromis nototaenia	F = 1.9659 SL - 105.22	F = 0.8115 W + 96.468	Duponchelle *et al.*, 2000b
Chromidotilapia guntheri	F = 2.6 SL - 64	F = 3.4 W + 25	Albaret, 1982
Copadichromis quadrimaculatus		F = 0.684 W - 0.8577	Duponchelle *et al.*, 2000b

TABLE 10.III. (CONT.)

Species	**F *vs* SL**	**F *vs* W**	**Source**
Cynotilapia afra	F = 0.6252 SL - 17.179	F = 1.9679 W + 6.3959	Duponchelle *et al.* (unpublished)
Diplotaxodon apogon		F = 0.6738 W - 1.0371	Duponchelle *et al.*, 2000b
Diplotaxodon argenteus	F = 0.306 SL - 11.866	F = 0.3006 W + 6.1836	Duponchelle *et al.*, 2000b
Genyochromis mento	F = 1.6346 SL - 94.359	F = 2.203 W + 0.8898	Duponchelle *et al.* (unpublished)
Labeotropheus fuelleborni	F = 0.6331 SL - 21.182	F = 1.1687 W + 7.7613	Duponchelle *et al.* (unpublished)
Labeotropheus trewavasae		F = 2.857 W - 15.549	Duponchelle *et al.* (unpublished)
Lethrinops argenteus	F = 2.5193 SL - 185.09	F = 1.7255 W + 21.72	Duponchelle *et al.*, 2000b
Lethrinops 'deep water albus'	F = 2.8885 SL - 178.91	F = 2.8411 W + 22.771	Duponchelle *et al.*, 2000b
Lethrinops gossei	F = 2.2518 SL - 147.31	F = 1.6832 W + 19.458	Duponchelle *et al.*, 2000b
Lethrinops longimanus	F = 2.7948 SL - 225.41	F = 2.9578 W - 43.716	Duponchelle *et al.*, 2000b
Lethrinops macrochir	F = 3.6833 SL - 267.1	F = 2.7129 W + 12.68	Duponchelle *et al.*, 2000b
Lethrinops 'oliveri'	F = 1.7657 SL - 72.585	F = 4.5704 W + 3.0726	Duponchelle *et al.*, 2000b
Lethrinops polli	F = 1.5365 SL - 83.52	F = 2.5654 W + 2.6796	Duponchelle *et al.*, 2000b
Mylochromis anaphyrmus	F = 2.7755 SL - 194.73	F = 1.9783 W + 25.864	Duponchelle *et al.*, 2000b
Nyassachromis 'argyrosoma'	F = 0.9259 SL - 29.05	F = 3.2835 W + 10.481	Duponchelle *et al.*, 2000b
Oreochromis niloticus	F = 111.92 SL - 993.64	F = 2.91 W + 277.7	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 53.507 SL - 308.55	F = 2.52 W + 164.4	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 129.9 SL - 1254	F = 3.64 W + 197.1	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 85.852 SL - 695.1	F = 3.61 W + 103.3	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 116.2 SL - 1095	F = 2.59 W + 337.2	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 81.871 SL - 633.54	F = 2.01 W + 368.6	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 122.43 SL - 1156.2	F = 3.14 W + 260.5	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 77.809 SL - 504.14	F = 3.78 W + 152.5	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 99.584 SL - 775.71	F = 2.69 W + 317.8	Duponchelle *et al.*, 2000a
Otopharynx 'productus'		F = 2.8372 W - 7.8469	Duponchelle *et al.*, 2000b
Otopharynx speciosus	F = 3.547 SL - 452.51	F = 1.0452 W - 25.644	Duponchelle *et al.*, 2000b
Pallidochromis tokolosh	F = 0.7106 SL - 78.13	F = 0.5496 W - 4.5233	Duponchelle *et al.*, 2000b
Petrotilapia 'fuscous'		F = 2.1274 W - 6.1381	Duponchelle *et al.*, (unpublished)
Placidochromis 'long'	F = 1.333 SL - 57.675	F = 6.8445 W - 12.583	Duponchelle *et al.*, 2000b
Placidochromis 'platyrhynchos'		F = 1.8798 W + 14.85	Duponchelle *et al.*, 2000b
Pseudotropheus 'aggressive blue'	F = 1.0151 SL - 46.016	F = 1.7042 W + 6.5604	Duponchelle *et al.* (unpublished)
Pseudotropheus callainos		F = 1.1263 W + 5.8628	Duponchelle *et al.* (unpublished)
Pseudotropheus heteropictus	F = 0.9346 SL - 34.827	F = 4.0141 W - 10.079	Duponchelle *et al.* (unpublished)
Pseudotropheus livingstonii	F = 3.1033 SL - 128.38	F = 6.4275 W + 1.2343	Duponchelle *et al.*, 2000b
Pseudotropheus tr. 'lilac'	F = 0.7236 SL - 23.059	F = 1.4092 W + 9.8755	Duponchelle *et al.* (unpublished)
Pseudotropheus tr. 'red cheek'	F = 0.6259 SL - 22.07	F = 2.0579 W - 4.9336	Duponchelle *et al.* (unpublished)
Pseudotropheus tropheops 'blue'	F = 1.6927 SL - 89.196	F = 3.596 W - 17.192	Duponchelle *et al.* (unpublished)
Pseudotropheus williamsi	F = 1.8937 SL - 104.3	F = 3.0137 W - 5.8688	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra	F = 0.8112 SL - 27.739	F = 1.9246 W + 6.6811	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'black dorsal'	F = 1.4866 SL - 74.477	F = 1.7705 W + 9.2223	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'red dorsal'	F = 0.9901 SL - 36.543	F = 2.1674 W + 6.981	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'yellow throat'	F = 1.1536 SL - 53.814	F = 2.3995 W - 1.8984	Duponchelle *et al.* (unpublished)
Sarotherodon melanotheron	F = 0.0008 LF 2.449	F = 1.72 W -15.0	Legendre & Écoutin, 1989 (unpublished)
Sarotherodon melanotheron	F = 2.7238 LF - 160.01	F = 1.948 W + 119.08	Panfili *et al.*, 2004a
Sarotherodon melanotheron	F = 2.8459 LF - 156.76	F = 2.111 W + 128.11	Panfili *et al.*, 2004a
Sciaenochromis alhi	F = 2.4762 SL - 200.07	F = 4.4172 W - 55.843	Duponchelle *et al.*, 2000b
Sciaenochromis benthicola	F = 1.0481 SL - 74.232	F = 1.264 W - 0.3265	Duponchelle *et al.*, 2000b
Stigmatochromis 'guttatus'	F = 1.1159 SL - 87.92	F = 1.4769 W - 8.0045	Duponchelle *et al.*, 2000b
Taeniolethrinops praeorbitalis	F = 2.0847 SL - 135.28	F = 0.9672 W + 74.587	Duponchelle *et al.*, 2000b
Tilapia guineensis	F = 0.1458 LF 1.9899	F = 18.61 W + 2018.0	Legendre & Écoutin, 1989 (unpublished)
Coptodon zillii	F = 49 SL - 2987	F = 28 W + 610	Albaret, 1982
Trematocranus placodon	F = 1.5364 SL - 62.449	F = 1.2303 W + 50.512	Duponchelle *et al.*, 2000b
Mastacembilidae			
Mastacembelus nigromarginatus	F = 8.4 SL -1468	F = 187 W + 67	Albaret, 1982

reproductive modes or styles. The general classification proposed by Balon (1975 and 1990), based on the degree of parental care (ethology) and reproductive sites (ecology) is generally accepted. The author identifies three broad sets within which there are etho-ecological subsets, regardless of the phyletic origin of the species (table 10.IV):

- fishes that do not guard their eggs once these have been released, among which we can distinguish fishes that lay eggs on open substrates or those that provide a modicum of protection by concealing them. These are generally fishes that are highly fecund and have an indirect form of development;
- fishes that guard their eggs in nests, either on pre-selected or pre-constructed substrates. These species generally have a few relatively large eggs, to which they provide different forms of parental care;
- fishes that bear their eggs for at least part of the embryonic period. In external brooders, the eggs are carried on the body surface or in the mouth, or in structures that open out. In internal brooders, the eggs are fertilized and transported within the body.

Each etho-ecologic section includes different reproductive guilds, of which we provide only a few examples (table 10.IV). These guilds are based on a combination of morphological, behavioural, and ecological characteristics.

TABLE 10.IV.
Simplified classification of reproductive styles in fish (from Balon, 1975).

NON-GUARDERS	**Open substrate spawners**		
		pelagic spawners	*Stolothrissa* *Limnothrissa* *Alestes* *Lates* *Ctenopoma* spp
		plant spawners	Small alestids and cyprinids *Epiplatys*, *Aphyosemion*
		rock and gravel spawners	*Opsaridium microlepis*
	Brood hiders		
		Annual fishes	*Nothobranchius*
GUARDERS	**Clutch tenders**		
		plant tenders	*Polypterus*
		rock tenders	many cichlids
	Nesters		
		froth nesters	*Hepsetus odoe* *Microctenopoma* spp.
		hole nesters	many cichlids some mormyrids *Protopterus*
		sand nesters	*Tilapia* spp. Tanganyikan lamprologine cichlids
		plant material nesters	*Gymnarchus niloticus* *Heterotis niloticus*
BEARERS	**External brooders**		
		mooth brooders	*Oreochromis spp.* *Sarotherodon spp* all haplochromines
		pouch brooders	freshwater pipefishes
	Internal live bearer		some asian poeciliids

An estimate of the proportion of different eco-ethological guides in African continental waters reveals a much higher number of guarders and bearers in the East African great lakes, which are characterized by relatively predictable physico-chemical systems. Meanwhile, a large percentage of non-guarder species are found in the rivers and wet zones, which have less predictable physical systems (Bruton & Merron, 1990).

To complete the reproductive guilds, we should also take into account the frequency of spawing and the period(s) during which spawning occurs. This usually takes place when the environmental conditions are, in principle, most conducive to the survival of eggs and larvae, and many species have a seasonal reproductive cycle. It is nonetheless possible to distinguish several options in reproductive behaviour (table 10.V).

TABLE 10.V.
Examples of main types of reproductive behaviour in African fishes (adapted from Lowe-McConnell, 1987).

Type of fecundity	Seasonality	Examples	Migratory behaviour / parental care
"big-bang"	once in the lifetime	*Anguilla*	long distance migrations, no parental care
total spawners	highly seasonal	*Alestes*	anadromous migrations
(very high fecundity)	(generally throughout the flood)	*Labeo*	open water spawners
		Schilbe	no parental care
partial spawners	throughout the flood	many cyprinids	
		Clarias	
		Protopterus	bottom nester
		Heterotis	egg garders
		Gymnarchus	floating nest (plant material)
		Hepsetus	floating nest (foam)
		anabantids	
small brood spawners	sometimes throughout the year	*Tilapia*	nest constructors and parental behaviour
(low fecundity)	sometimes throughout the flood	*Sarotherodon*	mouth brooders
	during the filling of ponds	*Nothobranchius*	annual species with resting eggs

One very rare behaviour is the "big bang" (Lowe-McConnell, 1987) which, like in eels, consists of reproducing once in a lifetime and then dying.

Several species, meanwhile, have a single short reproductive period every year. This is the case for many riverine species that practice reproductive migrations and spawn at the beginning of or during the flood, when conditions are optimal for juveniles that can find shelter and food in the flooded plains. This periodic strategy does include risks tied to climate variability and variations in flooding, making it difficult to predict the optimal period for reproduction. The species in question often release a very large number of eggs, and are sufficiently long-lived to reproduce for several consecutive years, thus minimizing the consequences of climate-related variations on the recruitment.

For other species, the reproductive season is spread out over the year. Scenarios differ depending on the group. Either individuals of a given species do not reach maturity at the same time, or eggs are spawned in batches at more or less regular intervals. This strategy tends to minimize the risks of a single spawning that may occur at an unfavourable period, and tends to benefit species with short lifespans.

Finally, other species spawn practically throughout the year. Most of these multiple spawners provide parental care, like the Cichlidae. Although a full reproductive cycle cannot be completed in 24 hours, certain phases follow a daily cycle. In particular, spawning can take place at certain hours, as has been observed in many fishes such as *B. macrolepidotus* which appears to reproduce before dark (Paugy, 1982a)

Cichlidae belonging to the genera *Tropheus* and *Simochromis* that live in the same habitats in Lake Tanganyika (between rocks, a few metres depth) and feed on Aufwuchs do not spawn at the same time of day. The former spawn early in the morning, while the latter spawn during daylight (Nelissen, 1977). Differences in spawning activity rhythms can contribute to limiting interspecies competition.

In the Nothobranchiidae *Nothobranchius guentheri*, reproductive behaviour follows a day-long cycle (Haas, 1976b). Reproductive activity is low very early in the morning, but increases 2.5 hours after dawn and reaches a peak 6 hours after dawn before waning.

The influence of lunar cycles has also been identified in the reproductive behaviour of certain fish species. The proportion of females ready to spawn among Lake Victoria *Oreochromis niloticus* is higher during the full moon than during the new moon (Okorie, 1973). In the Ethiop River in Nigeria, which has particularly clear waters, there is a marked synchronization of *Tilapia mariae* spawns with the lunar cycle, as 85% of spawning occurs during the last quarter of the lunar cycle, that is, between 0 and 6 days before the full moon (figure 10.2). Spawning before the full moon could contribute to improving larval survival owing to more efficient parental guarding during moonlit nights (Schwanck, 1987).

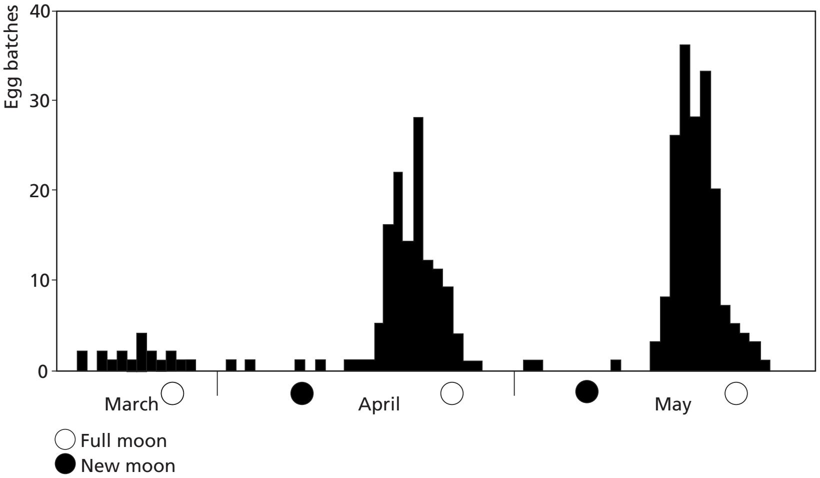


FIGURE 10.2.

Daily counts of egg batches in *Tilapia mariae* (from Schwanck, 1987).

Synchronization between reproduction and changes in the environment

Reproduction in fishes is a cyclic phenomenon, synchronized in many species, with seasonal environmental fluctuations that have an impact on fish physiology, as they can stimulate or inhibit certain stages of gametogenesis or spawning. Both are controlled by endocrine processes that are influenced by environmental factors such as temperature, photoperiod, rainfall, etc. Each species or species group can react differently to the environmental factors that affect their physiological rhythms.

This synchronization between the reproductive cycle and predictable changes in the environment is an adaptive process. As they evolved, fishes adapted their sexual cycle in order to reproduce at periods most favourable to the survival of their eggs. How did fishes program their reproductive cycle? What factors are responsible for gonad maturation in such a way that species are ready to spawn when conditions are favourable for the survival of eggs and larvae, thus granting them a selective advantage? We are still far from knowing the answers to all these questions, even though we suspect certain ecological factors of playing an important role, as reproduction is a complex phenomenon in which several abiotic factors are involved. In all likelihood, the chronology of the reproductive cycle is in fact a compromise between stimuli from different sources. Gametogenesis thus starts several months before spawning season, when conditions are not yet favourable to the survival of the young. Whatever the case, the synchronization of the reproductive cycle with environmental changes confers an adaptive advantage to species.

Single spawning species

Several authors have attempted to identify which factors in the physical system were involved in triggering maturation as well as spawning.

In the Niger basin, Bénech & Ouattara (1990) investigated the role of various environmental factors in the ovarian growth of *Brycinus leuciscus* by comparing the reproductive cycle in different natural conditions (different flood periods) between the sites of Mopti and Niamey. In Mopti, gametogenesis begins in week 20 at the same time as the climate changes induced by the movement of the intertropical front. The same thing occurs in Niamey in week 22. In both stations, the start of gonad development occurs once the water temperature has attained a maximum (29°C) in week 19, and water conductivity has stopped increasing with the appearance of the first rains. The gonado-somatic index reaches its peak in week 30 in Mopti, after which spawning begins and continues up to week 39. In Niamey, meanwhile, ovarian growth appears to be interrupted in week 22, then restarts again six to nine weeks later to reach a peak in week 35, with spawning occurring until week 45. In both sites, gonad development coincides with a decrease in conductivity after a period of warming and the start of the flood. Spawning occurs as water rises, a few weeks before the water level reaches its peak. It is nonetheless difficult to establish precisely which factor is responsible for triggering the different reproductive processes.

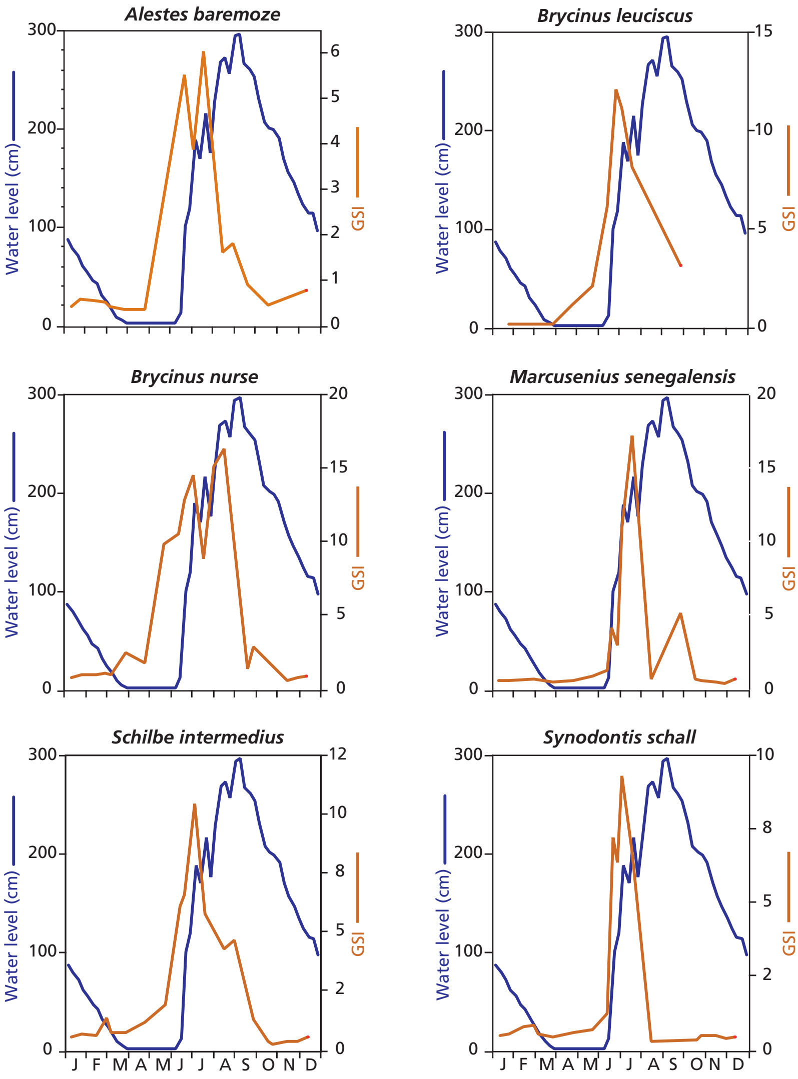


FIGURE 10.3.
Hydrological cycle and changes in the gonado-somatic index (GSI) of different fish species from the Baoulé River, a tributary of the Upper Senegal basin. Spawning occurs before the flood peak (from Paugy, 2002).

In aquarium conditions, Kirshbaum (1984) triggered Mormyridae gonad maturation by diminishing water conductivity, simulating rainfall, and increasing the water level, all factors identical to those that appear to be involved for *B. leuciscus*.

What stimuli trigger spawning? In large tropical rivers, the hydrological regime (or, to be precise, the set of climatic conditions prevailing at the start of the flood) appears to be the main regulator of reproduction. For many species, spawning coincides with the flood and can occur from the start of the flood up to its peak, but rarely during the recession. As such, most of the species present in the Baoulé (upper course of the Senegal) reproduce before the flood (figure 10.3), and this phenomenon has been seen in numerous species in various physical systems (Bénech & Quensière, 1985; Munro, 1990).

However, reproduction and flood are not always synchronized, which casts some doubt on the true role of this factor. In the Okavango delta, the flood occurs in the dry season, during winter months, as the flood wave takes a while to go from southern Angola via the Okavango River. In these conditions, *Hepsetus odoe* spawns in summer, with activity reaching a peak when waters are low (Merron *et al.*, 1990), which appears to indicate that the flood is not the primary stimulus triggering spawning in this species. A comparable situation exists in Lake Chad, where the lake floods in winter (December-January), several months after the flood peaks in the Chari River (September). Yet reproduction in most species takes place during the rainy season (July-August) which immediately follows the hot season (Bénech & Quensière, 1985). There are exceptions to this trend, as in *Brycinus macrolepidotus* and *Hydrocynus forskalii* of the 'Sahelo-Sudanian' basins found in the same latitudes. It is moreover customary in numerous equatorial species which indivudually have a single annual spawn, but without a precise spawning period when the entire population is considered. *Brycinus imberi* (figure 10.4) and *B. longipinnis* of the Côte d'Ivoire basins demonstrate such behaviour (Paugy, 1980a and 1982b).

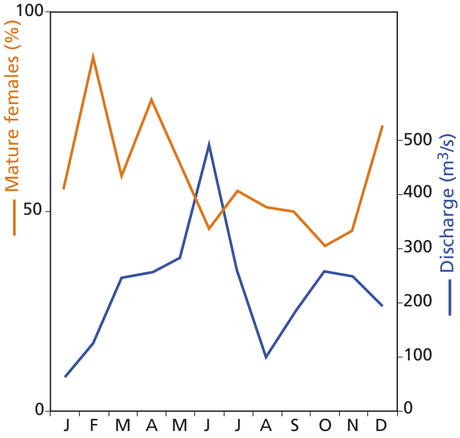


FIGURE 10.4.
Long breeding period of the populations of *Brycinus imberi* from Côte d'Ivoire. Throughout the year, more than half of fish are mature (from Paugy, 1980a).

Multiple spawning species

For species that have a reproductive period spread out over time (interval spawning or spawning throughout the year), it is rather difficult to identify the factors influencing the reproductive cycle (Jalabert & Zohar, 1982). This is especially the case for Cichlidae, which are theoretically capable of reproducing uninterruptedly in equatorial regions, though with a tendency to seasonal behaviour depending on latitude. In the Ébrié lagoon (Côte d'Ivoire), lagoon Tilapias (*Sarotherodon melanotheron* and *Tilapia guineensis*) reproduce throughout the year without displaying any clear seasonal variation in the intensity of sexual activity (Legendre & Écoutin, 1989). A high proportion of maturing fishes is observed throughout the year. However, in populations reared in parks in the lagoon, the sexual activity of *S. melanotheron* decreases significantly during the rainy season, from June to September (see box "Spawning frequency in cichlids"). Meanwhile, the sexual activity of *Oreochromis niloticus* shows marked seasonality in artificial reservoirs of Côte d'Ivoire, with a more spread-out season in the centre and south of the country than in the small agro-pastoral reservoirs of the north (Duponchelle *et al.*, 1999). In both north and south, periodicity of the reproductive season is nonetheless regulated by the photoperiod (see box "Influence of photoperiod on the reproductive cycle of cichlids"). On the other hand, in *O. niloticus*, fecundity rates are correlated with trophic availability in Côte d'Ivoire's artificial reservoirs. The highest fecundity rates are recorded when chlorophyll *a* concentrations are at their highest, just before the flood (Duponchelle *et al.*, 2000a).

Spawning frequency in cichlids (from Legendre & Écoutin, 1989)

In the lagoons of Côte d'Ivoire, where the two species reproduce throughout the year, the interval between two spawns is about two weeks in *Sarotherodon melanotheron*, and around three weeks in *Tilapia guineensis* (figure 10.5). Nonetheless, the frequency of spawning appears to be less regular in *T. guineensis,* which can go for nearly four months without spawning. For both species, the frequencies provided are averages that should be adapted, as relative frequency varies according to the seasons as shown in the figure below, where it is clear that a minimum is reached in both species during the rainy season, that is, June-July.

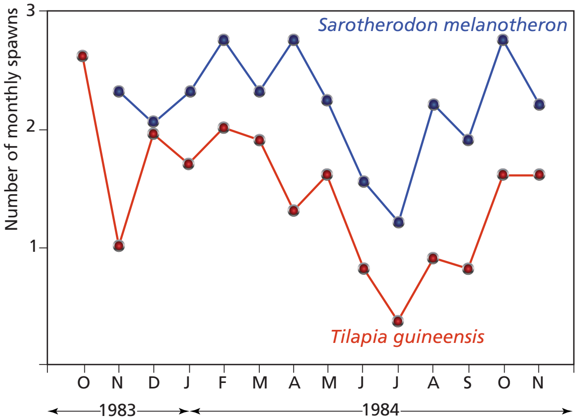


FIGURE 10.5.

Seasonal changes in the spawning frequency for *Sarotherodon melanotheron* and *Tilapia guineensis* in concrete tanks (redrawn from Legendre & Écoutin, 1989).

Several observations appear to reveal the existence of reproductive seasonality that is linked to the abundance of available food. In most of the zooplanktophagous haplochromines of Lake Victoria, there is a small proportion of mature females throughout the year, but there is a peak in reproductive activity during the dry period (June-October) when plankton production is highest owing to the mixing of waters (Goldschmidt & Witte, 1990). This situation is comparable to that of Lake Malawi where the zooplanktophagous 'utaka' spawn between March and July, when the waters mix (Iles, 1960).

A recent study in Lake Malawi confirmed that the reproductive season for these species occurs between March and December, with an additional peak of activity in December. These periods of sexual activity correspond to the ones where plankton production is highest (Duponchelle *et al.*, 2000b). Meanwhile, for the 37 other benthic or pelagic species studied that do not belong to the 'utaka' group, no correspondence has been found between the reproductive season and the annual cycles of temperature, photoperiod, oxygen concentration (for deep water species), conductivity, or phytoplankton abundance. Some species are capable of reproducing throughout the year, while others do so during well-defined seasons, regardless of the depth they inhabit. It appears

INFLUENCE OF PHOTOPERIOD ON THE REPRODUCTIVE CYCLE OF CICHLIDS

The influence of the photoperiod on the regulation of fish reproductive cycles is well-known in temperate systems, but it is often neglected in tropical and sub-equatorial environments where it remains relatively constant.

Yet in the artificial reservoirs of Côte d'Ivoire, the periodicity of the *Oreochromis niloticus* reproductive cycle is strongly correlated with the annual cycle of the length of day (figure 10.6). Analyses have shown that among the various environmental factors (precipitation, variations in water level, water temperature, chlorophyll *a* concentration) that are potentially involved in the regulation of the reproductive cycle of this species, photoperiod is the only factor that contributes significantly to the model.

Indeed, it accounts for 66 to 85% of the variation in reproductive seasonality, depending on the reservoir (Duponchelle *et al.*, 1999).

A good correlation was also observed with the annual cycle of chlorophyll *a* concentrations (used as an indicator of trophic availability), or with water temperature.

However, in experimental conditions, with optimized regular feeding, reproductive activity ceased when the photoperiod decreased (Baroiller *et al.*, 1997; Desprez & Mélard, 1998), even in optimal temperatures. These various results, in both natural and experimental conditions, led to the following hypothesis.

The reproductive season in Tilapias could be controlled at two levels: an upper level, controlled by a constant astronomical factor (photoperiod) which determines the periodicity of the reproductive season, and a lower level, regulated by the combination of different environmental variables (temperature, precipitation, availability of resources, etc.) which affect the inter-annual variations of reproductive duration and intensity (Duponchelle *et al.*, 1999).

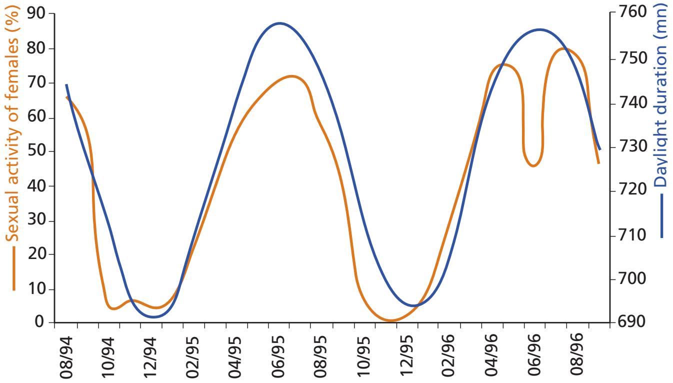


FIGURE 10.6.

Correlation between photoperiod and the reproductive seasonality of *Oreochromis niloticus* in small agropastoral reservoirs of Côte d'Ivoire (adapted from Duponchelle *et al.*, 1999).

that the reproductive modalities observed in these species, most of which feed on benthic invertebrates, are probably influenced by variations in the abundance of their preferred prey (Duponchelle *et al.*, 2000b). This also appears to be the case for species confined to rocky zones or 'mbunas' (Marsh *et al.*, 1986). These authors have noted that ten Cichlidae species, sexually active throughout the year, living in rocky physical systems, had a peak of reproductive activity during the spring (August-October) and a second one in early autumn (February-March), but were less active during cold periods (May-June). The spring peak coincides with significant algal development, whereas the autumn peak corresponds to a large biomass of epilithic algae.

It was also highlighted in the pelagic Clupeidae of Lake Tanganyika, *Limnothrissa miodon* and *Stolothrissa tanganicae*, which reproduce throughout the year, that the main period of juvenile production coincided with the period of maximum plankton development (Coulter, 1970). It appears that the maximum spawning period varies according to the lake's regions, in relation to zooplankton production (Chapman & Well, 1978).

In other cases, it is difficult to provide an interpretation based on food availability. For the three Tilapias endemic to Lake Malawi, which have a well-defined reproductive period (Lowe McConnell, 1987), *Oreochromis saka* and *O. lidole* spawn in shallow waters before the beginning of rains (October-November), in the hottest period of the year. Meanwhile, *O. squamipinnis* spawns during the rainy season (December-February) in deeper waters.

Flexibility of the spawning season

A species's spawning season can change if the conditions in the physical system change as well. This is the case for instance if a dam is built on a river. Thus, *Pellonula leonensis* (Clupeidae) which reproduces during the dry season in the Volta River, spawns all year round in Lake Volta. Likewise, *Physailia pellucida* (Schilbeidae), which spawns after the rainy season in rivers, also spawns throughout the year in the lake (Reynolds, 1974).

Other species use different strategies depending on geographic region, and thus according to climatic zones. Thus, all populations of *Brycinus imberi* (Alestidae) reproduce during the flood in the Zambezi (tropical regime) (Marshall & van der Heiden, 1977), while communities in Côte d'Ivoire (equatorial or subtropical regime) reproduce throughout the year with no specific synchrony with the flood regime (Paugy, 1982b). Moreover, potential fecundities differ significantly. We thus note that Ivorian individuals that may find more favourable conditions at some point in the year are individually less fecund than specimens from the Zambezi. There is thus a reproductive strategy adapted to the local conditions of the physical system.

Adaptive strategies

In some species, it has been noted that egg size is relative to parental size. In *Sarotherodon melanotheron* for example, the average weight of eggs is less than 5 mg for females weighing 50 g, but can reach 20 mg for 200 g females (Peters, 1963). A significant relationship between female size and egg size has also been observed in Lake Victoria Haplochromines (Glodschmidt & Witte, 1990). On the other hand, no relationship between egg size and female size was observed in *Oreochromis niloticus* in Côte d'Ivoire (Duponchelle *et al.*, 2000a), nor in 39 species of *Haplochromis* in Lake Malawi (Duponchelle *et al.*, 2000b).

The number and size of oocytes can also vary within the same species, and for individuals of the same size. Peters (1963) showed, for instance, that in laboratory conditions, a female *S. melanotheron* can produce either a large number of small eggs or a small number of large eggs. In the lagoons of Côte d'Ivoire, we have also noted that for females measuring 180-220 mm, the average weight of oocytes was 28 mg in the lagoon (F = 329 eggs per spawn and per female), from 15 to 18 mg in 'acadja' parks (F = around 500 eggs), and only 12 g in intensive-breeding fish parks (F = 726 eggs) (Legendre & Écoutin, 1989). Nonetheless, regardless of the spawning technique, the relative weight of gonads in relation to body weight remained the same, which suggests that the ovarian quantity generated during the reproductive cycle is a specific constant. That said, while this character is the least variable in *Oreochromis niloticus*, some inter-population and intra-population differences in successive years have been reported in Côte d'Ivoire (Duponchelle *et al.*, 2000a).

In Senegal, *S. melanotheron* populations show different reproductive and growth characteristics depending on the salinity of the estuaries they are in (Panfili *et al.*, 2004a). In the saltiest physical systems, size at first sexual maturity is smaller, relative fecundity is higher, oocytes are smaller, and growth slower. The most marked changes are observed in hyperhaline conditions (> 60 psu). Similar observations have been made in *Ethmalosa fimbriata* (Panfili *et al.*, 2004b). In this Clupeid species, the lack of genetic differentiation in the studied populations suggests that variations in reproductive and growth traits are not due to genetic isolation. Rather, they are probably phenotypic responses to marked fluctuations in salinity (Panfili *et al.*, 2004b).

CHANGES IN CICHLID REPRODUCTION INDUCED BY ENVIRONMENT

To test if the reproductive differences observed between *Oreochromis niloticus* populations from various artificial reservoirs in Côte d'Ivoire were induced by the environmental conditions encountered or if they had a genetic basis, two approaches were adopted:

- Fishes from two of the monitored reservoirs in Côte d'Ivoire, whose reproductive characteristics were among the most pronounced, were captured, marked, and placed in the same environment for five months. At the end of this period, they were sacrificed and their reproductive characteristics were compared.
- At the same time, the genetic characterisation of 300 specimens from each of the two populations was carried out using microsatellite markers.

No genetic difference was found between the two populations. After sharing the same environment for five months, no difference was found in the reproductive characteristics of the two populations.

Fecundity and oocyte size,which were very significantly different in their respective physical systems, were identical in the communal pond (figure 10.7). This led to the conclusion that the differences in reproduction observed between the two populations in natural conditions were a phenotypic response to their different environments. (Duponchelle *et al.*, 1998).

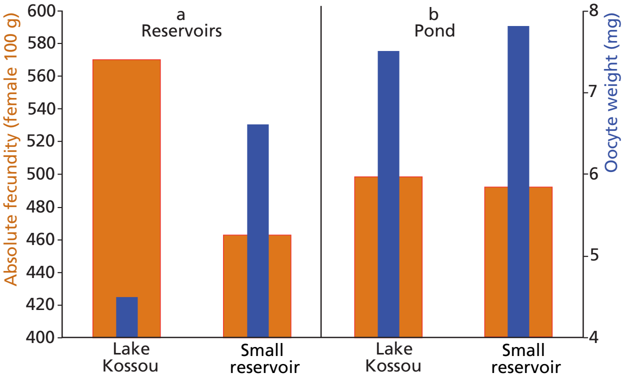


FIGURE 10.7.

Reproductive characteristics (fecundity and oocyte weight) of two populations of *Oreochromis niloticus* females in their respective reservoirs of origin in Côte d'Ivoire (a) and after 5 months of rearing in communal pond (b) (adapted from Duponchelle *et al.*, 1998).

In *Oreochromis niloticus*, marked variations in size at first sexual maturation (Duponchelle & Panfili, 1998), reproductive season (Duponchelle *et al.*, 1999), fecundity and egg size (Duponchelle *et al.*, 2000a) have been observed between populations of different artificial reservoirs in Côte d'Ivoire. Significant variations in reproductive characteristics have also been observed within each population over successive years. Genetic analyses and experiments in controlled environments (see box "Changes in cichlid reproduction induced by environment") have shown that the reproductive differences observed in the reservoirs were phenotypic responses to variations in the environmental conditions encountered (Duponchelle *et al.*, 1998).

The remarkable plasticity of the reproduction of *S. melanotheron* and *O. niloticus* depending on environmental conditions are illustrations of adaptive strategies that can be developed by Cichlidae. While the mechanisms involved in the regulation of their reproductive cycles have not yet been identified, a few elements can serve as a starting point. Vitellogenesis takes place very rapidly in Cichlidae. In *O. niloticus*, for example, a full gonadal cycle lasts 27 days on average and can be as short as 15 days in non-incubating females (Tacon, 1995). The rapidity of their gonadal cycle thus allows Cichlidae to adapt their reproductive characteristics very quickly in reaction to changes in their environment (see box "Rapid phenotypic changes in Nile tilapia, *Oreochromis niloticus*").

RAPID PHENOTYPIC CHANGES IN NILE TILAPIA, *OREOCHROMIS NILOTICUS*

DUPONCHELLE & LEGENDRE, 2001

In Côte d'Ivoire, one of the major characteristics of certain artificial lakes is the presence of a large number of dead tree stumps.
To find out if the resulting spatial structure can influence the reproductive characteristics of *Oreochromis niloticus*, fishes from the same parents were placed for two months in concrete tanks with three different types of spatial organization:

- bare concrete tanks serving as controls;
- tanks with a sand-covered bottom;
- tanks with an artificial reef created from concrete blocks.

After two months, analysis of the fishes showed that Tilapias were capable of adapting to the organization of their living space by modifying their living traits. Females had lower fecundity in the tanks with reefs than in the control tanks (figure 10.8). An opposing trend was noted for egg size. These results also suggest that spatial organization, through the increase in the number of shelters and nesting sites, exercises a greater influence on Tilapia reproduction than the intrinsic quality of the spawning substrate does.

Even more significantly, it is the first time than an experiment demonstrated such a swift adaptive response in fishes. It occurred within one to two reproductive cycles, that is, around four to six weeks for the species (Duponchelle & Legendre, 2001).

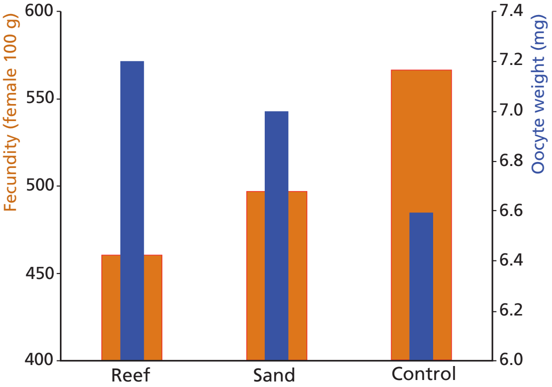


FIGURE 10.8.
Fecundity of *Oreochromis niloticus* females and mean oocyte weight depending on rearing environment.
For clarity, values were equated for 100 g standard females (redrawn from Duponchelle & Legendre, 2001).

Parental care

Parental care refers to any assistance provided by parents whith the purpose of ensuring better survival of eggs after fecundation. Such assistance may range from the construction of nests to the brooding of eggs and fry, including egg ventilation to ensure oxygenation or to remove silt.

Only 22% of teleost families (Blumer, 1982), especially ones with freshwater presence, provide a form of parental care. Care is more often provided by males (11% of teleost families) than by females (7% of families), while biparental care is seen in 4% of families (Sargent & Gross, 1992) (see box "Types of parental care").

TYPES OF PARENTAL CARE

Parental care in fishes takes many forms:

- guarding eggs and larvae by chasing off other fishes and predators,
- construction and maintenance of a nest,
- incubation of eggs and larvae in the mouth or gill cavity,
- transport of eggs from one site to another, generally in the mouth,
- cleaning of spawning sites,
- ventilation of eggs using fins to ensure better oxygenation and remove deposited sediments.

It has been suggested that parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990) or densely-populated systems characterized by significant predation on eggs and juveniles. Such parental care practices helped reduce hazards, but this theory ought to be backed by observations. The main function of parental care is to protect the young from predators and a wide variety of behaviours exist in substrate brooders and mouth brooders.

Substrate brooders keep their spawn on or near a substrate and watch over their youngs until they are independent, while mouth brooders transport their youngs in the mouth from spawning until they are also independent. There are paternal, maternal, and biparental incubators (see box "Incubation period for cichlids").

The number of eggs that can be incubated in the mouth varies depending on species and individual size. In *O. macrochir*, females measuring 300-350 mm LS incubate up to 800 eggs (Marshall, 1979). Similar values have been observed in the paternal mouth brooder *S. melanotheron* (Legendre & Écoutin, 1989).

The practice of parental care is fairly widespread in African fishes (Blumer, 1982) and particularly in Cichlidae (Keenleyside, 1991). Many Cichlidae substrate brooder species are widely distributed in north and west Africa, and several species are also present in Lake Tanganyika, while the majority of mouth brooder Cichlidae species (over 70% of Cichlidae) are limited to the East African great lakes (see box "Biparental mouth brooder").

INCUBATION PERIOD FOR CICHLIDS

Substrate brooders

The sticky eggs are deposited on a hard surface, fertilized, and hatch a few days after the two parents guard the eggs with great vigilance. Eggs are smaller but more numerous than in mouth brooders. After hatching, the young larvae are hidden in a hole or in vegetation. When they can swim freely, they remain grouped near the substrate under the watchful eye of the parents.

Mouth brooders

There are three broad categories:

- ***maternal mouth brooders*** constitute the most common system. Spawning takes place on a substrate often prepared by the male, and the non-sticky eggs, released individually or in small batches, are rapidly taken into the mouth by the female. The male releases its sperm as the female collects the eggs, or fertilizes them in the mouth. The female then incubates the eggs until they are fully independent. In some cases, the female abandons them from time to time in order to feed, then takes them back again into the mouth. This behaviour has been observed in numerous Cichlidae in the East African lakes;
- ***paternal mouth brooders*** are found in only a few species. It is the case for *Sarotherodon melanotheron*;
- ***biparental mouth brooders*,** that is, mouth brooding by both parents from spawning until the young are independent, is also rare in Cichlidae. It has been observed in *Sarotherodon galilaeus*.

There are of course many variants for each type of mouth brooding.

The number of eggs that can be incubated depends on the size of the oral cavity. For *S. melanotheron*, a paternal mouth brooder, the number of eggs that can be incubated in relation to the number of eggs released depends on the size of the male compared with the female. It has indeed been shown that the volume of the male's oral cavity increases faster with the male's size than the size of the spawn with the female's size (Legendre & Trébaol, 1993). As a result, smaller males cannot incubate all the eggs released by a female of the same size, as they would occupy 90% of the oral cavity. Incubation is thus more successful when females pair off with larger males.

BIPARENTAL MOUTH BROODER

Xenotilapia spiloptera is an endemic Cichlidae species in Lake Tanganyika that is a biparental mouth brooder (Konings, 1992).

The species forms shoals but, as the reproductive season approaches, each shoal separates into several couples that seek a rocky habitat.

The couple is established by repeated courtship between the male and the female, and then settles in a small territory about 30 cm in diameter that is defended against other fishes.

A few days prior to spawning, there is a noticeable increase in mutual courtship, and a slight change in colour pattern.

At the time of spawning, the female cleans the site and deposits a few eggs. The male, which usually waits behind her about 3 cm above the substrate, then positions himself above the eggs and fertilizes them. The female waits for the male to go away then takes the fertilized eggs in her mouth.

After a brief pause during which the male chases off intruders, the female swims to the substrate again, waits for the male to position himself behind her, and releases a new series of eggs. The spawn may have 40 eggs, but it appears that quantity depends on the buccal capacity of the female.

The first nine or twelve days after spawning, the female incubates the embryos and does not eat. After this period, the larvae are transferred to the mouth of the male, which incubates them for another ten days. At the end of incubation, the male releases the fry in the territory defended by both parents. In the first few days, the youngs can seek shelter in the male's mouth, but they generally remain on the substrate and navigate within the territory. Youngs measure around 1.5 cm at the time of release, and it takes two years for them to reach the adult size of 10 cm.

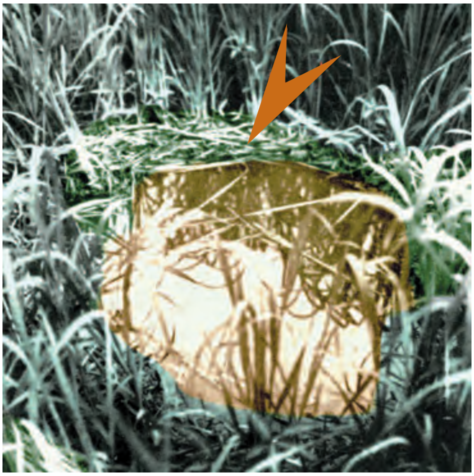
There are a few exceptions such as *Oreochromis* and *Sarotherodon*. The paternal mouth brooder *S. melanotheron* is a species common to all brackish waters along the West African coast, while the biparental mouth brooder *S. galilaeus* is widely distributed in the north of tropical Africa.

Fishes build nests

A form of protection for eggs and larvae is to place them in a nest that may or may not be guarded by the parents. There is a wide variety of nests in fishes. Some are constructed depressions as with *Heterotis niloticus*) (see box "Nest of *Heterotis niloticus*"), or consist of burrows, as with *Protopterus annectens* (see box "Nest of *Protopterus annectens*"). Floating nests are a fairly common form in physical systems presenting a risk of anoxia. This is the case for nests of *Gymnarchus niloticus* built using plants, and Mormyridae nests that are also built using plant matter (see box "Nest of *Gymnarchus niloticus*"). In *Pollimyrus petricolus*, a species endemic to Niger, males actively guard the nest built from decomposing roots and branches of *Echinocloa stagnina*, which allows development of micro-invertebrates that serve as food for their young. Floating foam nests are also built by *Hepsetus odoe*.

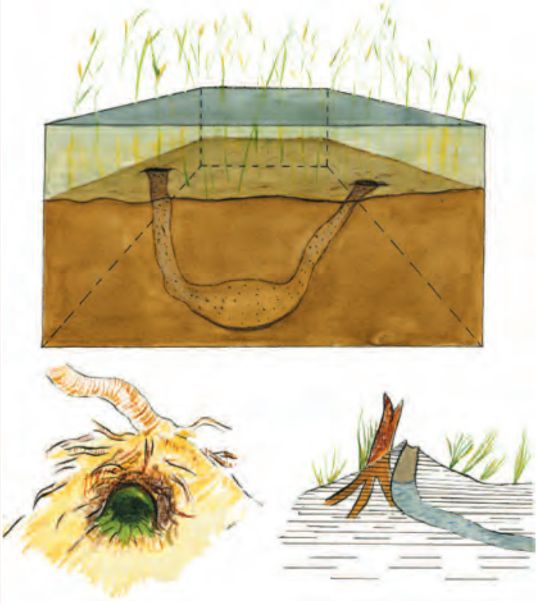
NEST OF *HETEROTIS NILOTICUS*

The nests of *Heterotis niloticus* are built in herbaceous vegetation.
They are comparable to small basins measuring about 1.2 m in diameter, with a slightly excavated centre located at a depth of about 30 cm.
The bottom is bare and flat.
The compact rims are about 20 cm thick at the top and projects slightly above the water surface.
They are constructed using plant stems that have been removed from the centre of the nest. Parents stay near the nest once the eggs have been released.



Eggs are fairly small (2.5 mm in diameter) and orange.
They hatch about two days after release.
Youngs have long, dark red gill filaments that extend outside the gill cover.
They rapidly form a shoal around 30 cm in diameter occupying the centre of the nest.
On the fifth or sixth day, they leave the nest, still in a dense shoal, and under the protection of the parents (Svensson, 1933).

NEST OF *PROTOPTERUS ANNECTENS*



The lungfish burrows into the bottom to reproduce. Nests are generally built in shallow areas covered by herbaceous plants. The most common type is a **U**-shaped tube with two openings, one measuring 20 to 30 cm in diameter and the other 10 to 15 cm only. The nest is about 40 cm deep and the internal diameter is identical to that of the smaller opening. It contains a larger chamber (20-30 cm in diameter) containing the eggs and larvae.

There is some variability in nest shape. Some may have three openings, while others may be constructed on the bank and have only one.

The male guards the nest until the youngs have left it. He also ventilates the water inside the nest.

It has been observed that eggs inside the nest may be of different sizes. It is thus possible that the nest may be used by more than one female, or if not, that the female has intervals in spawning.

NEST OF *GYMNARCHUS NILOTICUS*

Gymnarchus niloticus is only found in the Nilo-Sudanian zone. It can reach a length of 1.60 m, and its pale yellow spherical eggs are very large (9 to 10 mm in diameter).

In the Niger floodplain, during the flood, *Gymnarchus* builds a floating nest in prairies of burgu millet (*Echinocloa stagnina*, also named hippo grass) submerged in depths of 1.5 to 2.2 m. The nest is formed from burgu millet stalks that are 2 to 3 m long, cut at the base and folded in on each other to define a cavity of about 50 cm length by 20 cm width. It forms a sort of floating pouch that measures around 150 cm by 80 cm and floats on the surface of the water. The parents enter the nest through a tunnel and deposit about a thousand eggs. Hatching is thought to take place some five days later, and the young leave the nest after 18 days, when the yolk sac has been completely resorbed. When they hatch from the egg, youngs have external gills that extend out of the brachial cavity, but they are quickly resorbed.

Parents are never far from the nest in order to protect it from other fishes, particularly lungfish which appear to have a liking for *Gymnarchus* eggs (Daget, 1952).

Origin and evolution of parental care

Fishes that do not provide parental care lay a large quantity of small eggs that are dispersed in the pelagic environment. This is the case for many species belonging to the Clupeidae, Alestidae, Cypriniformes, etc. families. In running water, these eggs drift downstream and the larvae colonize fluvial annexes where they find both food and shelter. There is little chance that pelagic eggs need to withstand anoxic conditions, but they are exposed to much predation. This reproductive mode may represent ancestral conditions. Encouraging dispersion could increase the chances of survival in an unstable environment.

Reproduction by dispersion does not encourage the development of parental care, and it is possible that during evolution, some species found it more advantageous to recognize and select sites that were conducive to spawning. This is especially true for freshwater habitats that are very temporally and spatially heterogeneous, with some of the biotopes less favourable to egg development than others. In reality, many species that do not practice parental care do not lay their eggs at random, but deposit them among plants, in gravel, in holes, etc.

Once favourable habitat has been identified and regularly used, there may be an adaptive advantage to staying there, which is the key step in the appearance of territorial behaviour as well as site preparation and defensive behaviour, in order to monopolise the sites that are most favourable to reproduction.

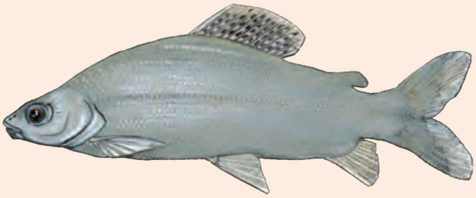
Substrate brooding, which is seen in both riverine and lacustrine species, is considered an ancestral behaviour in Cichlidae. Their very adhesive eggs, compared with those of mouth brooders, tend to support the hypothesis of a more ancient origin on the phylogenetic level.

Mouth brooding, meanwhile, is more specialized and more recent. It probably derives from an ancestral substrate brooding behaviour in which the act of taking the eggs in the mouth to transport them from one site to another could have become a fixed component of reproductive behaviour. The adaptive advantage is that it keeps embryos away from predators and limits competition for reproductive sites. We may also see a means of escaping the need for a substrate to reproduce, when benthic space is highly sought after (Balon, 1978).

In the beginning, among substrate brooders, parental care was probably provided by both parents. Mouth brooding evolved independently in phylogenically distant groups such as Ariidae, various Anabantidae, Arapaimidae, and Cichlidae. For the great majority of Teleosts, the male is most often the mouth brooder (Blumer, 1982). In Cichlidae, meanwhile, the female provides the care, and this investment may be an innovation in this family (Stiassny & Gerstner, 1992). In some haplochromines of Lake Malawi, it has been observed that mouth brooding can last until the young reach a length of 3 cm (Turner, 1994; Duponchelle *et al.*, 2000b). This long period of parental care given to the young after spawning, as observed in Cichlidae, is also unusual in teleost fishes.

A special case is that of species whose parents place the eggs in floating nests made from plants or foam (for instance *Hepsetus odoe*). This behaviour may be interpreted as an adaptation to development in anoxic waters (as eggs are placed on the better-oxygenated water/air interface) but may also be considered an adaptation to an unstable environment.

Growth and ontogeny



Christian Lévêque

Growth is one of the most complex processes for an organism. On the metabolic level, part of the energy consumed will be devoted to increasing its weight, but the proportion of energy used to generate living matter depends on the age of the individuals, their physiological state, their environmental conditions, etc.

First stages of development

Little is known about the first stages of development in African fishes. A review of literature shows that data is only available for 18 of 74 identified families (Cambray & Teugels, 1988).

ONTOGENY AND MAIN STAGES OF DEVELOPMENT

Ontogeny is the process of differentiation of the different stages of development in the life of an organism. We usually distinguish several periods in the life of a fish. (Balon, 1981, 1984 and 1986):

- the embryonic period which begins with fertilization and is characterized by exclusively endogenous nutrition from the egg yolk;
- the larval period which begins with the progressive but rapid transition from an endogenous food supply to exogenous feeding. This period is characterized by the presence of temporary larval organisms;
- the juvenile period begins when the fins are well-differentiated and when all temporary organs are replaced by final organs. This stage ends with the first maturation of gametes. This is usually a period of rapid growth sometimes characterized by a specific colouration;
- the adult period begins with the first maturation of gametes. It is characterized by a decrease in somatic growth rate;
- finally, there is sometimes a period of senescence.

Balon (1985; 1990) distinguishes two broad types of ontogenic trajectories. In the indirect development or "altricial" model, eggs are generally small and produced in large numbers. They yield small, underdeveloped young larvae with only a small volume of yolk that is not sufficient for producing the final phenotype. These young larvae must feed rapidly on small particles to complete their development and are highly vulnerable during this period. The Alestidae *Alestes baremoze* is a good example of this type of fish (Durand & Loubens, 1971) (figure 11.1), as are *Clarias gariepinus* (Bruton, 1979a) and *Heterobranchus longifilis*.

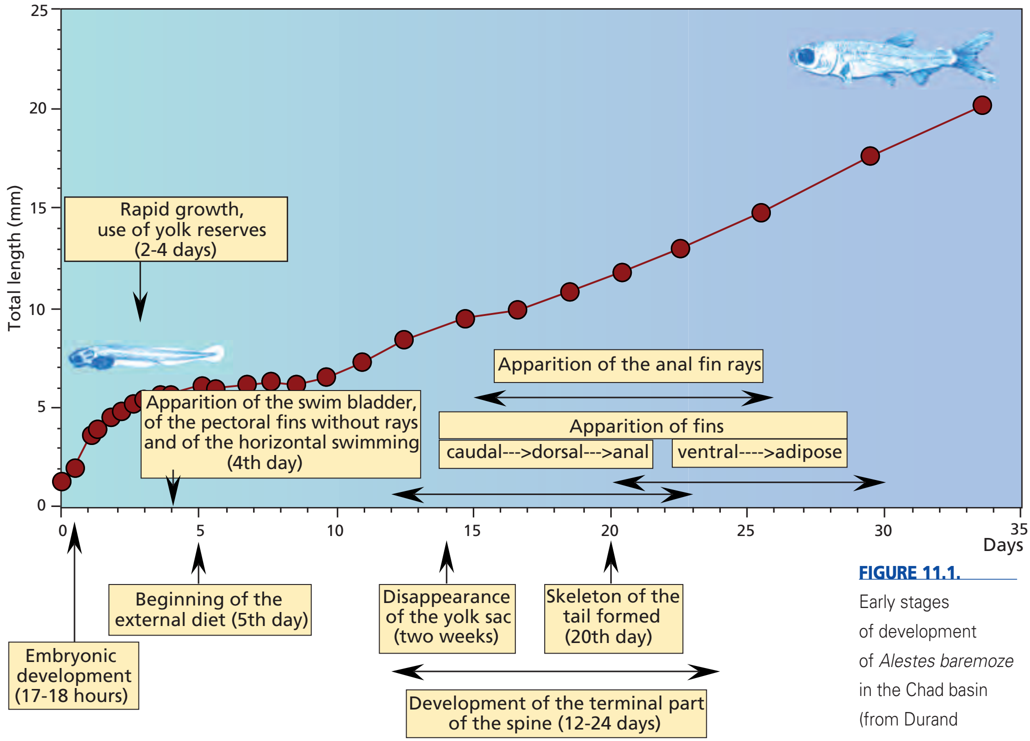


FIGURE 11.1.
Early stages of development of *Alestes baremoze* in the Chad basin (from Durand & Loubens, 1971).

In the direct development ("precocial") model, fishes produce a limited number of large eggs with a large amount of yolk, which allows the embryo to develop to an advanced stage. This shortens or eliminates the larval period, and juveniles are already well-formed and thus less vulnerable when they start seeking an external diet. *Labeotropheu*s, a Cichlidae mouth-brooder from Lake Malawi, is a good example of this type of fish that releases a large juvenile (14% of adult size) only 31 days after fertilization (Balon, 1977) (see box "First stages of development in *Labeotropheus*"). *Cyphotilapia frontosa* illustrates an even more advanced style, as embryos already start consuming an external diet even while in the buccal cavity where they still have a yolk reserve (Balon, 1985).

FIRST STAGES OF DEVELOPMENT IN *LABEOTROPHEUS* (FROM BALON, 1977)

Labeotropheus is an endemic Cichlidae in Lake Malawi. It is a mouth-brooder for eggs and juveniles. Just after spawning, 30 to 50 oval-shaped eggs (3 mm in diameter and 4.4 mm long) are immediately collected in the mouth by females. They are fertilized in the oral cavity of the female which is almost completely filled by eggs.

The eggs are incubated for 6 days before hatching. At birth, juveniles have a large yolk sac and stay in the oral cavity where they develop and acquire their main morphological structures (skeleton, fins, etc.). The yolk sac is absorbed 21-22 days after fertilization, but embryos stay in the oral cavity of the female up to the 31st day. At this age, they are very well-formed, autonomous, large (approximately 15 mm, i.e., 14% of the adult size) and begin their exogenous foraging.

There are, of course, intermediate modes between the two broad styles discussed above. *Pollimyrus isidori* (table 11.I) is an example.

TABLE 11.I.

Comparative characteristics in the development of some African fish species.

References. 1: Durand & Loubens, 1971; 2: Cambray, 1985; 3: Bruton, 1979; 4: Legendre & Teugels, 1991; 5: Kirshbaum, 1987; 6: Balon, 1977; 7: Balon, 1985. Gonado-somatic index (GSI)

	Altricial development				**Intermediate development**	**Precocial development**	
Species	*Alestes baremoze*	*Barbus trevelyani*	*Clarias gariepinus*	*Hetrobranchus longifilis*	*Pollimyrus isidori*	*Labeotropheus trewavasae*	*Cyphotilapia frontosa*
References	1	2	3	4	5	6	3
Egg size (mm) Egg number	1-1.3 x 10,000	1.5	1.6-1.9 x 10,000	1.5-1.8 x 100,000	2 120	3 x 4.3 30-50	5.6x4.0
GSI	9 %		7-10 %	20-23 %			
Parental care	no	no		no	nest protected (male)	mouth-brooder (female)	mouth-brooder (female)
Embryonic development	< 1 day	2.8 days	1 day	1 day	3 to 4 days	6 days	5 days
Exogenous diet Size (mm)	5 days 6 mm	? 7 mm	3-4 days 6.2 mm	3 days 10 mm TL	15 days 8 mm	25-30 days 15 mm	14 days 15 mm
Disappearance of the yolk sac Size (mm)	12 days 7 to 8	11.5 days 7.1	3 days 6.2	3-4 days	14 days 8	21 days 13-14	
End of larval time Size	30 days 17.5 mm	50-60 days 20 mm	14 days ? 12.1 mm		40 days 15 mm		feeding oral cavity
Juvenile freedom Size						31 days 15 mm	54 days 23 mm LT

Growth estimation

Growth can be estimated using changes in size or biomass in a given time interval. It corresponds to the organism's energy intake that is not used for maintaining metabolism.

There is a great deal of literature on growth estimation methods, and researchers agree that it is difficult to determine the age of tropical fish. Marks on bony structures are harder to read and interpret than on temperate fishes (Mérona *et al.*, 1988). Nonetheless, certain investigations have shown that growth marks generally coincide with drops in temperature, which often occur during low water periods. In some cases, growth marks can be associated with gonad maturation which generally follows a long period of fasting. Formation of marks on bony structures is thus the result of various physiological disturbances, and it is necessary to determine which ones are at play for a given species.

Determination of growth and age were long considered key elements for models of fish stock dynamics. As a result, a large number of growth curves were calculated for African fishes (Mérona *et al.*, 1988), but most did not attempt to account for the relationships between growth and other biological parameters. Consequently, many of these results are of limited use to understand species biology.

Growth models

Annual growth can be described as an asymptotic curve, and the most widely used is von Bertalanffy's model (1938). It is based on bioenergetic principles, with the hypothesis that growth rate is equal to the difference between the anabolic rate and the catabolic rate. The von Bertalanffy model is expressed as the equation:

$$Lt = L_\infty \left\{1 - e^{-K(t-t_0)}\right\}$$

where **L_∞** is the asymptotic length, Lt fish length at age t, K is a constant that describes the rate of growth, and t_0 is the hypothetical time at which size is zero.

Similarly, fish weight at time t is given by the equation:

$$Wt = W_\infty \left\{1 - e^{-K(t-t_0)}\right\}$$

While von Bertalanffy's model provides us with a smooth annual growth curve, growth is not a continuous process. At times there are long periods in a year during which growth stops or is sharply reduced. In other words, growth can take place during rather short periods. For instance, 75% of the growth of young *Oreochromis andersoni* and *O. macrochir* in the Kafue River occurs during the six weeks of peak water levels (Dudley, 1972). During the dry season, growth is very slow but does not stop (Kapetsky, 1974).

Welcomme & Hagborg (1977) proposed a growth model for fishes in flood zones, which takes into account a rapid initial increase in length followed by a slower growth period. In the formula $L_{t+t'} = L_t + G\,(e^{t'})$, the values of L_t for successive years are the same as the ones provided by the von Bertalanffy model, but growth during the year is calculated for each week. This gives a growth curve that is a more accurate representation of what happens on the field.

Growth in length and weight gain are not always correlated. Weight gain includes the creation of fat reserves, for instance, or gonad development, phenomena that do not necessarily involve an increase in length (table 11.II).

TABLE 11.II.

Some growth data about African fish (from Mérona *et al.*, 1988.
S: sex (m: male, f female, t: sexes blended);
L: length (TL: total length; SL: standard length; FL: fork length);
M: size at first maturation; A: average longevity (years);
AMS: average maximal size; MSO: maximal size observed;
L_∞, K and t_0: parameters of the von Bertalanffy equation.

Species	Sex	Locality	L	M	A	AMS	MSO	L_∞	K	t_0
Mormyrus rume	t	Niger-Benue	TL	425	6,0	785		2 048	0.071	- 0.483
Petrocephalus bovei	t	Côte d'Ivoire	SL	65	2,5	95	110	99	1.104	- 0.203
Hepsetus odoe	m	Lake Liambezi	FL	200		305	370	307	1.712	- 0.237
Hepsetus odoe	f	Lake Liambezi	FL	250	5,0	413	470			
Hydrocynus vittatus	m	Lake Bangweulu	FL	390	8,0	605		796	0.266	- 0.337
Hydrocynus vittatus	f	Lake Bangweulu	FL	390	11,0	689		740	0.229	- 0.145
Alestes baremoze	m	Chad	SL	180	5,0	231	285	252	0.696	- 0.243
Alestes baremoze	f	Chad	SL	205	6,0	263	326	292	0.518	- 0.318
Bagrus meridionalis	m	Lake Malawi	TL	340	11,0	607	890	1 048	0.092	+ 0.017
Bagrus meridionalis	f	Lake Malawi	TL	360	17,0	832	970	1 092	0.091	+ 0.017
Oreochromis niloticus	t	Lake Mariut	TL		5,0	376		426	0.460	+ 0.541
Coptodon zillii	m	Niger	TL	200	6,0	300	320	310	0.531	+ 0.226
Coptodon zillii	f	Niger	TL		6,0	269		274	0.603	+ 0.252
Lates niloticus	f	Chad	SL	24				953	0.191	- 0.749

Length-weight relationships and coefficient of condition

The relationship between fish length and weight takes the form:

$$\log W = \log a + b \log L$$

where W is the weight, L the length, a and b are constants.

When growth is isometric, that is, when the fish shape does not change with growth, b is equal to 3. A value below 3 indicates that weight gain is inferior to increase in length. The opposite holds true if b is above 3 (table 11-III).

TABLE 11-III.

Length-weight relationships of some African fish species.
Constant values: a and b.

Species	log a	b	Range size (mm)	Geographical origin	Source
Polypetridae					
Polypterus senegalus	4.556	2.760	375	Nile	Hickley & Bailey, 1986
Mormyridae					
Hyperopisus bebe	5.972	3.370	400	Nile	Hickley & Bailey, 1986
Marcusenius furcidens	4.459	2.785	75-225	Côte d'Ivoire	unpublished
Marcusenius senegalensis	4.951	3.040	75-205	Côte d'Ivoire	unpublished
Marcusenius ussheri	4.342	2.746	20-235	Côte d'Ivoire	unpublished
Mormyrus cashive	5.074	3.010	585	Nile	Hickley & Bailey, 1986
Mormyrus rume	4.389	2.706	20-430	Côte d'Ivoire	unpublished
Petrocephalus bovei	4.533	2.907	30-120	Côte d'Ivoire	unpublished
Arapaimidae					
Hetrotis niloticus	4.973	3.030	880	Nile	Hickley & Bailey, 1986
Hepsetidae					
Hepsetus odoe	5.460	3.258	90-290	Côte d'Ivoire	unpublished
Alestidae					
Hydrocynus forskalii	4.714	2.943	75-275	Côte d'Ivoire	unpublished
Hydrocynus forskalii	4.781	2.930	470	Nile	Hickley & Bailey, 1986
Alestes baremoze	4.875	2.987	30-250	Côte d'Ivoire	unpublished
Alestes dentex	4.485	2.790	360	Nile	Hickley & Bailey, 1986
Brycinus nurse	4.492	2.935	30-210	Côte d'Ivoire	unpublished
Brycinus nurse	4.464	2.900	155	Nile	Hickley & Bailey, 1986
Brycinus imberi	4.616	3.031	28-153	Côte d'Ivoire	unpublished
Brycinus macrolepidotus	4.554	2.940	23-308	Côte d'Ivoire	unpublished
Brycinus macrolepidotus	4.513	2.880	315	Nile	Hickley & Bailey, 1986
Brycinus longipinnis	4.792	3.115	42-104	Côte d'Ivoire	unpublished
Micralestes acutidens	4.628	2.960	48	Nile	Hickley & Bailey, 1986
Citharinidae					
Citharinus citharus	4.357	2.910	310	Nile	Hickley & Bailey, 1986
Citharinus latus	4.369	2.950	430	Nile	Hickley & Bailey, 1986
Ichthyborus besse	5.993	3.133	185	Chad	Durand *et al.*, 1973
Ichthyborus besse	5.486	3.270	185	Nile	Hickley & Bailey, 1986
Nannocharax fasciatus	4.786	2.994	30-52	Côte d'Ivoire	unpublished
Distichodontidae					
Distichodus rostratus	4.576	2.950	670	Nile	Hickley & Bailey, 1986
Cyprinidae					
Barbus trispilos	4.238	2.766	27-72	Côte d'Ivoire	unpublished
Labeo coubie	4.178	2.825	60-305	Côte d'Ivoire	unpublished
Labeo niloticus	4.448	2.890	390	Nile	Hickley & Bailey, 1986
Labeo parvus	4.311	2.888	40-205	Côte d'Ivoire	unpublished
Labeo senegalensis	4.471	2.934	35-275	Côte d'Ivoire	unpublished
Raiamas senegalensis	4.791	2.995	40-150	Côte d'Ivoire	unpublished
Bagridae					
Bagrus bajad	4.696	2.890	530	Nile	Hickley & Bailey, 1986

TABLE 11-III. (CONT.)

Species	log a	b	Range size (mm)	Geographical origin	Source
Clatoteidae					
Chrysichthys maurus	4.391	2.862	30-205	Côte d'Ivoire	unpublished
Clarotes laticeps	4.561	2.940	400	Nile	Hickley & Bailey, 1986
Auchenoglanis biscutatus	4.573	2.990	375	Nile	Hickley & Bailey, 1986
Clariidae					
Clarias gariepinus	4.432	2.750	78	Nile	Hickley & Bailey, 1986
Schilbeidae					
Schilbe mandibularis (M)	4.535	2.804	30-230	Côte d'Ivoire	unpublished
Schilbe mandibularis (F)	4.648	2.869	30-230	Côte d'Ivoire	unpublished
Schilbe intermedius	5.541	3.312	26-305	Côte d'Ivoire	unpublished
Schilbe niloticus	5.323	3.150	350	Nile	Hickley & Bailey, 1986
Mochokidae					
Synodontis schall (youngs)	3.793	2.562	35-105	Côte d'Ivoire	unpublished
Synodontis schall (adults)	4.969	3.149	105-200	Côte d'Ivoire	unpublished
Synodontis schall	5.021	3.200	330	Nile	Hickley & Bailey, 1986
Synodontis bastiani	4.362	2.837	30-205	Côte d'Ivoire	unpublished
Synodontis clarias	5.501	2.420	290	Nile	Hickley & Bailey, 1986
Synodontis frontosus	4.543	3.000	285	Nile	Hickley & Bailey, 1986
Amphiliidae					
Amphilius atesuensis	4.242	2.703	20-54	Côte d'Ivoire	unpublished
Nothobranchiidae					
Epiplatys spilargyreius	3.987	2.420	36	Nile	Hickley & Bailey, 1986
Latidae					
Lates niloticus	4.669	3.018	100-799	Lake Chad	Loubens, 1974
Lates niloticus	4.479	2.945	100-799	Chari	Loubens, 1974
Lates niloticus	4.474	2.930	1280	Nile	Hickley & Bailey, 1986
Cichlidae					
Hemichromis bimaculatus	4.217	2.885	16-93	Côte d'Ivoire	unpublished
Hemichromis fasciatus	4.601	3.061	32-150	Côte d'Ivoire	unpublished
Hemichromis fasciatus	4.281	2.900	145	Nile	Hickley & Bailey, 1986
Hemichromis letourneuxi	4.388	2.960	63	Nile	Hickley & Bailey, 1986
Oreochromis niloticus	4.463	3.040	400	Nile	Hickley & Bailey, 1986
Oreochromis niloticus	1.055	2.990	Long. totale	Lake Turkana	Harbott & Ogari, 1982
Chromidotilapia guntheri	4.366	2.971	29-125	Côte d'Ivoire	unpublished
Sarotherodon galilaeus	4.158	2.906	25-180	Côte d'Ivoire	unpublished
Sarotherodon galilaeus	4.216	2.950	255	Nile	Hickley & Bailey, 1986
Sarotherodon galilaeus	1.055	3.010	Long. totale	Lake Turkana	Harbott & Ogari, 1982
Haplochromis loati	4.295	2.870	70	Nile	Hickley & Bailey, 1986
Coptodon zillii	4.205	2.924	20-170	Côte d'Ivoire	unpublished
Coptodon zillii	4.405	3.020	210	Nile	Hickley & Bailey, 1986
Mastacembelidae					
Mastacembelus nigromarginatus	5.111	2.775	55-175	Côte d'Ivoire	unpublished

The index K, also called the coefficient of condition, is the relationship between body weight (W in g) and length (L in cm):

$$K = \frac{W}{L^3}$$

This coefficient does not change with length if growth is isometric, which is rarely the case. In many species, however, there may be a variation in body shape or weight during growth, depending for instance on the reproductive cycle or the availability of food. The coefficient of condition makes it possible to monitor the fish's weight. It is thought to be a good instrument for comparing the overall physiological state of populations during a seasonal cycle or between basins with different ecological conditions.

Longevity, size and growth

An important characteristic of fishes is that growth never stops during their lifetime but only slows down with age or size, unlike in mammals and birds. One thus cannot associate an absolute average size to a species and, instead, the maximum size observed (MSO) is most often mentioned. Another characteristic is the great variability in growth at an individual level as well as at the level of populations living in physical systems with different ecological characteristics (food, space, temperature, competition, etc.).

We can posit that the larger a fish, the older it is. If this is the case, there should be a relationship between characteristic growth parameters and a parameter expressing maximum age or size. This indeed holds true, and there is a significant relationship between the maximum size observed (MSO) in wild populations and estimated lengths at 1 year (L1) and 2 years (L2) (Legendre & Albaret, 1991) (figure 11.2). They are, respectively, L1 = 0.205 MSO + 45.57 and L2 = 0.333 MSO + 63.86 for 58 value pairs. These models have been validated experimentally using 6 farmed species.

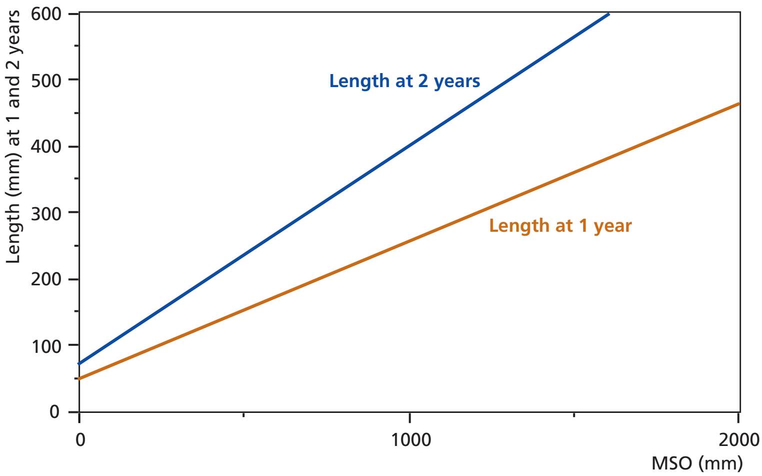


FIGURE 11.2.
Relationship between the maximum size observed (MSO in mm) and the length at 1 and 2 years old for various fresh- and brackishwater African fish species. (data from Legendre & Albaret, 1991).

These results show the existence of a strong positive correlation between the MSO and lengths L1 and L2, which indicates that fishes with a high MSO have a higher growth rate than fishes with a lower MSO.

The ratios L1/MSO and L2/MSO indicate that African fishes reach about a third and then half their maximum size at the end of the first and the second year, respectively (Legendre & Albaret, 1991). These observations agree with the results obtained by de Mérona (1983) who underscored a similar relationship between the asymptotic length, $L\infty$, and the coefficient K of the von Bertalanffy equation: $\log K = 2.186 - 1.048 \log L\infty$ which can be simplified to $K = 153/L\infty$. In order to apply this relationship to field data, de Mérona (1983) also established an empirical relationship between $L\infty$ and the maximum average size (MAS) of the population, which is the average value (or mode) of the largest individuals observed in the population: $L\infty = 1.248$ MAS. The combination of these two ratios allows a rough estimate of the growth curve of African fishes (Mérona *et al.*, 1988), which serves as a quick model for estimating growth. Data available for African fishes appear to show that fishes in tropical regions do not grow faster than those in temperate zones, contrary to common belief, but this would merit further investigation.

If the above results highlight general trends, it should be nonetheless recalled that there is high inter-species variability as well as large differences between populations of the same species living in different hydrographic basins. That said, the MSO remains a practical tool for rapid assessment of growth rates in the absence of other data.

Size and age at first maturity

Puberty is an important event in the life of an animal, and is accompanied by a reduction in somatic growth. Sexual maturation is costly in terms of energy. The reserves accumulated up to that point are used for gonad development, gamete production, development of secondary sex characteristics, etc.

As a result, there are potential conflicts in energy use between:

- continued growth of the individual, who could then produce more eggs;
- immediate production of descendants, which is another type of demographic strategy.

The age at which the fish reaches sexual maturity thus has evolutionary implications. In stable populations, it is believed that the age at first reproduction evolved in order to maximize reproductive success throughout the fish's lifetime. The average size at first reproduction, defined as the size class in which at least 50% of the individuals are mature, is often mentioned. This average size may vary depending on the type of physical system and may not be the same for both sexes (see table 11.II).

Do fishes reach sexual maturity at a given age or size? This question was the object of much discussion but is probably not highly relevant after all, as fishes mature within an age or size range that is probably defined by the combined influence of genetics and environment. For some cichlid species living in different physical systems, growth and age or size at first maturation, as well as MSO, can also be very different (Noakes & Balon, 1982). For *O. niloticus*, the size at first maturation may vary from 140 mm to 390 mm in the natural environment, and for *C. zillii* and *O. mossambicus*, this size can go from 70 and 45 mm respectively in an aquarium, and 135 and 300 mm in a lake or reservoir (table 11.IV).

TABLE 11.IV.
Comparison of size at sexual maturity, maximum size observed and longevity for different populations of cichlids. Data from Noakes & Balon (1982) for *C. zillii* and *O. mossambicus;* from Trewavas, (1983) for *O. niloticus.*

Species	Locality	Size at maturation (mm)	Maximal size (mm)	Longevity (years)
Coptodon zillii	Lake Kinnereth	135	270	7
	Egypt,ponds	130	250	
	Lake Naivasha	90		
	aquarium	70		
Oreochromis mossambicus	Lake Kariba	300	390	8
	South Africa		390	11
	Sri Lanka	150	340	
	Egypt		300	7
	Hong Kong	165	310	4
	aquarium	45		
Oreochromis niloticus	Lake Turkana	390	640	
	Lake George	280	400	
	Lake Albert	280	420	
	Lake Edward	250	360	
	Lake Baringo	180	360	
	Egypt	200	330	9
	Buhuku lagoon	140	260	

Size and age at maturation are thus influenced by the environmental conditions in which the fish grows. Thus, most Tilapias are known for their capacity to reproduce at a smaller size when they are in an environment that does not fully suit them. For four wild populations of *O. mossambicus* living in small pools of water with different sets of environmental characteristics, the age at first maturity varies from 1 to 3 years, and the size at first maturity ranges from 118 to 236 mm for females (James & Bruton, 1992) (table 11.V).

TABLE 11.V.
Biological traits of four South African populations of *O. mossambicus* in different types of habitats (from James & Bruton, 1992).

Habitat	SL 50 % maturity (mm)	Maximal SL (mm)	Weight (g) at SL 50 %	Age (years)	Average size of layings (nb of eggs)	Average size of eggs	Average number of eggs / g
Kowie lagoon							
males	223	289	410	3+			
females	212	262	345	3+	2662	2.9	4.27
Rufanes pond							
males	110	281	40	1+			
females	118	250	49		376	2.4	6.92
Lake Bradshaw							
males	168	266	170	2+			
females	186	246	239	2+	1374	2.8	2.63
Lake Mill Farm							
males	265	356	842	2+			
females	263	359	820	2-3+	3113	3.5	3.32

For Cichlidae, changes in the size at first maturity (SFM) are also influenced by fishing pressure. In Lake George, for instance, intensive fishing is thought to have led to the decrease in the SFM of *Oreochromis niloticus* from 27.5 cm TL in 1960 to only 20 cm in 1972 (Gwahaba, 1973). Likewise, in Lake Turkana, the SFM of *O. niloticus* went from 39 cm in the 1950s to only 29.6 cm in the 1970s (Harbott & Ogari, 1982).

There are many other examples of variations in age or size at first maturity for a single species. But the reasons for the shift from a demographic tactic favouring growth to another one favouring early reproduction have not yet been identified in a convincing manner. Diet-related factors are often mentioned. In fact, field data have shown that Tilapias in poor physiological condition have a strong tendency to reproduce at a smaller size than those in better condition. Such a phenomenon has been observed for *Oreochromis niloticus* in different African lakes (Lowe, 1958), and for *Sarotherodon melanotheron* in the lagoons of Côte d'Ivoire (Legendre & Écoutin, 1996) (figure 11.3).

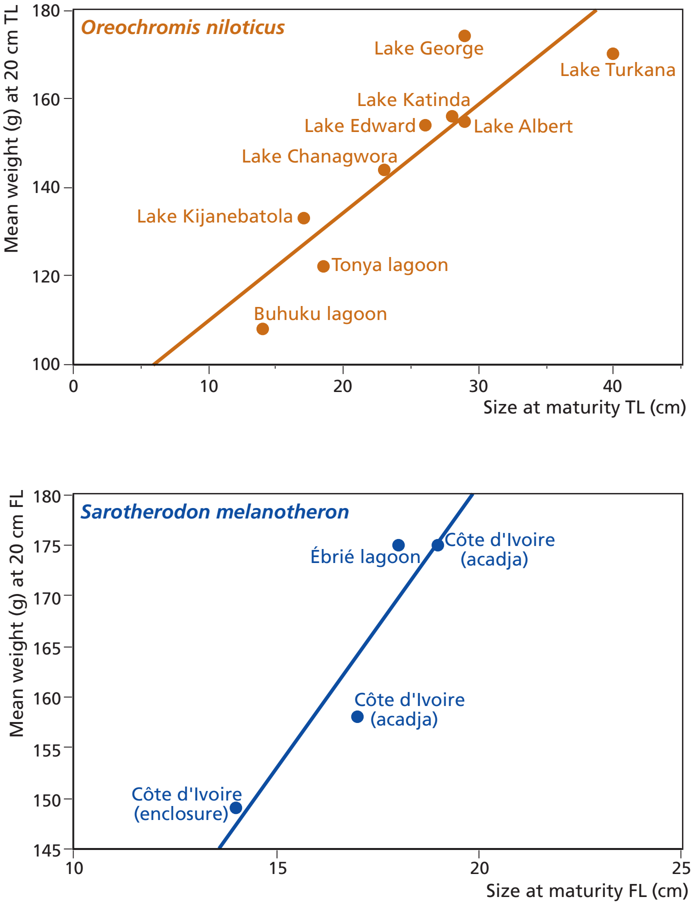


FIGURE 11.3.
Relationships between the mean weight of a 200 mm TL specimen and the size at first maturity (from Legendre & Écoutin, 1996). TL: total length; FL: fork length. *Oreochromis niloticus* populations from several African aquatic environments (data from Lowe, 1958). *Sarotherodon melanotheron* from Côte d'Ivoire (from Legendre & Écoutin, 1996).

Dwarf populations

The existence of dwarf populations that reproduce at much smaller sizes than those customarily observed has also been found in non-cichlid fishes.

In Lake Chad, *Brycinus nurse dageti* is a dwarf population of *Brycinus nurse nurse* and the two species coexist in the lacustrine environment (Bénech & Quensière, 1985). Likewise, in Lake Turkana, *Brycinus nurse nana* is also a dwarf population of *B. nurse* (Paugy, 1986). There are also dwarf populations of *Schilbe niloticus* in Lake Chad (Bénech & Quensière, 1985) and of *Ethmalosa fimbriata* in some bays of the Ébrié lagoon in Côte d'Ivoire (Albaret & Charles-Dominique, 1982). These phenomena have not been well explained to date. The cline detected in *Schilbe mandibularis* (Lévêque & Herbinet, 1982) that leads to dwarf populations in Liberia has not been explained either.

A distinctive aspect of dwarfism is that of "stunted" populations: fishes are not small for their age, but old for their size (Noakes & Balon, 1982). These populations have an accelerated ontogeny which manifests as very early sexual maturity. Thus, *Coptodon zillii* which usually reaches sexual maturity at around 2 or 3 years and a size of 200-300 mm can become mature in a few months at a size below 100 mm when it is introduced into small pools (Fryer & Iles, 1972). In a hot spring, Hecht & Zway (1985) observed a population of *O. mossambicus* in which the largest individual was a male measuring 105 mm SL, while the smallest mature female measured 35 mm SL at one year of age. This "stunting" phenomenon has been observed in nature when shallow lakes dry out, or when small pools are isolated from the main water mass. In Lake Turkana, where *O. niloticus* is mature at an average size of 280 mm TL, it has been observed that populations living in springs isolated from the lake reproduced at 80 mm TL (Harbott & Ogari, 1982). Here, the mechanisms at play are not well-identified either.

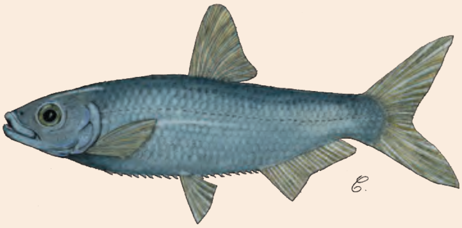
Environmental conditions and growth characteristics

Most species have developed a type of demographic strategy matching a habitat that is favourable to them, as they live there and have adapted to it. Nonetheless, when some species find themselves in worse conditions, they can modify their reproductive behaviour, sometimes within large margins.

The phenotypic plasticity of *Oreochromis mossambicus*, which is found in a large variety of habitats, is well known. Its level of investment in the protection of eggs and young varies depending on the conditions of the physical system. By studying four populations living in physical systems that differed greatly in their abiotic and biotic characteristics, James & Bruton (1992) showed that the species is able to shift from its usual mode of direct development to an indirect one when the conditions of the habitat are more drastic. The populations of the Kowie lagoon and of Mill Farm lake become mature at a length around 70% of their maximum size, which is typical of Cichlidae living in stable physical systems and who have an indirect mode of development. The population in the Rufanes pool, meanwhile, showed early maturity and smaller eggs, characteristics typical of an indirect mode of development. Populations in Rufanes and Lake

Bradshaw, habitats presenting more difficult conditions, are much more fecund than the others. Generally speaking, when all the biological characteristics are taken into account, there is a shift from a direct development style in Mill Farm lake to an indirect one in Rufanes pool.

Diets and food webs



Didier Paugy

Christian Lévêque

All animals use food as their sole source of energy. The search for food is thus a key activity for fishes, which devote a significant portion to their time to this quest, and perhaps even the bulk of their activities.

A major problem for fish is deciding when and where to feed, for how long, identifying the most suitable prey (in terms of size and nutritional value), and finding and capturing such prey. That is the reason why some view feeding strategies as decision-making systems (Cézilly *et al.*, 1991). A fundamental axiom is that such strategies were shaped during natural selection, and that any decision tends to optimize variables such as the rate of energy assimilation, which is correlated with the concept of "fitness" (Pyke, 1984). Thus, given the different options available in their natural environment, animals do not choose their food at random. On the contrary, they carry out activities that provide the highest reproductive success (Pulliam, 1989). As a corollary, food research strategies are adaptations that allow fishes to address, as efficiently as possible, different environmental constraints such as competition, food scarcity, and unpredictable variations in resources.

Some results also suggest that fishes have the capacity to learn and use alternative behaviours that allow them to be more efficient in finding prey, and therefore live longer (Hart, 1986).

Diets and trophic groups

Characterizing a fish's diet requires a qualitative and quantitative description of prey found in its stomach. The simplest assessment method is noting the presence or absence of a type of prey in stomachs. The data is then used to calculate the percentage of occurrence which is the ratio of the number of stomachs in which one type of prey is found with the total number of stomachs studied.

COMPARATIVE ADVANTAGES OF THE METHODS USED FOR THE ANALYSIS OF STOMACH CONTENTS

Methods	Advantages	Failures
Occurrence	simple, easy, quick	rudimentary does not take into account the volume and the relative abundance of prey
Numerical	simple, quick	does not take into account the volume of each prey small-sized prey digested more quickly than large-sized prey difficulty of counting prey during digestion
Volumetric	determines the respective volume of each type of prey gives the most representative picture of the diet	difficult and long to implement difficulty to separate taxa after ingestion and/or at the beginning of digestion
Gravimetric	provides later knowledge of the caloric value of each type of prey	long to implement possible sources of error overestimates the contribution of large size prey
Subjective • dominances • points	allows quick integration of several parameters integrates numerical and volumetric methods	too subjective difficult comparison depending on the users and/or the "encoders"

(from Hynes, 1950 and Hyslop, 1980)

The numerical method consists of counting the number of individuals in a category of prey for the entire sample, then expressing it as a percentage of the total number of prey.

The volumetric or gravimetric methods consist of determining the relative importance in volume or weight of a category of prey in relation to the total volume (or total weight) of all prey.

Subjective methods consist of attributing points to each prey according to its presence or dominance in relation to all examined stomachs.

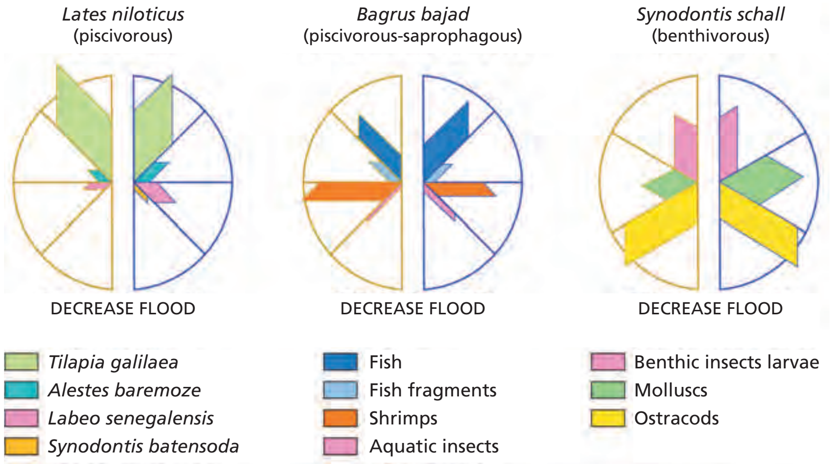
Lauzanne (1976) proposed the use of a Feeding Index (FI) that uses both the percentage of occurrence (%OC) and the volumetric method (%V):

$$\mathrm{FI} = \frac{\%\,\mathrm{OC} \times \%\,\mathrm{V}}{100}$$

This index, which varies from 0 to 100, allows researchers to identify preferences and compare the relative importance of different prey in the diet. It is useful for comparing the diets of a single species according to size, seasons, or biotope, and lends itself well to a clear graphic representation (figure 12.1).

Following Lauzanne (1977, 1983), a few major trophic categories could be recognized in Lake Chad, and this classification can be extrapolated to most riverine tropical African fish communities.

FIGURE 12.1.
Diet composition of *Lates niloticus*, *Bagrus bajad* and *Synodontis schall* in Lake Chad (from Lauzanne, 1976).



Dominant primary consumers

- phytoplanktivorous filter feeders consuming mainly planktonic algae, such as *Sarotherodon galilaeus*;
- grazers or macrophyte consumers such as *Brycinus macrolepidotus*;
- browsers eating the superficial layer of sediment usually composed of sedimented algae, or the periphyton growing on rocky substrates, e.g. *Labeo senegalensis*, *Citharinus citharus*, *Distichodus rostratus*;
- detritivores such as some tilapiines;

Dominant secondary consumers

- the zooplanctivores filtering zooplankton with their gill rakers: *Alestes baremoze*, *Synodontis batensoda*, *Synodontis membranaceus*;
- the benthivores, feeding mainly on benthic invertebrates: *Synodontis schall*, *S. clarias*, *Hyperopisus bebe*, *Heterotis niloticus*. A few species such as *Tetraodon lineatus* feed almost exclusively upon molluscs ;
- surface feeders, eating predominantly terrestrial invertebrates: *Brycinus macrolepidotus*;

Top consumers

- strictly piscivorous fish, feeding exclusively on living fish, such as *Lates niloticus* and all *Hydrocynus* species;
- less strictly piscivore species consuming both fish, shrimps and other invertebrates: *Schilbe mystus*, *Bagrus bajad*, and young *Hydrocynus*.

In practice, species feed on prey available in the ecosystem they inhabit, and diet can change from one site to another or according to the season . As a result, the above classification is only broadly valid (primary, secondary, top). Given this capacity of adaptation to available resources it is possible, for West Africa, to retain just six broad trophic categories: limnivores, micro- and macrophytophages, zooplanktophages, invertivores, omnivores, and ichtyophages (Paugy, 1994).

The food habits of African fish have been the subject of much investigation, and the main findings are given below (table 12.I).

● Item almost exclusively consumed ◉ Item a major constituent of the diet ○ Item occuring regularly in the diet but not dominant

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
Primary consumers														
Citharinus citharus	Lake Chad	13		◉										
Citharinus latus	Sudd	6		◉										
Citharinus latus	Niger	3		◉	○									
Citharinus citharus	Niger	3		◉	○									
Citharinus eburneensis	Bandama	3		◉	○									
Citharidium ansorgii	Niger	3		◉	○									
Citharinops distichoides	Niger	3		◉	○									
Distichodus brevipinnis	Lake Kainji	2	◉		●									
Distichodus engycephalus	Lake Kainji	2	◉		◉									
Distichodus engycephalus	Senegal	25	◉		◉									
Distichodus rostratus	Lake Kainji	2	◉		◉									
Distichodus rostratus	Sudd	6	◉		◉									
Distichodus rostratus	Senegal	25	◉		◉									
Labeo niloticus	Sudd	6		◉										
Labeo parvus	Bandama	20		◉										
Labeo parvus	Senegal	25		●										
Labeo senegalensis	Lake Chad	13		◉										
Labeo senegalensis	Senegal	25		●										
Labeo roseopunctatus	Senegal	25		●										
Oreochromis niloticus	Lake Turkana	5	●											
Sarotherodon galilaeus	Lake Chad	13	●											
Sarotherodon galilaeus	Sudd	6	●	○	○									
Coptodon zillii	Sudd	6	◉		◉									
Secondary consumers														
Polypterus senegalus	Sudd	6					○	●			○	○		
Heterotis niloticus	Lake Chad	13			○	○				◉		○		
Heterotis niloticus	Sudd	6	○	○	◉			○						
Hyperopisus bebe	Lake Chad	12			○				●	○				
Brienomyrus brachyistius	Mono	26						●						
Brienomyrus brachyistius	Cross	11						●						
Brevimyrus niger	Lake Chad	15				◉		◉			○			
Brevimyrus niger	Chari	15				○		◉			○			
Brevimyrus niger	Nigeria	9				◉		◉						
Hyperopisus bebe	Senegal	25						●						
Marcusenius mento	Senegal	25						●						
Marcusenius senegalensis	Senegal	25						●						
Mormyrops anguilloides	Senegal	25						●						
Mormyrus rume	Senegal	25						●						
Marcusenius brucii	Mono	26						●						
Marcusenius bruyerei	Bandama	20						●						
Marcusenius senegalensis	Nigeria	9						●						
Marcusenius furcidens	Bandama	20						●						

TABLE 12.I

Selected data on the dominant food habits of adult fish from north tropical Africa.

Bibliographic references:
1: Adebisi, 1981;
2: Arawano, 1982;
3: Daget, 1962a;
4: Ghazai *et al.*, 1991;
5: Harbott, 1982;
6: Hickley & Bailey, 1987;
7: Hopson, 1982;
8: Hopson *et al.*, 1982;
9: Hyslop, 1986;
10: Im, 1977;
11: King, 1989;
12: Lauzanne, 1975a;
13: Lauzanne, 1976;
14: Lauzanne, 1977;
15: Lek, 1979;
16: Lek & Lek, 1977;
17: Lek & Lek, 1978a;
18: Lock, 1982;
19: McLeod, 1982;
20: Merona, unpublished;
21: Mraja, 1982;
22: Nwadiaro & Okodie, 1987;
23: Ogari, 1982;
24: Pandare & Romand, 1989;
25: Paugy, 1994;
26: Paugy & Bénech, 1989;
27: Robinson & Robinson,1969;
28: Sagua, 1979;
29: Thiero Yatabary, 1983;
30: Tobor, 1972;
31: Vidy, 1976.

TABLE 12.I (CONT.)

● Item almost exclusively consumed ◉ Item a major constituent of the diet ○ Item occuring regularly in the diet but not dominant

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
Mormyrops anguilloides	Mono	26						◉		○				
Mormyrus rume	Mono	26						●						
Petrocephalus bane	Lake Chad	15				◉		◉						
Petrocephalus bovei	Mono	26						●						
Petrocephalus bovei	Bandama	20				○		●						
Petrocephalus bovei	Chari	15				○		◉		○				
Petrocephalus bovei	Lake Chad	15				◉		◉		○				
Petrocephalus bovei	Nigeria	9				◉		●						
Petrocephalus bovei	Senegal	25						●						
Pollimyrus adspersus	Nigeria	9				◉		◉						
Pollimyrus isidori	Lake Chad	15				◉		◉						
Pollimyrus isidori	Chari	15				○		◉			○			
Alestes baremoze	Lake Chad	13				●								
Alestes baremoze	Lake Turkana	7				◉	○	◉						
Alestes baremoze	Senegal	25				○	◉	◉		○				
Alestes dentex	Lake Chad	13			○	●		○						
Alestes dentex	Sudd	6				◉		◉	○				○	
Micralestes acutidens	Chari	16				◉		◉						
Micralestes acutidens	Lake Chad	27				●								
Brycinus leuciscus	Niger	4					◉	◉			◉			
Brycinus longipinnis	Mono	26					◉	◉						
Brycinus macrolepidotus	Mono	26					●	○			◉			
Brycinus macrolepidotus	Lake Chad	13			◉		◉	○						
Brycinus macrolepidotus	Senegal	25			○		○	◉		○	○			○
Brycinus nurse	Mono	26						●						
Brycinus nurse	Senegal	25				○	◉	◉		○				
Brycinus imberi	Mono	26					○	●			○			
Micraleste acutidens	Sudd	6				○		◉						
Nannocharax fasciatus	Senegal	25						●						
Barbus ablabes	Mono	26						●						
Barbus macrops	Senegal	25				○	○	◉						
Barbus chlorotaenia	Mono	26						●						
Barbus callipterus	Mono	26						●						
Barbus bynni	Lake Turkana	21						◉	◉	◉				
Barbus sacratus	Senegal	25				○	○	◉						
Leptocypris niloticus	Senegal	25						●						
Raiamas senegalensis	Senegal	25						●						
Raiamas steindachneri	Senegal	25						●						
Chrysichthys auratus	Mono	26						◉	◉					
Chrysichthys auratus	Nigeria	22				○		●						
Chrysichthys auratus	Senegal	25						●						
Chrysichthys maurus	Bandama	20						●	○					
Auchenoglanis occidentalis	Senegal	25						●						
Clarotes laticeps	Sudd	6						◉	◉			◉	○	
Schilbe mystus	Bandama	20					◉	◉						
Schilbe mystus	Mono	26					○	◉					○	
Schilbe mandibularis	Bandama	31					◉	◉						
Amphilius atesuensis	Bandama	20						●						
Amphilius atesuensis	Senegal	25						●						
Clarias agboyiensis	Mono	26						●						

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1: Adebisi, 1981;
2: Arawano, 1982;
3: Daget, 1962a;
4: Ghazai *et al.*, 1991;
5: Harbott, 1982;
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24: Pandare & Romand, 1989;
25: Paugy, 1994;
26: Paugy & Bénech, 1989;
27: Robinson & Robinson,1969;
28: Sagua, 1979;
29: Thiero Yatabary, 1983;
30: Tobor, 1972;
31: Vidy, 1976.

TABLE 12.I (CONT.)

● Item almost exclusively consumed ◉ Item a major constituent of the diet ○ Item occuring regularly in the diet but not dominant

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
Heterobranchus isopterus	Mono	26					○	◉			○		○	
Heterobranchus isopterus	Senegal	25			○		○	◉		○			○	
Synodontis batensoda	Lake Chad	13				●		○						
Synodontis membranaceus	Lake Chad	13				●								
Synodontis clarias	Lake Chad	12					○	○	●	○				
Synodontis frontosus	Sudd	6		○				◉	◉					
Synodontis schall	Lake Chad	13					○		●	○				
Synodontis schall	Lake Turkana	18				◉		○	○	○		○	○	
Synodontis schall	Niger	29				◉		○	○	◉				
Synodontis schall	Bandama	20					○	◉	◉					
Synodontis frontosus	Lake Chad	10									◉			◉
Synodontis frontosus	Lake Chad	30						◉	◉		◉			
Synodontis frontosus	Chari	10									◉			○
Synodontis obesus	Mono	26						●						
Synodontis ocellifer	Senegal	25						●						
Synodontis schall	Senegal	25						●						
Nothobranchius	Sudd	6				◉		◉						
Aphyosemion geryi	Guinea	24					◉	◉						
Chromidotilapia guntheri	Bandama	20				○		●	○					
Chromidotilapia guntheri	Senegal	25				○		◉		○				
Nematogobius maindroni	Senegal	25						●						
Ctenopoma petherici	Sudd	6			○			●						
Mastacembelus nigromarginatus	Bandama	20						●						
Tetraodon lineatus	Lake Chad	14							●					
Top consumers														
Mormyrops anguilloides	Ogun	1										○	●	
Gymnarchus niloticus	Lake Chad	30											●	
Hepsetus odoe	Ogun	1						○					●	
Hydrocynus brevis	Lake Chad	13											●	
Hydrocynus forskalii	Lake Chad	13						○				◉	◉	
Hydrocynus forskalii	Lake Turkana	8											●	
Hydrocynus forskalii	Senegal	25											●	
Ichthyborus besse	Lake Chad	17						○				◉	◉	◉
Bagrus bajad	Lake Chad	13						○				◉	◉	
Bagrus bajad	Lake Turkana	18										◉	◉	
Bagrus docmak	Lake Turkana	18						○				◉	◉	
Schilbe niloticus	Lake Chad	13					◉	○		○		○	◉	
Schilbe niloticus	Mono	26					○	◉			◉		○	○
Schilbe uranoscopus	Lake Chad	13					○	○		○		○	◉	
Schilbe uranoscopus	Lake Turkana	18										◉	◉	
Schilbe mystus	Senegal	25					◉	◉		◉			○	
Malapterurus electricus	Lake Kainji	28											●	
Parachanna obscura	Sudd	6			○			○					◉	
Parachanna obscura	Senegal	25											●	
Lates niloticus	Lake Chad	13										◉	●	
Lates niloticus	Senegal	25											●	
Lates longispinis	Lake Turkana	19										◉	◉	
Haplochromis macconneli	Lake Turkana	23										◉	○	
Hemichromis fasciatus	Ogun	1						○					◉	
Hemichromis fasciatus	Senegal	25						○					◉	

Bibliographic references:

1: Adebisi, 1981;
2: Arawano, 1982;
3: Daget, 1962a;
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19: McLeod, 1982;
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23: Ogari, 1982;
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25: Paugy, 1994;
26: Paugy & Bénech, 1989;
27: Robinson & Robinson,1969;
28: Sagua, 1979;
29: Thiero Yatabary, 1983;
30: Tobor, 1972;
31: Vidy, 1976.

In the East African great lakes, fishes have developed particular trophic specializations as part of adaptive radiations. It seems that all available resources are used by Cichlidae, and even used exclusively by them. This leads us to distinguish numerous trophic categories (Witte & van Oijen, 1990; Yamaoka, 1991) (figure 12.2):

- detritivores, bottom feeders eating a mixture of planktonic and benthic components;
- phytoplanktivores;
- epilithic (rocks) and epiphytic (plants) algal grazers;
- phytophagous, eating plants;
- molluscivores, consuming shells and gastropods; including oral crushers and pharyngeal crushers;
- zooplanktivorous;
- insectivorous;
- prawn and crab eaters;
- piscivorous;
- paedophages eating eggs and embryos from other species;
- scale eaters consuming mainly scales from other species;
- external parasite eaters…

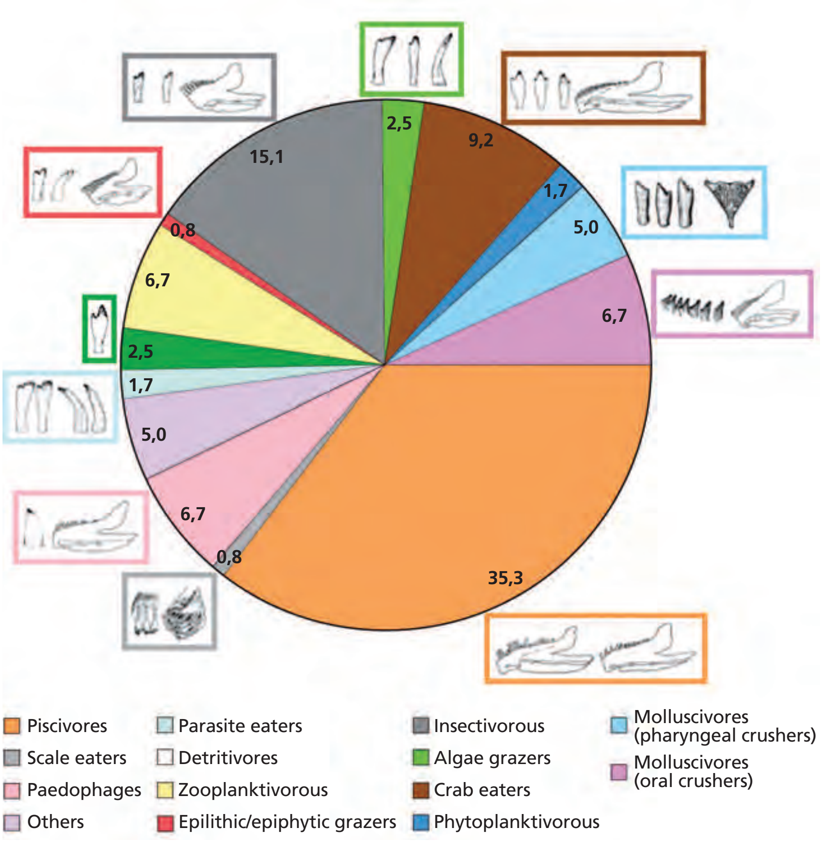


FIGURE 12.2.
Trophic specializations among haplochromines in Lake Victoria. Relative number of species and relationship between diet and teeth (data from Witte & van Oijen, 1990).

Morphological adaptations to feeding behaviour

If species ended up occupying equivalent ecological niches in different types of ecosystems, they would theoretically have displayed similar adaptive responses to identical selective pressures. For diet, scientists thus advanced the hypothesis that there could be a correlation between the general morphology of species and their diet. For African fish, studies on morphology-diet relationships are scarce, with most only providing descriptions of the general diet of the taxa being analysed. Nonetheless, a few studies show that there is indeed a significant relationship between diet and species morphology (Winemiller *et al.*, 1995 ; Hugueny & Pouilly, 1999). More specifically, some morphological characteristics appear to be associated with the type of diet.

These include, for instance:

- mouth size and body size in piscivorous fish;
- gut length correlated with the behaviour of detritivores ;
- orientation or position of the mouth explaining both benthic and detritivore diets.

Similar results were obtained from observations of the same family (Winemiller *et al.*, 1995) or in a community composed of different taxons belonging to different families (Hugueny & Pouilly, 1999). They thus seem to refute the common idea that ecomorphological studies only provide valid results when they are limited to comparisons between families (Douglas & Matthews, 1992).

Later in the chapter, we shall provide examples of close correlations between diet and different morphological characteristics.

Head and mouth morphologies

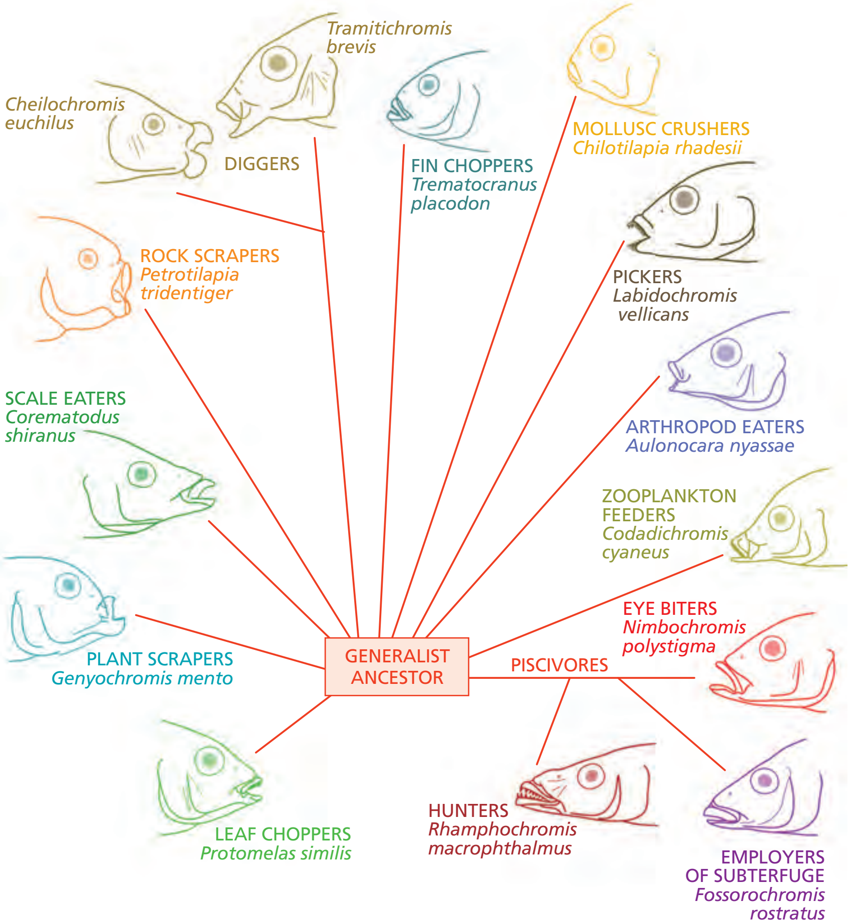
It has been suggested that one key innovation, the pharyngeal mechanism, was one of the major reasons for the extraordinary explosive speciation undergone by the cichlid fish in the African Great Lakes (Liem, 1973). The sharpest morphological specialization concerns adaptations to the head to collect different types of prey. Adaptive changes in the jaws are particularly striking, for example in the huge difference between the elongated mandibles of the piscivorous *Rhamphochromis*, and the squat, almost square-cornered jaws of the scraper *Labeotropheus* (Fryer, 1991) (figure 12.3).

In many species of cyprinids, there are feeding adaptations in the shape of the mouth. In the so-called *Varicorhinus* mouth form, the horny (or keratinized) lips are adapted for scraping algae and aufwuchs from submerged rocks or other hard substrates. The complex ventral mouths of *Labeo*, with homodont pharyngeal teeth which are set close together to form a single grinding surface, are specialized to feed on epibenthic algae.

Length of the gut

There is a correlation between the diet and the length of the gut relative to body length (Kapoor *et al.*, 1975). Carnivorous fish usually have a large stomach

FIGURE 12.3.
Example of adaptive radiation (morphological adaptation of the shape of the mouth) for a few cichlids of Lake Malawi (redrawn from Fryer & Iles, 1972).



and a short gut (ratio less than 1). That is the case for *Lates* and *Hydrocynus*, but also for many invertebrate feeders. Conversely, in sediment browser fish such as *Labeo*, the stomach is often absent or small, and the gut is usually more than ten times longer than the body length (table 12.II). Generally speaking, omnivorous fish, zooplankton feeders or invertebrate feeders have fairly short intestines, less than three times the length of the body. Furthermore, it seems that there is no significant relationship between these types of diet and the length of the gut (Paugy, 1994).

Electric organs

Peculiar adaptations have been developed among electric fish. The catfish *Malapterurus electricus* is a sluggish swimmer, but it feeds almost exclusively on fish. A powerful volley of high frequency electric organ discharges emitted close to fish can paralyse its prey (see box "Electric organ of *Malapterurus electricus*"). This explains why *M. electricus* is a more effective predator of fish in general (Sagua, 1979).

TABLE 12.II.

Relative length of the gut and dominant diet in various African fish species (from Paugy, 1994).
LG: length of the gut; SL: standard length.

Species	Diet	LG/SL
Notopteridae		
Papyrocranus afer	omnivore	0.18
Mormyridæ		
Brienomyrus brachyistius	invertivore	0.45
Hyperopisus bebe	invertivore	0.67
Marcusenius mento	invertivore	0.55
Marcusenius senegalensis	invertivore	0.74
Mormyrops anguilloides	invertivore	0.46
Mormyrus rume	invertivore	0.78
Petrocephalus bovei	invertivore	0.68
Alestidæ		
Alestes baremoze	omnivore	0.89
Brycinus macrolepidotus	omnivore	1.16
Brycinus nurse	omnivore	1.31
Hydrocynus forskalii	piscivore	0.85
Hydrocynus vittatus	piscivore	1.06
Distichodontidæ		
Distichodus engycephalus	micro/macrophyt.	4.71
Distichodus niloticus	micro/macrophyt.	2.77
Distichodus rostratus	micro/macrophyt.	2.79
Hemistichodus mesmaekersi	invertivore	0.42
Hemistichodus vaillanti	invertivore	0.37
Ichthyborus besse	piscivore	1.10
Nannocharax fasciatus	invertivore	0.43
Nannocharax lineomaculatus	invertivore	0.37
Nannocharax occidentalis	invertivore	0.34
Nannocharx ansorgii	invertivore	0.52
Paradistichodus dimidiatus	micro/macrophyt.	1.83
Xenocharax spilurus	omnivore	1.83
Citharinidæ		
Citharidium ansorgii	micro/macrophyt.	5.67
Citharinops distichoides	micro/macrophyt.	4.48
Citharinus citharus	micro/macrophyt.	6.13
Citharinus congicus	micro/macrophyt.	4.40
Citharinus eburneensis	micro/macrophyt.	7.00
Citharinus gibbosus	micro/macrophyt.	5.29
Citharinus latus	micro/macrophyt.	6.78
Citharinus macrolepis	micro/macrophyt.	4.46
Cyprinidae		
Raiamas senegalensis	invertivore	0.38
Acapoeta tanganicae	micro/macrophyt.	5.00
Barbus anoplus	omnivore	0.80
Barbus macrops	omnivore	0.82
Barbus sacratus	omnivore	1.63
Chelaethiops elongatus	zooplanktivore	0.75
Chelaethiops minutus	zooplanktivore	0.70
Coptostomobarbus wittei	zooplanktivore	0.80
Garra congoensis	micro/macrophyt.	4.50
Garra dembensis	micro/macrophyt.	4.50
Labeo horie	limnivore	16.75
Labeo lineatus	limnivore	16.10
Labeo niloticus	limnivore	16.90
Labeo parvus	limnivore	10.00
Labeo roseopunctatus	limnivore	13.39
Labeo senegalensis	limnivore	13.36
Labeo variegatus	limnivore	17.00
Leptocypris modestus	invertivore	0.93
Leptocypris niloticus	invertivore	0.52
Opsaridium chrystyi	invertivore	0.73
Raiamas moorei	invertivore	0.73
Raiamas steindachneri	invertivore	0.32
Claroteidæ		
Auchenoglanis occidentalis	invertivore	0.88
Chrysichthys auratus	invertivore	1.98
Schilbeidæ		
Schilbe mystus	omnivore	0.86
Amphiliidæ		
Amphilius atesuensis	invertivore	0.51
Clariidæ		
Clarias anguillaris	omnivore	0.86
Heterobranchus isopterus	omnivore	1.32
Mochokidæ		
Synodontis ocellifer	invertivore	2.18
Synodontis schall	invertivore	1.96
Channidæ		
Parachanna obscura	piscivore	0.55
Latidæ		
Lates niloticus	piscivore	0.52
Cichlidæ		
Chromidotilapia guntheri	omnivore	3.01
Haplochromis adolphifrederici	invertivore	1.68
Haplochromis astatodon	micro/macrophyt.	2.84
Haplochromis gracilor	omnivore	1.56
Haplochromis graueri	invertivore	1.92
Haplochromis kamiranzovu	micro/macrophyt.	3.05
Haplochromis nigroides	omnivore	1.88
Haplochromis olivaceus	micro/macrophyt.	3.32
Haplochromis paucidens	invertivore	1.42
Haplochromis scheffersi	omnivore	1.72
Hemichromis fasciatus	piscivore	0.78
Oreochromis mossambicus	micro/macrophyt.	6.80
Sarotherodon galilaeus	micro/macrophyt.	6.54
Coptodon zillii	micro/macrophyt.	5.03
Gobiidæ		
Nematogobius maindroni	invertivore	0.37

ELECTRIC ORGAN OF *MALAPTERURUS ELECTRICUS* (SOURCE FRESSARD, 1958)

The African *Malapterurus*, like nearly 250 species of marine and freshwater fish, can emit an electric discharge in a close conducting space.
The shock produced by the electric discharge is significant because it can reach 450 volts. This value ranks this species among those presenting the highest electrical discharges. Only the electric eel (*Electrophorus electricus*), in the Amazon River emits stronger discharges (550 volts).Specific observations have shown that *Malapterurus* has a constant and coordinated use of its discharge in its feeding behaviour. Thus, a *Malapterurus* emitting no discharge released 110 in two hours when it was in the presence of prey. Small fish become inert when subjected to the discharges, and are suffocated when their breathing stops. After, the predator often touches its prey with the anterior portion of its organ.
At the same time, it curves its body to the same side to form a loop discharge with maximum efficiency.
Then, after having rejected and caught its prey several times, it swallows the prey, continuing meanwhile to emit some discharges.
Finally, when the animal is sated, no stimulus, even provoked, seems able to cause a reaction, and no more electric discharge is emitted.

Species	Common names	Habitat	Discharge power (V)
Raja undulata	painted ray	marine	4
Torpedo marmorata	electric ray	marine	45
Torpedo californica	electric ray	marine	50
Uranoscopus scaber		marine	0.2-0.4
Astroscopus spp.		estuarine	5-50
Apteronotus albifrons		freshwater	0.0003-0.001
Electrophorus electricus	electric eel	freshwater	115 (200 mm)
Electrophorus electricus	electric eel	freshwater	500 (1000 mm)
Gymnarchus electricus	aba	freshwater	3-7
Malapterurus electricus	electric catfish	freshwater	30 (50 mm)
Malapterurus electricus	electric catfish	freshwater	350 (500 mm)
Mormyres	elephant fish	freshwater	0.1
Mormyrus kannume	elephant fish	freshwater	2

Body form and feeding types

Behavioural strategies for foraging are constrained by morphology, including mouth shape and position as well as body form.

Webb (1984), while looking for correlations between locomotor morphology and the feeding niche, distinguished three basic functional locomotory mechanisms which may be linked to foraging (figure 12.4):

- to exploit food widely distributed in space and time, fish have to move at speeds that sample the greatest volume for the least expenditure of energy. This applies both to macrophage and filter-feeders that have, generally, a streamlined anterior body and a very forked caudal fin. The typical example for African fish is *Alestes baremoze* that filters zooplankton in the lacustrine environment (Lauzanne, 1970) and is an excellent swimmer able to perform long-distance migrations.

- to exploit very vagile food, fish have to catch their prey very quickly before they can escape and reach shelter. Therefore, they must be able to accelerate

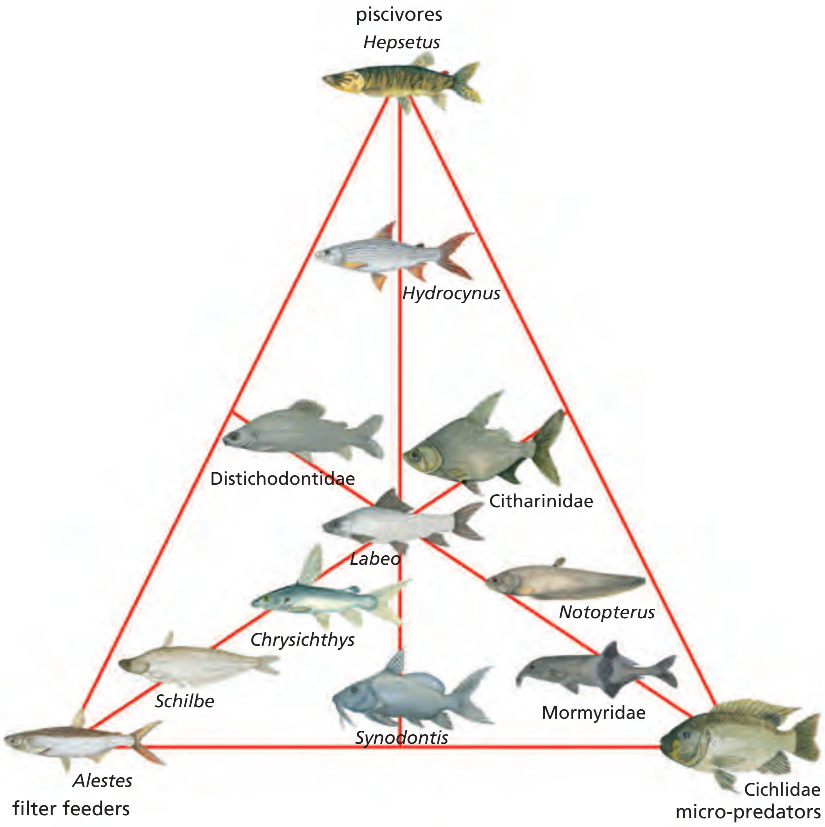


FIGURE 12.4.
Ternary diagram "function-morphology" representing the different types of fish swimming. Angles of the triangle are three major modes of foraging; the species closer to the centre are more generalist (adapted from Webb, 1984).

rapidly. In Africa, the typical example is *Hepsetus odoe* (African pike), which has a flexible body and very secluded dorsal fin to accelerate very briefly but with unbelievable speed;

- to exploit prey sometimes hidden in holes or lying on bottom, fish have to swim in very restricted spaces. The median and paired fins allow better manoeuvrability. Many cichlids fit these characteristics as well as mormyrids, notopterids, etc.

It is not possible to combine all the optimum features for the different types of swimming in one fish: the optimum design for manoeuvring excludes the elements that favour high performance in accelerating or in cruising. The three basic design are therefore mutually exclusive. Locomotor specialists represent only a small proportion of fish species and the majority of fish are locomotor generalists.

However, locomotor adaptations for food capture are of diminished importance among locomotor generalists, and other adaptations (e.g. suction or protrusible jaws) which are vital to food selection and the extension of diet breadth, are more common in foraging.

Prey selection

The best prey for a predator is theoretically one that, in a given context, provides it with the greatest amount of energy for the least cost of capture.

Zooplanktivorous fish have two different feeding modes (Lazzaro, 1987):

- particle feeders attack and ingest individual prey that have been visually selected;
- filter feeders do not detect prey individually but retain plankton in their gill rakers. They thus engage in passive selection of prey, and efficient filtration depends to a large extent on gill structure and the size of the particles.

Field workers have used "electivity indices" (E) such as that devised by Ivlev, expressed as

$$E = \frac{(r_i - p_i)}{(r_i + p_i)}$$

where r_i is the proportion of food item i in the diet, and p_i the proportion of item i in the environment. This index is useful when investigating whether a prey species is or is not being eaten in proportion to its abundance in the habitat, but does not distinguish mechanisms behind any selection revealed.

In filter feeders like *Synodontis batensoda* in Lake Chad, the smallest captured prey measured 80 µm, but the proportion of rotifers and nauplii retained by the gill rakers increases progressively with size, up to 260 µm. The selection of the largest planktonic crustaceans depends essentially on their ability to avoid predators. In this respect, the large cladoceran *Moina micrura,* with poor mobility, is easily captured whereas the more vagile diaptomids are hardly ever caught (Gras *et al*., 1981). Meanwhile, large *Alestes baremoze* adults do not retain small nauplii or rotifers in their gill rakers, but only particles larger than 400 µm. Above 880 µm all planktonic elements are retained (Lauzanne, 1970). These two zooplanktonivorous fish species thus have different behaviours and do not consume the same type of prey in the physical system where they live in sympatry.

In Lake Victoria, it has also been shown that the decrease in the proportion of shrimp *Caridina nilotica* in the stomach contents of *Lates niloticus* is partly a result of larger spaces between gills as the fish grows larger (Hughes, 1992). Beyond 70 cm LT, the spaces are too large to retain the shrimp.

Benthic fishes can also exert selective pressure on prey species. Three benthivore species of Lake Chad, *Synodontis clarias, S. schall,* and *Hyperopisus bebe*, essentially consume small molluscs, as shown in the comparison of size distribution of molluscs in the benthos and in the stomach contents of predator fishes (figure 12.5) (Lauzanne, 1975a).

Still in Lake Chad, up to 50 mm LS *Tetraodon lineatus* consumes mainly micro-crustaceans and insect larvae, then, up to 125 mm LS, larger lunged molluscs living in vegetated areas (*Gabbia* sp., *Anisus* sp., *Bulinus* spp). Beyond 200 mm LS, *T. lineatus* only consumes benthic molluscs with thicker shells (*Bellamya unicolor, Melania tuberculata, Corbicula africana*) (Lauzanne, 1977)

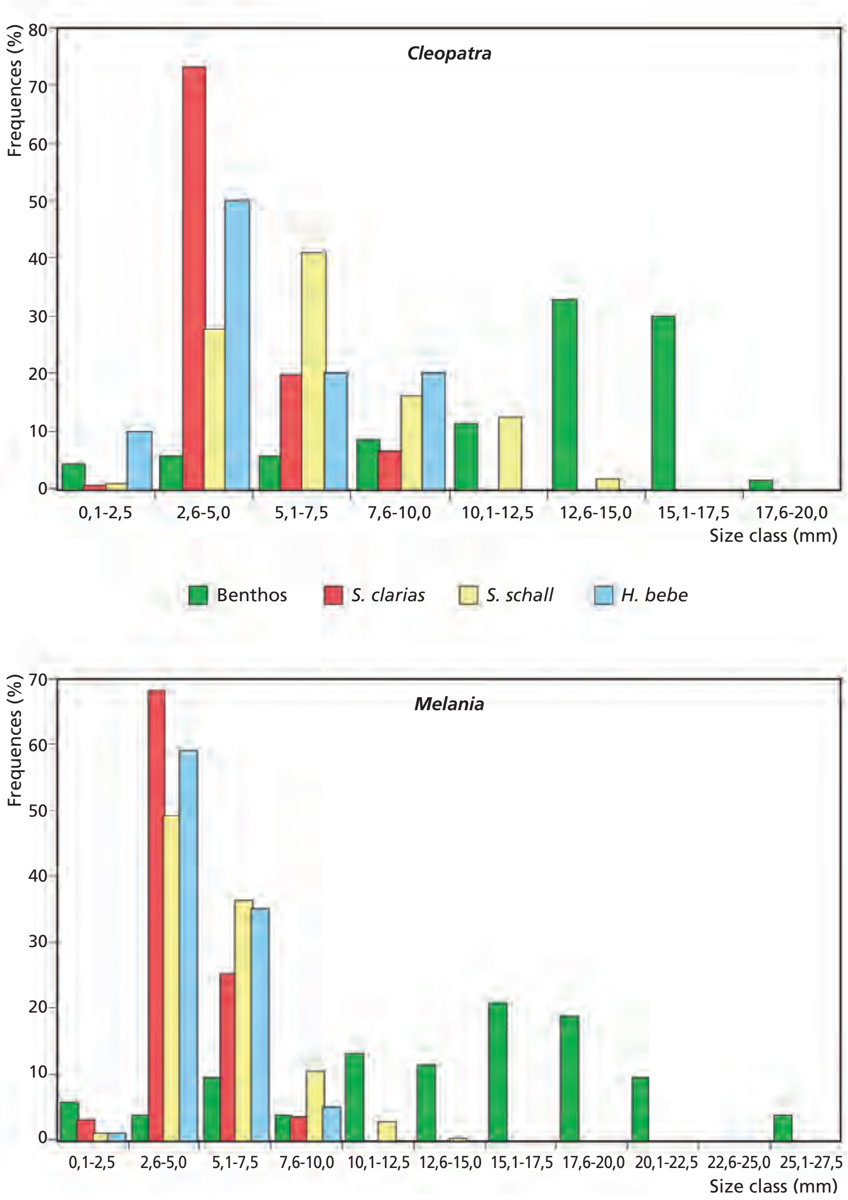


FIGURE 12.5.
Comparison of size distribution of two species of benthic molluscs (*Cleopatra bulimoides* and *Melania tuberculata*) in the Lake Chad benthos and in the stomach contents of three malacophagous fish species *(Synodontis clarias*, *S. schall* and *Hyperopisus bebe*) (from Lauzanne, 1975a).

(figure 12.6). Similar behaviour has been observed in the lagoon fish *Trachinotus teraia* (Trébaol, 1991). Up to 125 mm LS, it feeds on Clupeidae larvae and juvenile shrimp, while larger individuals consume mainly *Corbula trigona* bivalves in Ébrié lagoon (Côte d'Ivoire).

The impact of selective predation on the dynamics of planktonic or benthic natural populations may thus be significant (see chapter *Role of fish in ecosystems functioning* and chapter *Species introductions*).

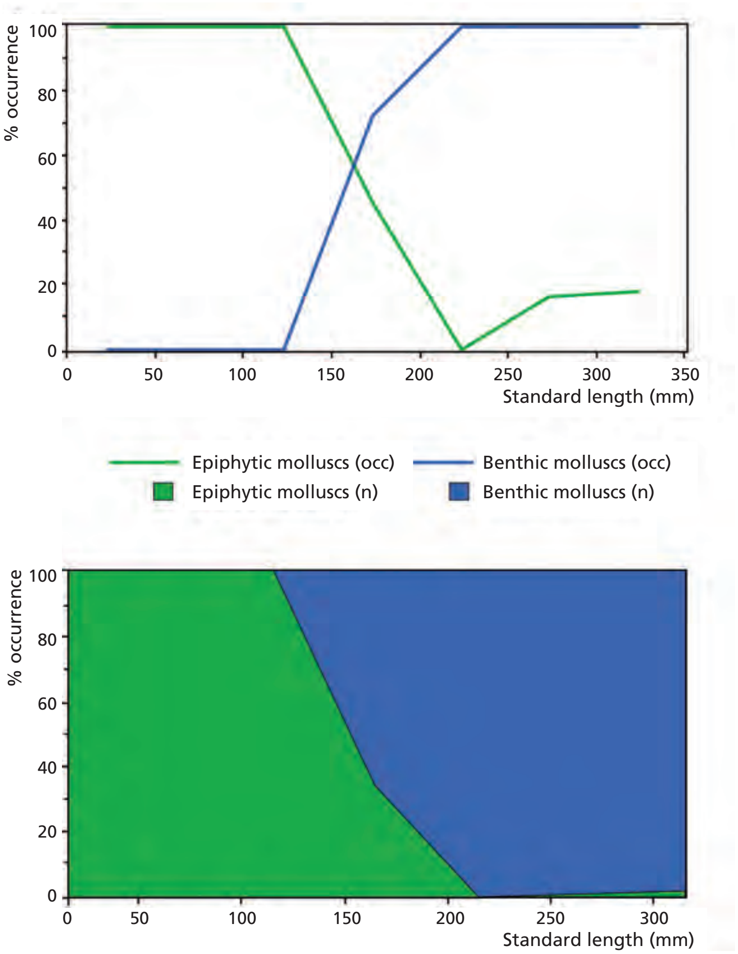


FIGURE 12.6.
Ontogenic change in diet of *Tetraodon lineatus* in Lake Chad (from Lauzanne, 1977).

Ontogenic shifts in feeding behaviour

Most fish species vary greatly in body size during their lifetimes and often undergo drastic changes in ecology as they grow. Their dietary requirements and their feeding behaviour also undergo changes which are usually related to the ability of growing animals to handle particular food types. Several studies on African fish have highlighted these ontogenetic changes. We have already discussed the case of *Tetraodon lineatus*. Examples also exist in piscivorous species. Thus, in the Chari River, juveniles of *Hydrocynus forskalii* are strictly zooplanktivorous up to 30 mm in length. Between 30 and 45 mm, they consume both zooplankton and insects. Over 50 mm, they become frankly piscivorous. In the Southeast archipelago of Lake Chad, the pattern is the same, but the transition from one diet to another occurs in larger sizes (figure 12.7).

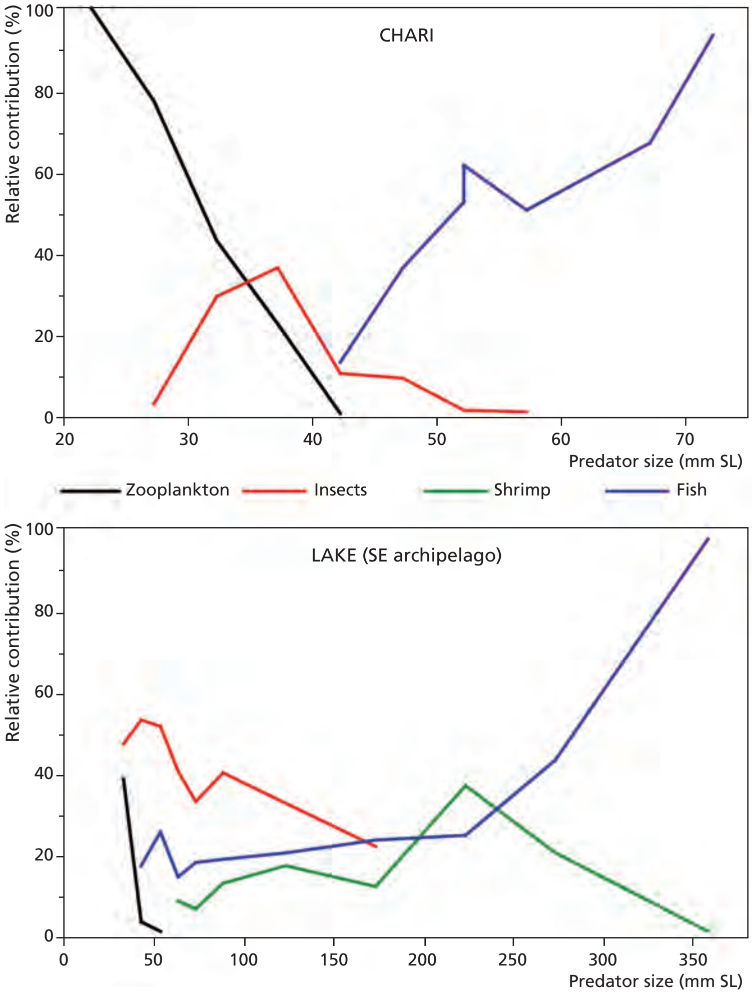


FIGURE 12.7.
Hydrocynus forskalii: change in the proportion of food items depending on size in the Chari and Lake Chad (Southeast archipelago) (from Lauzanne, 1975b).

Diet also changes with individual growth in cichlids. A peculiar behavioural and morphological development has been reported for *Docimodus evelynae*, a cichlid species from Lake Malawi, in which small juveniles (less than 50 mm SL) are facultative cleaners, removing fungi from other cichlids. From 50 to 70-80 mm SL, they are no longer cleaners, and feed upon plankton, insects and aufwuchs. Above 80 mm SL, their dentition changes (the juvenile tricuspid teeth are replaced by adult unicuspid teeth) and adult *D. evelynae* alter their diet to feed upon scales, fins and skin of their fish prey. Field data has also provided evidence that as *D. evelynae* grow, they move into deeper water. As a result of the depth restricted distributions observed for many species in Lake Malawi, the cichlids cleaned by juvenile *D. evelynae* in shallow water are not the same as those preyed upon by adults in deeper water (Ribbink, 1990).

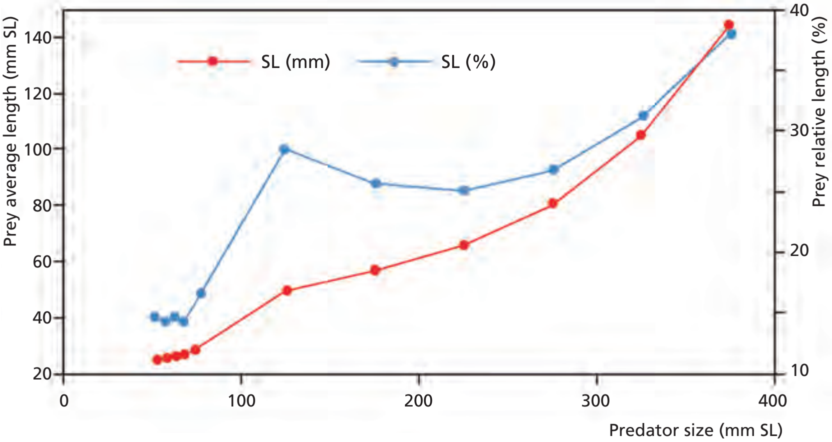
Relationship between predator size and prey size

For many fishes, there is a prey size that minimizes cost of capture by providing the greatest amount of energy to the predator. This type of relationship has been especially studied in piscivorous fishes, which are the most eclectic from this point of view. Generally it can be observed that the relative prey size (size of the prey in relation to the predator) is greater in small and large predators. The relationship thus follows a U-shaped curve.

The relationship between the length of *Lates niloticus* and the size of prey was studied by Hopson (1972). *Lates* at all lengths are able to eat fish up to approximately one-third of their own length. The largest prey in relative size were eaten by the smallest *Lates*, 30 to 40 mm TL. Relative prey size fell steeply from 38% in the smallest *Lates* to 6% in the 30-36 cm TL group. Between 300 and 800 mm TL there was a slight increase in the relative size of prey from 6 to 10%. A marked change was noted in *Lates* over 850 mm TL with prawns and small characins virtually disappearing from the diet. The result is a steep rise in both relative size and average size.

In Lake Chad, the mean relative prey size of *Hydrocynus forskalii* is about 10% for small fish (50-75 mm SL) eating mainly invertebrates, but varies between 20 and 33% for fish from 100 to 400 mm SL (Lauzanne, 1975b) (figure 12.8). A relationship between predator size and prey size has also been recorded for *Ichthyborus besse*, a less common predator than those cited previously. The mean relative size of prey varies from 20 to 30% for individual fish less than 100 mm SL and from 30 to 40% for *I. besse* above 100 mm SL. The highest relative prey length observed was 50% that of the predator (Lek & Lek, 1978b).

FIGURE 12.8.
Hydrocynus forskalii: relationship between the length of the predator and the size of the prey in Lake Chad (from Lauzanne, 1975b).



Variability in diet of adults

Different field studies have suggested that many fish may vary their diet according to the seasons or environments. It seems that fish broaden their diet to include less preferred prey as the availability of the preferred prey declines. In other words, when food is scarce, they are less demanding about its quality.

For example, *Synodontis batensoda*, a detritivorous fish in the river systems of the Chari (Blache *et al.,* 1964), the Nile (Sandon & El Tayib, 1953) and the Niger (Daget, 1954), was exclusively a filter feeder in Lake Chad before the drought period (Lauzanne, 1972; Tobor, 1972). When the food offered is composed of zooplankton and floating organisms, *S. batensoda* swim on their backs in order to filter the food at the water surface. If the food offered is composed of benthic detritus and mud, the fish swims in a ventral position and filters sediment. In 1974, during the drying phase of Lake Chad, when the zooplankton became less abundant, lake populations of *S. batensoda* exhibited both these feeding behaviours (Im, 1977).

Alestes baremoze is strictly zooplanktivore in Lake Chad (Lauzanne, 1976) and Lake Turkana (Hopson, 1982). In rivers, where zooplankton is scarce, it becomes partly phytophagous in the Chari River as well as in the Niger River but with a significant component of emerging insects (Daget, 1952). In Côte d'Ivoire, aquatic insects and terrestrial invertebrates constitute the bulk of the diet of *A. baremoze* in rivers (Paugy, 1978), whereas in the Kossou man-made lake, this species is zooplanktivore (Kouassi, 1978).

More broadly, many species adapt their diets according to the restrictions of the physical system. For samples taken from different ponds of a temporary watercourse in Mali, it was shown that for the majority of species, diet similarities are greater within a sample than between same species from different samples (Paugy, 1994). This indicates that to survive in sometimes extreme conditions, species adapt – within certain limits – their diets to the available dominant resources. We can thus show that when faced with poor food diversity which is also related to poorer quality, species use the most abundant resources, and when prey becomes more numerous, fishes feed on a larger number of prey taxa. In other words, food diversity which depends on the richness of ingested prey is apparently dependent on the prey available in the environment (figure 12.9).

There is a large body of literature on the degree of trophic specialization of endemic Cichlidae in the East African lakes. It appears that the majority of species can consume a much wider range of food than their morphological specialization would initially suggest.

In fact, many of the Malawi Cichlidae can use one resource or another, based on availability, and are quite opportunistic (Ribbink, 1990). Species that usually graze on the biological surface layer of rocks can shift to a planktonic diet and even consume eggs or larvae of another species. Contrary to a number of common beliefs, the trophic specialization of these Cichlidae does not limit their dietary range, but could give them a competitive advantage in using

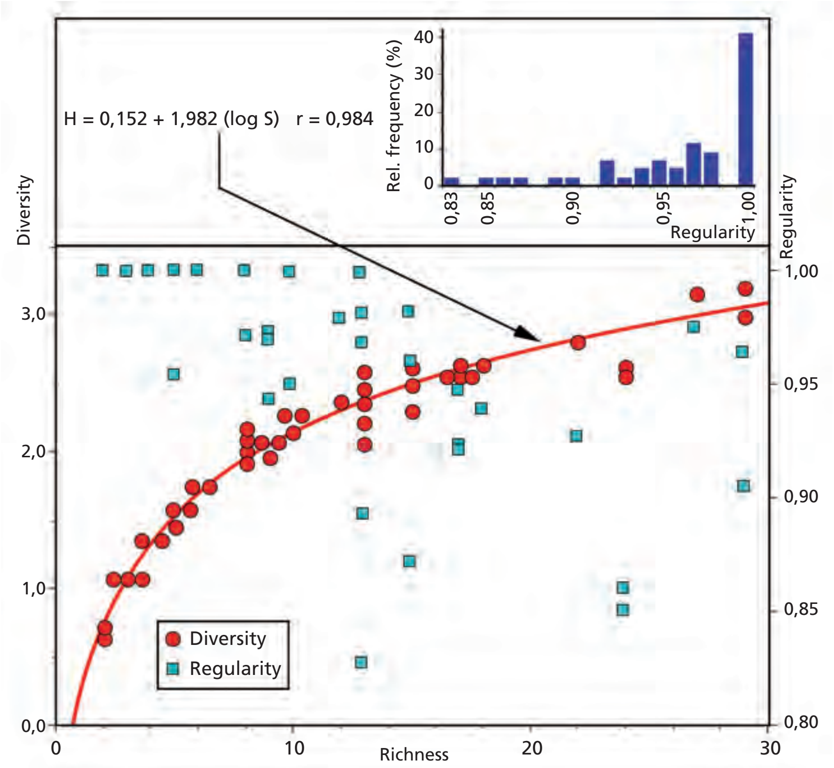


FIGURE 12.9.
Fish of the Baoulé River (Upper Senegal River in Mali): relationship between the diversity (Shannon index) or the regularity of feeding (ratio between diversity of items and the maximal theoretical diversity for a same number of taxa; also called equitability) and the richness of ingested preys (from Paugy, 1994).

certain types of food, particularly during food shortages, given that they are able to switch to a more general or opportunistic diet at any time (Witte, 1984).

Other groups have also developed this capacity to share resources by "adapting" their morphology. An example is the *Barbus* (Cyprinidae) species flock in Lake Tana where each of the 14 species studied has developed a specific food strategy that avoids interspecies competition. The morphological study carried out on these 14 species also led to the creation of a predictive food model (FFM: *Food-Fish Model*) whose results are consistent with the biological reality observed in the stomach contents of different *Barbus* (Sibbing & Nagelkerke, 2001).

Feeding activity patterns

Change in fish activity during a 24-hour period is a well-known phenomenon. It is generally linked to feeding habits. There are species that are mainly active during the day, or at night or during periods of rapidly changing light intensity (dawn and dusk) (table 12.III).

Major foraging activities include movements between resting sites and foraging areas as well as movements to follow, if necessary, daily activity patterns of prey. For example, vertical migrations of Lake Victoria haplochromines are

TABLE 12.III.

Feeding activity of African fish species (from Lévêque, 1997a).

Species	Basins	Sources	Diel feeding activity
Diurnal diet			
Alestes baremoze	Lake Chad	Lauzanne, 1977	diurnal feeder; peak stomach fullness in the afternoon
Alestes baremoze	Lake Turkana	Hopson, 1982	chiefly diurnal feeder
Brycinus leuciscus	Niger River	Ghazaï *et al.*, 1991	chiefly diurnal feeder, but less during the full moon
Hydrocynus forskalii	Lake Turkana	Hopson *et al.*, 1982	diurnal feeder; peak fullness in the afternoon
Labeo parvus	Bandama	Mérona, unpub. data	diurnal feeder; stop feeding at night
Lates longispinis	Lake Turkana	McLeod, 1982	non-feeding between sunset and midnight; peak fullness in the afternoon
Oreochromis niloticus	Lake Turkana	Harbott, 1982	diurnal feeder; marked diel feeding pattern
Oreochromis niloticus	Lake George	Moriarty, 1973	diurnal feeder; marked diel feeding pattern
Sarotherodon galilaeus	Lake Chad	Lauzanne, 1977	diurnal feeder
Trachinotus teraia	Ébrié Lagoon	Trébaol, 1991	diurnal feeder
Nocturnal diet			
Bagrus bajad	Lake Turkana	Lock, 1982	peak stomach fullness at night but feeding occurs also during the day
Synodontis batensoda	Lake Chad	Lauzanne, 1977	nocturnal feeder
Hydrocynus brevis	Lake Kivu	Losseau-Hoebeke, 1992	feeds on haplochromines at night and usually hides between rocks during the day
Malapterurus electricus	Niger River	Belbenoit *et al.*, 1979	nocturnal feeder; peak hunting and feeding period of 5-6 h immediately following sunset
Schilbe uranoscopus	Lake Turkana	Lock, 1982	peak stomach fullness at night; most active at sunset and during the early part of night
Syndontis schall	Lake Turkana	Lock, 1982	peak stomach fullness in the dawn and morning; little feeding in the afternoon
Diurnal and nocturnal diet			
Aphyosemion geryi	Guinea	Pandaré & Romand, 1989	feeds both day and night, but a peak of feeding between 10-19 h

assumed to follow the migration of the prey *Chaoborus* larvae which stay in the muddy bottom during the day and migrate to the water surface during the night to feed on the zooplankton (Witte, 1984).

Similarly, in Lake Kariba, field observations and echo-sounding surveys demonstrated that the clupeid *Limnothrissa miodon*, which feeds principally on *Bosmina longirostris*, shows a pattern of diurnal vertical migration similar to that of its prey (Begg, 1976).

In species that detect prey visually, lunar phases may have an influence on circadian dietary rhythms. For example, in *Brycinus leuciscus* which usually feeds during the day, feeding activity tends to be limited during the full moon, even though feeding has no nocturnal importance. In fact, it appears that diurnal feeding decreases owing to gregariousness that occurs in preparation for the migratory phase that follows the full moon (Ghazaï *et al.*, 1991).

Food webs

Food webs are diagrams depicting which species in a community interact in feeding. "Food webs are thus caricatures of nature" (Pimm, 1982) but they give a picture of the processes at work in ecosystems. According to Cohen (1989) "If an ecological community is like a city, a web is like a street map of the city: it shows where road traffic can and does go."

A food chain describes the energy transfer through different trophic levels, from producers (vegetation for example) to top consumers. The energy transfers are subject to the laws of thermodynamics: at each link, considerable energy is dissipated from the system in the form of heat. Chain lengths are usually short and include four to five links.

In aquatic environments, there are basically two major types of food chains depending of the main energy source represented by primary producers or detritus:

- grazing food chain: in lakes, the food webs of the pelagic zone are fundamentally based on the primary production by phytoplankton;
- detritus food chain: in contrast, the food webs in the benthic zone are usually based on organic material, including living and dead organisms, imported from pelagic communities, or of allochthonous origin.

In small streams and rivers, the food webs are often heavily dependent on allochthonous organic material, falling into the water or washed in by rains (leaves and terrestrial insects for example). In contrast, in large rivers with a slow flow, the primary production of indigenous origin is more important.

Phytoplanktivore communities

The shortest food chain could be illustrated by simple fish communities feeding on phytoplankton. However, Bowen (1988) pointed out that the majority of African fish do not feed directly on living plant material but depend either on zooplankton or benthic invertebrates for food. True primary consumers only belong to some genera (*Labeo, Citharinus, Distichodus, Tilapia, Oreochromis* and *Sarotherodon*), that is to say fewer than 7% of the total species.

The cichlid *Alcolapia grahami* is endemic to Lake Magadi where it feeds on benthic filamentous cyanophytes, insect larvae and copepods. It was introduced in the 1950s into Lake Nakuru to control mosquito breeding. There it is the only fish species, and quickly became one of the major filter feeders exploiting the high standing crops of the cyanobacterium *Spirulina platensis* which provide 95% of its diet.

Phytoplankton, mostly blue-green algae, is very abundant in Lake George. It was mainly consumed by two species, *Oreochromis niloticus* and *Haplochromis nigripinnis*, which largely dominated the fish biomass (Gwahaba, 1975).

Relatively simple trophic webs: pelagic fish communities of East African Great Lakes

The trophic hierarchy among the pelagic fish of East African Great Lakes is relatively simple because few fish species are adapted to the pelagic zone of inland waters. For example, in Lake Tanganyika the trophic web is mainly organized from phytoplankton which is consumed by zooplankton (Coulter, 1991). The latter is the main food of two clupeid species, *Stolothrissa tanganicae* and *Limnothrissa miodon*, which appear from their diet and life history to be narrowly specialized for pelagic life and are key members of the pelagic food chain, linking planktonic and piscivorous trophic levels (figure 12.10). Juveniles of *Limnothrissa* are zooplanktivores, but adults feed regularly on juvenile and adult *Stolothrissa*. The two clupeids are the prime food for predators, which are essentially two species of *Lates*. An alternative is in a phytoplankton-shrimp-fish food web (figure 12.10).

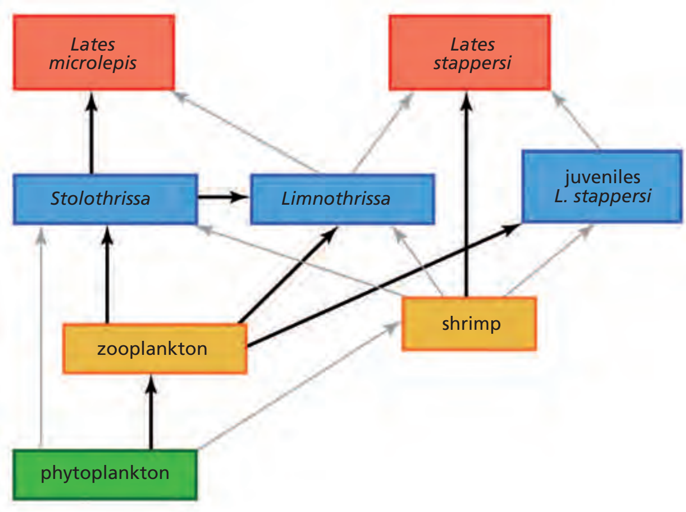


FIGURE 12.10.
Food web of the pelagic fish community of Lake Tanganyika (from Coulter, 1991). Heavy arrows for major food preference, grey arrow for secondary food preference.

It is interesting to highlight that the pelagic food web of Lake Tanganyika is marine in nature: the primary grazer is a diaptomid copepod just as in many productive marine systems, and the primary planktivores (Clupeidae) are also of marine origin, as are the main predators, *Lates*, which also belong to a family of marine origin (Hecky, 1991).

In Lake Kivu, the pelagic food web is relatively simple including the introduced zooplanktophage *Limnothrissa miodon* (from Lake Tanganyika), the microphytophage *Haplochromis kamiranzovu*, the micropredator *Raiamas moorei* (feeding on insects but also on juvenile fish), and the piscivore *Haplochromis vittatus* (Ulyel, 1991).

Trophic webs can sometimes change without necessarily becoming more complicated. A striking example can be seen in Lake Victoria. In some zones, after the introduction of *Lates niloticus*, the stock of *Haplochromis spp.* which served as the essential food for predators has almost totally disappeared (Ligtvœt & Witte, 1991). Since then, although certain species still exist, they are no longer the major prey, and the predator, which now often exhibits cannibalistic behaviour, feeds almost exclusively on a single Cyprinidae species (see chapter *Fish communities in East African rift lakes*).

More complex food webs of shallow lakes

In Lake Chad, before the drought of the early 1970s, trophic webs – including in free waters – were much more complex than in the pelagic zones of the great lakes owing to the shallowness of the waters. Lauzanne (1976 and 1983) distinguishes two closely intertwined chains in the open waters of Lake Chad. The first one, planktonic, starts with phytoplankton, and the second one, benthic, is partly of detritic origin. The planktonic network leads to planktivorous Alestidae (*Micralestes acutidens, Brycinus nurse, Alestes baremoze*), Mochokidae (*Synodontis membranaceus, Synodontis batensoda*), and Mormyridae (*Pollimyrus isidori*). In turn, these fishes are prey to several predator species (figure 12.11) that consume relatively few of the species from the detritivore and benthic chain (see also box "Ecopath"). Therefore, as in Lake Tanganyika, zooplanktivorous fishes serve as the main food source of *Lates* and *Hydrocynus*. Similar results were obtained in Lake Turkana (Hopson & Ferguson, 1982).

It should be noted that terrestrial invertebrates that fall on the open waters of Lake Chad, sometimes tens of kilometres from the coast, play an important role in the diets of a few species such as *Schilbe niloticus*, which on several occasions has been observed to have stomachs full of crickets. This observation has also been made, to a lesser degree, in *Schilbe uranoscopus* and *Bagrus*

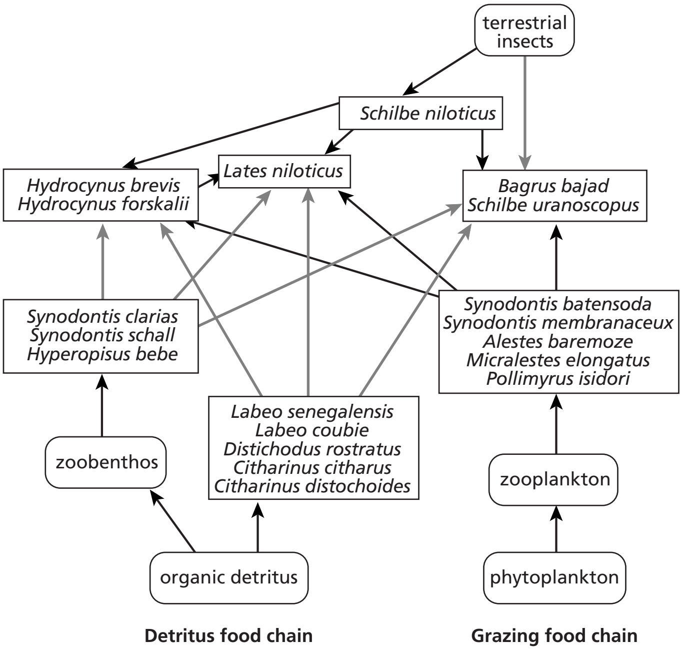


FIGURE 12.11.
Food webs in the open waters of Lake Chad (modified from Lauzanne, 1983).

bajad. Similar observations on the diet of *Schilbe niloticus* have been made in Lake Albert (Worthington, 1932). *S. niloticus* plays an important role in the diet of other predators in Lake Chad, and in a way represents the main link of a third trophic chain, one that connects external sources to top predators.

Prior to the introduction of *L. niloticus*, certain areas on the edge of Lake Victoria provided an example of a relatively complex trophic web.

ECOPATH

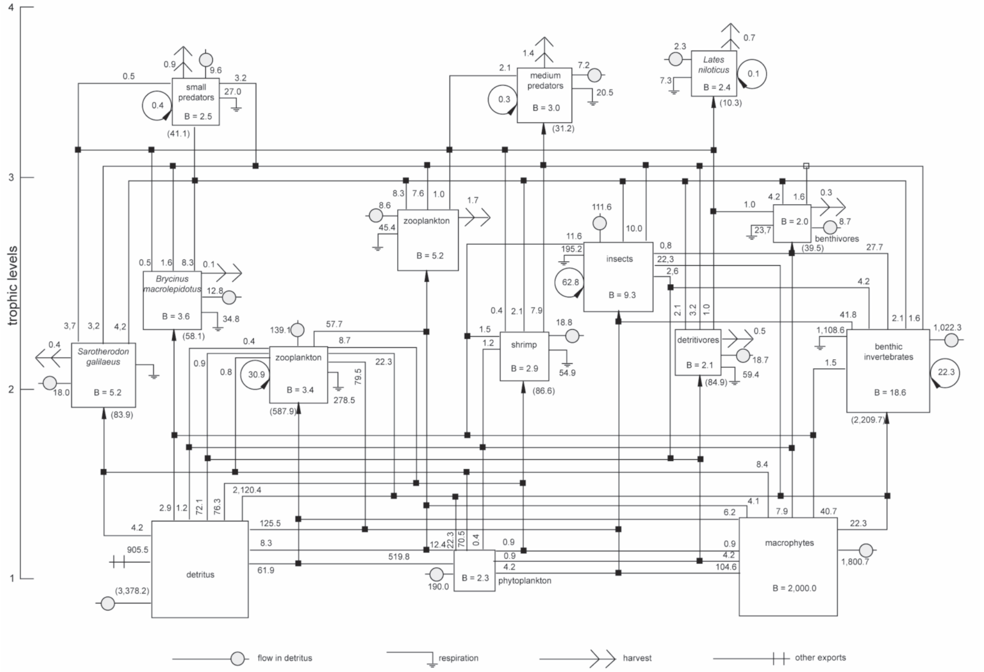
It is often useful to quantify the energy transfers that occur, rather than limiting oneself to a simple description of a trophic web, in order to obtain a partial (by level) or general appraisal that takes all the supposed players into account.

An initial attempt to model this led to the creation of the first "ECOPATH" programme (Polovina & Ow, 1983 ; Polovina, 1984 and 1985). A new version of the initial attempt was recently proposed under the name "ECOPATH II" (Christensen & Pauly, 1993 ; Pauly *et al.*, 1993), which resurrected the initial model and simplified it to include only easily-obtained parameters, in order to characterize the relative consumption of different fish populations as faithfully as possible.

As an example, we present below the modelling of a relatively complex web: Lake Chad (Palomares *et al.*, 1993) (figure 12.12). This model estimates total biomass to be 26 t. km^{-2}, a reasonable figure when compared with the value for total captures, estimated at 6.4 t. km^{-2}. Likewise, the relative dominance of species (*B. macrolepidotus* and zooplanktivores) is quite consistent with previous observations (Durand, 1983). Nonetheless, this model should not be considered universal, as it only reflects the "normal" period of Lake Chad's evolution; neither can it be applied to other systems of the ecoregion.

FIGURE 12.12.

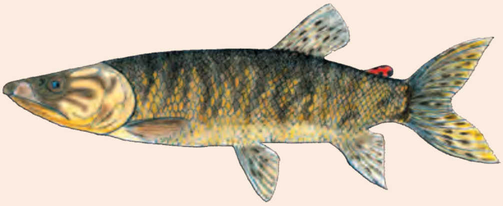
Ecopath II: model of Lake Chad during the "normal" period (from Palomares *et al.*, 1993).



Diversity of responses to environmental constraints and extreme environmental conditions

Christian Lévêque

Didier Paugy



The prevailing environmental conditions in aquatic habitats often allow different fish species to coexist. In certain conditions, however, an environmental factor can change in such a way that it becomes an intolerable constraint that leads to the elimination of most of the species. Some of the species that have developed adaptive solutions to such constraints can nonetheless tolerate extreme conditions, at least within certain limits and/or for a given period that allows them to await the return of more favourable conditions.

Unlike birds and mammals, fish do not regulate their body temperature, but can exhibit great flexibility in their responses to environmental changes and in traits such as growth, age at first reproduction, life span, and other life-history traits. The nature of the responses of organisms to changing environmental conditions is a central problem in biology and the meaning of "adaptation" has been widely discussed (Løvtrup, 1988; Endler & McLellan, 1988).

This chapter is concerned with some of the major environmental constraints to which tropical freshwater fish have become adapted since diversity of conditions enhances biodiversity.

Temperature

Because of its effect on the velocity of chemical reactions, environmental temperature is perhaps the most pervasive of the abiotic factors. It has major influences on many biological processes, such as maturation and spawning, growth, development rate, metabolism, etc. Fish are faced with a simple choice in responding to temperature changes: either to move to another habitat when possible (a behavioural response), or to adapt their metabolic processes to the new situation (metabolic responses).

Temperature preferences and thermal tolerance ranges

Changes in temperature occur less abruptly in water than in air, but fish can nevertheless be exposed to large temperature variations.

Adult fish can survive over a limited range of temperatures bounded by the upper and lower incipient lethal temperature (UILT and LILT). The LILT for *Coptodon zillii* which occur in Lake Huleh (Israel), is 6.5°C, and the UILT is 42.5°C, but mortality begins when the temperature exceeds 39.5°C (Philippart & Ruwet, 1982). *O. niloticus* can also tolerate a temperature of 8°C for several hours and an upper tolerance limit of 42°C has been reported. These species, and probably also *O. aureus* and *S. galilaeus* which tolerate a wide range of temperatures, are typically eurythermal species. On the other hand, species such as *T. guineensis* (14°-33°C) and *S. melanotheron* (18°-33°C) which live in a narrower range of temperatures are more stenothermal.

It is not perhaps the thermal tolerance limits which are so important for wild populations, but rather the temperature preferenda at which maximum biological performance can be expected. It is generally accepted, for instance, that tilapias cease growing significantly at temperatures below 20°C, and feeding stops completely around 16°C. On the other hand, maximum swimming performance occurs at 28°C in *C. zillii*, 28-32°C in *O. niloticus* and 32°C in *S. galilaeus* (Fukusho, 1968).

The effect of temperature has an important consequence on the egg stage. At low temperatures, the development time from fertilisation to hatching is extended. For *Heterobranchus longifilis*, the thermal optimum for incubation and egg hatching ranges from 25 to 29°C (Legendre & Teugels, 1991). In contrast, the range of optimal temperatures for egg development is much wider for *Clarias gariepinus*: 19 to 31°C (Bruton, 1979b). This better tolerance of low temperature may be explained by (or may explain) the wider distribution range of this species, which is recorded from South Africa to Israel.

Temperature and feeding

Temperature affects both the rate of food consumption and the rate of gastric evacuation. At low temperatures the fish may cease to feed, but the rate of consumption increases with increasing temperature.

For *Sarotherodon galilaeus* in Lake Chad, the gut repletion coefficient and rate of gastric evacuation increased with temperature (figure 13.1), but a quite different situation was observed in the same lake with *Alestes baremoze* (figure 13.1). For this latter species gut repletion and gastric evacuation rates were negatively correlated with temperature (Lauzanne, 1969). Lauzanne (1977) tentatively suggested that it could be related to differences in spawning periods, but this explanation is not convincing. What is clear is that the daily food consumption rate (expressed as the ratio of the weight of ingested food to fish weight x 100) decreases with temperature for *Alestes* (1.77% at 19.6°C, 1.43 at 21.6°C, and 1.18 at 30.6°C), whereas it increases for *Sarotherodon* (1.5% at 19.5°C, 3.3 at 26.1°C and 6.1 at 30°C).

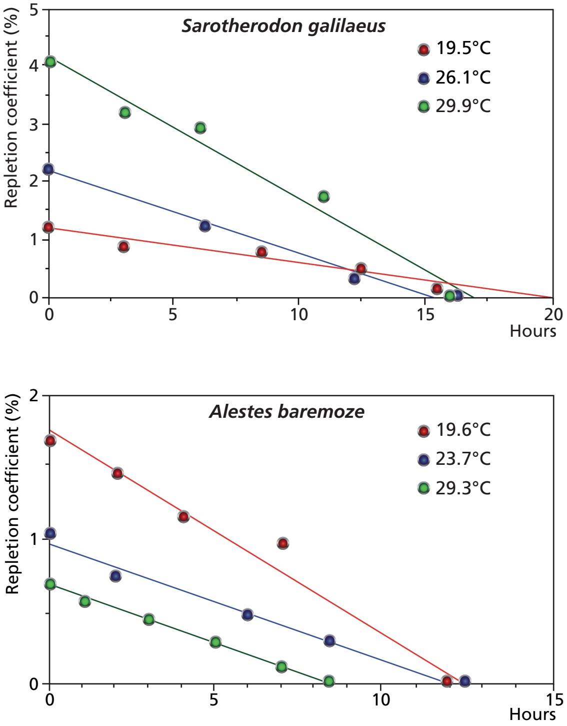


FIGURE 13.1.
Effect of temperature on gastric evacuation rates for two species from Lake Chad, *Alestes baremoze* and *Sarotherodon galilaeus*. The repletion coefficient is expressed as % of the body weight. (from Lauzanne, 1969 and 1977).

Behavioural responses to environmental temperature changes

It is usually assumed, but apparently not really tested with quantitative data, that fish are able to select the temperature regime in which they would maximize their lifetime production of offspring (Wootton, 1990).

When juveniles of *O. niloticus* and *C. rendalli* are submitted experimentally to a thermal gradient in tanks from 24 to 40°C, they respond positively to the warm water and swim actively towards water which is only slightly cooler than their lethal temperature tolerance (Caulton, 1977, 1982). In tilapias living in lakes, the juveniles, and above all the alevins, make daily cyclical movements between the shallower littoral zones, occupied during the day, and the deeper zones towards the open water, occupied by night. For instance, in Lake McIlwaine (Zimbabwe), the juveniles move in the morning from the deep homothermal waters where they stay overnight, into shallow coastal waters where the temperature exceeds that of the homothermal waters (28°C at midday). Large schools of juveniles are eventually found in warm waters at midday. In the late afternoon, a reverse movement is observed, and the juveniles move back into the deeper, homothermal water. The ecological significance and the survival value of these daily migrations have been much discussed. They may be a tactic for avoiding predators present in deep water during the day, or for reducing food competition by the successive exploitation of different habitats in the course of the day. An elegant explanation based on careful energy budgets was proposed by Caulton (1982) who claimed that thermal oscillations were beneficial to the growth of juvenile cichlids. The offshore-inshore migration tends to maximize growth: faster growth rates are achieved when fish move into warm inshore areas during the day (faster feeding and digestion rates), while when they retreat to cool deeper areas at night, the energy demands are less than if the fish remained at constant temperature.

Temperature creates distinct boundaries which may act as physical barriers to fish movement. Details of thermal structure contribute to defining the amount of suitable habitat available at a given time. Knowledge of the thermal structure of a waterbody is therefore important for understanding fish distribution and abundance.

Adaptations to the lack of oxygen

With few exceptions, fish essentially have aquatic respiration. The poor solubility of oxygen in water means that the quantity of oxygen available to fishes is always very limited and may still decrease considerably (in which case there is hypoxia) as a result of various factors: water warming, pollution, water stratification, etc. In particular, it is not rare for oxygen content to be a limiting factor in stagnant waters, particularly when they contain much organic matter whose decomposition generally consumes large amounts of oxygen.

When oxygen availability decreases, fish increase their gill ventilation rate. Depending on their choices or available options, fish can either attempt to move to better-oxygenated zones or use physiological, behavioural, or morphological adaptations to face this deoxygenation. In the worst case, the fish will die of asphyxiation.

Morphological and physiological adaptations

Some fishes are able to use oxygen in the air when its concentration in water becomes critically low. Most of them have organs that are adapted to these two modes of respiration. *Protopterus* spp and *Polypterus* spp possess a true lung, whereas *Gymnarchus, Heterotis, Papyrocranus, Phractolaemus*, have a modified swim bladder (air bladder) that allows them to use aerial respiration when needed. There is an arborescent breathing organ in the gill cavity of *Clarias*, and a labyrinth organ in *Ctenopoma* (Anabantidae).

Aerial respiration occasionally represents 90 to 95% of normal respiration in *Protopterus aethiopicus* even in well-oxygenated waters (Lenfant & Johansen, 1968), whereas this is only a compensatory mechanism when gill respiration is insufficient in *Clarias gariepinus* and *Polypterus senegalus* (Babiker, 1979 ; 1984). The *Protopterus* spp breathe through the mouth, swallowing air into the mouth cavity to send it to the lung. In water, *Protopterus* breathes every five to seven minutes, whereas in air it breathes every one to three minutes.

Generally speaking, Tilapias are resistant to low oxygen content, which explains why some species can live and reproduce in swamps or shallow lakes that may become temporarily anoxic. According to Bénech & Lek (1981) for instance, *O. niloticus,* which is capable of extracting oxygen in poorly oxygenated waters,

ADAPTATIONS TO AERIAL RESPIRATION

Adaptation of the gill or pharyngeal cavity

- **gill modifications**: Synbranchidae (*Monopterus*); Mastacembelidae (*Mastacembelus*)
- **vascularised epithelium in a suprabranchial chamber**: Channidae (*Parachanna*)
- **labyrinth organ**: Anabantidae (*Ctenopoma*)
- **arborescent organ**: Clariidae (*Clarias*)

Modified swim bladders

- Arapaimidae: *Heterotis niloticus*
- Notopteridae: *Papyrocranus afer*
- Gymnarchidae: *Gymnarchus niloticus*
- Phractolaemidae: *Phractolaemus ansorgii*

True lungs

- Polypteridae: *Polypterus senegalus*, *Erpetoichthys calabaricus*
- Protopteridae: *Protopterus*

can survive for a few hours in very hypoxic conditions (less than 0.5 mg l^{-1}), but their behaviour changes and the fish becomes lethargic. Once it is placed in favourable oxygenation conditions, it quickly reverts to its normal behaviour.

Behavioural responses to reduced oxygen availability

Some fishes living in poorly oxygenated physical systems have developed behaviours that allow them to face periods of hypoxia and await improved conditions.

For instance, certain species living in swampy habitats use the superficial layer of water which is comparatively richer in oxygen than the rest of the water column, because of exchanges with the atmosphere. This appears to be the case with *Synodontis membranaceus* and *Synodontis batensoda* (Green, 1977), as well as for *Sarotherodon* spp. (Bénech & Lek, 1981). Use of the superficial layer is undoubtedly facilitated by head shape and the location of the mouth (Kramer, 1983). Thus, Cyprinodontiformes with their flat heads and an upturned mouth are also adapted to this kind of behaviour.

In addition to using the superficial water layer, other species also take water bubbles into their mouth, as in *Synodontis membranaceus* (Roberts, 1975) and *Brevimyrus niger* (Bénech & Lek, 1981).

Another adaptation to hypoxic systems consists of laying eggs in floating nests. *Hepsetus odoe* deposits its eggs at the air-water interface, in a floating foam nest, and the young larvae possess structures that allow them to remain attached to the nest (figure 13.2) (see also chapter *Reproduction*). *Ctenopoma damesi* also

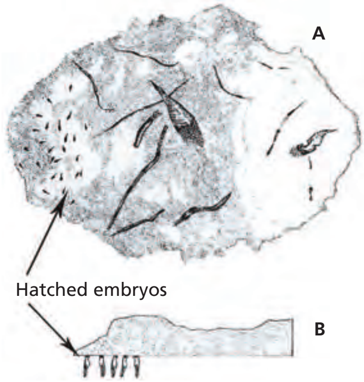


FIGURE 13.2.
Foam nest of *Hepsetus odoe*, with hatched embryos. Newly hatched embryos are suspended below the nest via a cement gland (B). Top view (A) and cross section (B) from Merron *et al.*, 1990).

lays eggs in floating foam nests guarded by the male, who ensures the eggs remain oxygenated, while *C. muriei* produces floating eggs.

Adaptations to salinity

Many fishes live in fresh or salt water, but numerous so-called amphihaline (or euryhaline) species can move from fresh to salt water and back. The internal fluids of freshwater fish are more concentrated than freshwater, so they have a tendency to lose ions (Na^+, Mg^{++}, Cl^- in particular) and acquire water through all permeable surfaces such as gills or oral mucosa. Conversely, in salt water, they tend to acquire ions and lose water. Osmoregulation is the phenomenon that allows animals to regulate plasma concentrations of ions and water, and to maintain a constant osmotic pressure in their internal fluids despite variations in ambient conditions.

Gill epithelium is subjected to an uninterrupted flow of water, and the transfer of salts primarily occurs here. For example, in *O. mossambicus* the exchange rate increases nearly two hundred fold when the species is transferred directly from fresh to salt water. But the physiological mechanisms that allow adaptation to salinity are still poorly understood (Prunet & Bornancin, 1989). Nonetheless, we know that adaptation to salinity can be modulated by numerous environmental factors. Very early exposure to high salinities is believed to increase adult resistance to salinity (Watanabe *et al.*, 1985).

Fish species that can live in continental salt waters are rare, and many belong to the Cichlidae of marine origin which may explain their great euryhalinity. Several Tilapias such as *Tilapia guineensis* and *Sarotherodon melanotheron* live and reproduce in the coastal waters of West Africa, in salinities of up to 30‰. In Casamance, Albaret (1987) even observed populations of *Sarotherodon melanotheron* and *Tilapia guineensis*, in 90‰ waters during a period of drought. East African species such as *Oreochromis mossambicus*, *O. urolepis,* and *O. placidus* also have high tolerance for salinity. *O. mossambicus* has been observed to reproduce in waters with a salinity of 69‰, twice that of sea water.

A few Tilapia species are well-adapted to the high salinities found in some lakes. This is the case for *Oreochromis amphimelas* in Lake Manyara (58‰), *Alcolapia grahami* endemic to Lake Magadi (40‰), and *A. alcalica* in Lake Natron (30 to 40‰) (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*). *Coptodon zillii* which usually lives in fresh water reproduces in Lake Quarun, in Egypt, where salinity varies from 10 to 26‰, and can survive in waters with a salinity of up to 44‰.

Among the Cyprinodontidae, *Aphanius fasciatus* lives in waters reaching a salinity of 40‰ in North Africa. Mormyridae, meanwhile, are strict freshwater fishes that cannot tolerate even low salinities. Thus, in Lake Chad, Mormyridae are confined to waters whose conductivity remains below 400µS cm^{-1} (Bénech *et al.*, 1983). Mormyridae are also not found in Lake Turkana where conductivity is around 3500 µS cm^{-1}, even though the rest of the ichthyofauna has strong nilotic affinity (Lévêque *et al.*, 1991). It is also believed (Lowe-McConnell, 1987) that the existence of a single species of Mormyridae in Lake Tanganyika may be the result of past events marked by an increase in water salinity that led to the elimination of other species of the same family.

Adaptations to drought

Africa has numerous temporary aquatic physical systems that dry up seasonally. In general, there is a seasonal cycle related to rainfall and flooding, but in some extreme cases, water is supplied much more sporadically. Meanwhile, in wet tropical areas, small puddles such as those found in the footprints of elephants or cattle can appear and disappear several times a year (see chapter *Life-history strategies*).

A small number of species have adapted to survive total desiccation. The West African lungfish (*Protopterus annectens*) has long been known to survive long periods of desiccation of its habitat (Johnels & Svensson, 1954).

THE LUNGFISH

When the water level decreases, the West African lungfish (*Protopterus annectens*) digs a vertical burrow in the soft mud as well as a round chamber in which it secretes copious quantities of mucous. When the mud dries up, the mucous also becomes dehydrated, forming a cocoon around the fish which thus becomes dormant. The fish remains immobile, folded upon itself, breathing air through a small opening at the top of the cocoon (figure 13.3).

In nature, *Protopterus annectens* can aestivate for seven to eight months, depending on the length of the dry season. In aestivating *Protopterus aethiopicus,* the rate of oxygen consumption decreases progressively to 10% of an active fish's consumption, and the heart rate decreases to around three beats per minute (Beadle, 1981).

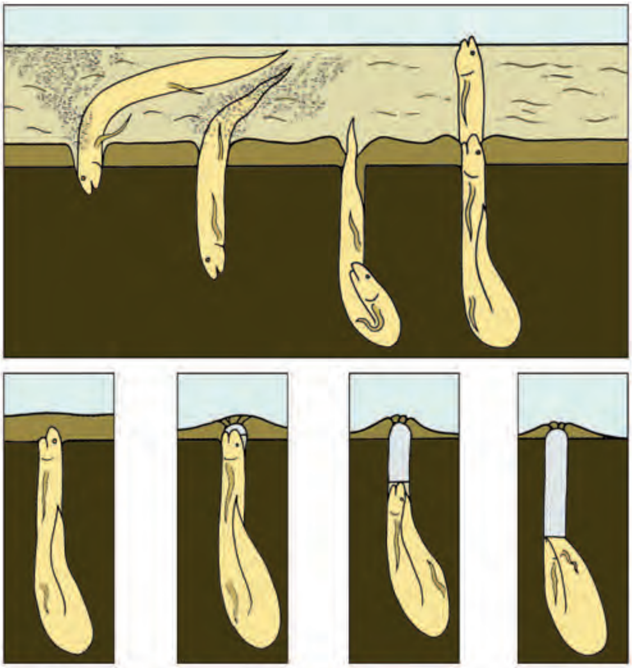


FIGURE 13.3.

Schematic views of aestivating and cocooned *Protopterus annectens* (redrawn from Johnels & Svensson, 1954).

Catfish of the genus *Clarias* are also known to survive in sand or wet mud, but not in fully dried up areas (Bruton, 1979b). Their capacity to recolonize recently flooded areas probably comes from the fact that they are able to travel several hundred metres in wet prairies.

Fishes of the Cyprinodontiformes order are particularly well-adapted to life in temporary habitats, and certain species of the genera *Nothobranchius* and *Aphyosemion* live in the temporary ponds of tropical Africa. Adults only live there for a few months, that is, during the high water period, and the reproductive cycle must be completed during this period. Resistance to drought in this case takes the form of eggs enclosed in a thick membrane. They can resist for several years while buried in the ground and develop once the physical system is filled with water again. Growth after hatching is very rapid, and for *Nothobranchius*, sexual maturity can be reached in less than one month (Haas, 1976a). *Nothobranchius rachovii* can thus spawn at the age of 4 weeks and a size of 9 mm (Simpson, 1979), while *N. guentheri* reaches maturity 7 to 8 weeks after hatching (Bailey, 1972).

DIAPAUSE IN CYPRINODONTIFORMES

In Cyprinodontiformes living in temporary physical systems, hatching can be delayed by several days; that is, the fry remains in the egg instead of hatching out. In some species of *Aphyosemion* and *Epiplatys*, this period does not exceed several days, whereas it can reach up to 70 days in *Aphyosemion batesii* (Brosset, 1982).

We have also seen that eggs of Cyprinodontiformes can enter diapause, that is, suspend development at well-defined stages (Wourms, 1972). Pre-incubation diapause has been observed in *Aphyosemion batesii* (Brosset, 1982), and diapause in an embryo that was ready to hatch has been seen in other annual species such as *Fundulopanchax arnoldi, F. fallax, F. walkeri*.

Genus and species names have been updated from the ones used by Brosset.

Blind fish

Life in total darkness, as in underground caves, can lead to the regression or disappearance of eyes. It is generally believed that these "troglobionts" evolved from surface species with eyes and which, for various reasons, were trapped underground. This resulted in loss of pigmentation, a slower metabolism, and a decrease in eye size that is increasingly pronounced with the duration of the cave colonization (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*).

There are few known blind fish species in Africa (see chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*). In a large group of caves in the region of Thysville in DRC, belonging to the Kouilou system, scientists discovered *Caecobarbus geertsii*, *Chanallabes apus* and *Dolichallabes microphthalmus* (Heuts, 1951 ; Heuts & Leleup, 1954). *Barbopsis* *devecchi* and *Uegtiglanis zammaranoi* were captured in wells in Somalia and Ethiopia. Two fully blind species of cave-dwelling Eleotridae were discovered in Madagascar, in karst formations in the south-western part of the island (Kiener, 1963).

Blind fishes have also been found in rapids, and a hypothesis worth verifying is that the loss of eyes and pigmentation could be due to the fact that they spend their lives under rocks. This is the case of *Platyallabes tihoni* (figure 12.3) and *Mastacembelus brichardi*, two species from Stanley Pool living under rocks or in cracks.

A new blind fish species (*Glossogobius anakaranensis* Banister, 1994) was discovered in an underground river of the Ankarana massif in the north of Madagascar. It is the third blind fish species recorded in the "Grand Île"; the other two were Eleotridae discovered in the southwest of Madagascar.

Light attenuation and darkness

African river waters are generally turbid and fish cannot use their sight to orient themselves. They have thus developed adaptations that allow them to communicate while in motion.

In electric fish, discharges create an instantaneous electric field around the fish (figure 13.4). The presence of an object in the immediate surroundings of the fish concentrates or disperses the lines of the field, depending on its electric conductivity compared with water. Disturbance of the field owing to the presence of the object is sensed by the fish, whose cerebellum processes messages transmitted by its electroreceptors. Various experiments carried out with *Gymnarchus* in particular have proven that the fish are able to use this detection system to avoid obstacles, but it is only effective within a radius of about 10 centimetres in Mormyridae. The adaptive value of this system is obvious for fish living in murky waters and which are often nocturnal. It allows them to orient themselves and to find prey to feed upon.

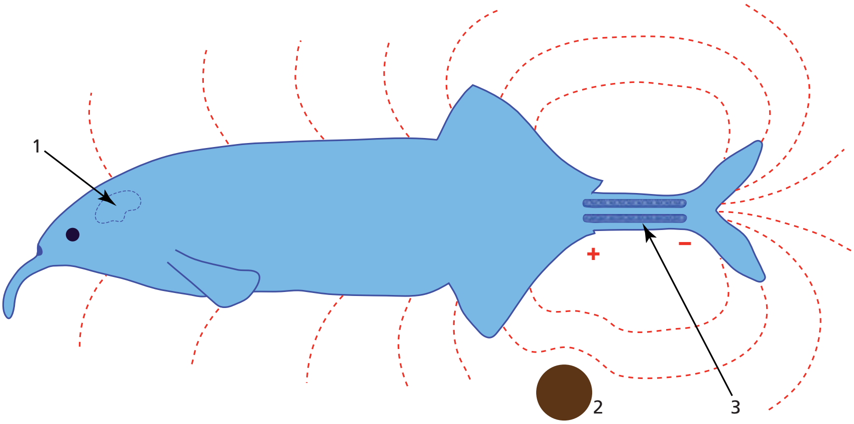
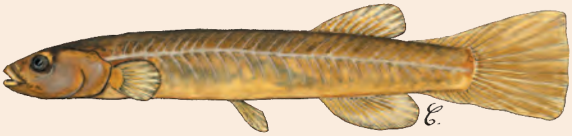


FIGURE 13.4.
Principle of electrolocation in a mormyrid fish. The electric organ (3) which is monitored by electroreceptors (1) found in pores of the anterior surface, produces electric discharges. The dotted lines give the current flow associated with electric organ discharge. Each object (2) with conductivity different from that the surrounding water distorts the current pattern and thus modifies the fish information.

Ethology



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Ethology calls on a wide range of disciplines including genetics, physiology, ecology, developmental biology, and evolution to converge in an integrated view of the organism, its function, and its interactions with its physical system. Among the vertebrates, bird and mammal behaviour have been the subject of much investigation, whereas fish behaviour is still relatively unknown barring a few exceptions, in particular species that are popular with aquarium enthusiasts. The majority of studies on African fishes focus on two families, the Mormyridae because of their particular means of communication (electric signals), and the Cichlidae, owing to their economic importance and significance in evolutionary science with the "species flocks" in the African great lakes (see box, "History of the ethology of African fishes"; chapter *Diversity of African fish: a heritage of evolution*).

Functions and structure of behaviour

Behaviour is composed of a series of specific actions in response to information, and favourable to sustaining an individual or species. This stimulus may be external (provided by the environment: changes in the physical conditions of the system, presence of a predator or congener, etc.) or internal (provided or possessed by the individual: change in serum hormone levels, etc.) To be efficient, these actions must be spatially and temporally organized. It is therefore necessary to have the response coincide with the stimulus (Guyomarc'h, 1995). Behaviours are generally subdivided into four broad categories (Guyomarc'h, 1995):

- so-called maintenance behaviours (resting phases);
- food behaviours (exploratory strategies, capture, etc.)
- so-called agonistic behaviours (to ward off intra- or interspecific competitors from a territory where the animal feeds and/or reproduces);
- reproductive behaviours (mating, arrangement of spawning site, nest construction, spawning, parental care, etc.).

HISTORY OF THE ETHOLOGY OF AFRICAN FISHES

As early as 1950, Baerends & Baerends von Roon pioneered in the behavioural study of Cichlidae, but the most significant work on Tilapias *sensu lato* was carried out by researchers from the Université de Liège, with Ruwet & Voss (1966), then Voss (1977, 1981). This enabled not just the acquisition of data on systematics, but also led to direct applications in the establishment of fishfarming for this "African carp". At around the same time, Wickler (1962) began studying mimetism in these fishes.

Studies expanded in the 1980s-90s to the fishes of the great lakes: Tanganyika (Kawanabe *et al.*, 1997), Malawi (Ribbink *et al.*, 1983; Hert, 1989), and Victoria (Crapon de Crapona, 1982; Crapon de Crapona & Fritzsch, 1984; Goldschmidt, 1991; Fermon, 1997), as scientists attempted to determine if behaviour was one of the keys to understanding species flocks, as already hypothesized by the preliminary work of Fryer & Iles (1972) and Greenwood (1991). Investigations continue to this day and focus on sexual selection, colouring patterns, and sex partner selection, territoriality, and male competition (Maan, 2006; Djikstra *et al.*, 2007; Blais *et al.*, 2009; Baldauf *et al.*, 2011; Ding *et al.*, 2014; Sefc *et al.*, 2015, etc.).

Meanwhile, Mormyridae attracted the attention of researchers because of their ability to produce electricity. Initial investigations on these fishes focused mainly on physiological and neurological aspects in order to understand how they produced and used electricity.

Later studies showed that discharges could have specific characteristics, also varying according to the social behaviour, physiological state, and sex of the fish, much like the role of songs in birds.

For a full bibliography, the following references can be consulted: Kramer, 1990, 1996; Hopkins, 1986; Moller, 1995; Feulner, 2006; Arnegard *et al.*, 2010).

Functions of behaviour

An organism can act directly on its biotic or abiotic environment. This is a direct action: fleeing a predator, seeking food, building a nest, and so on. These are known as first-order behaviours that contribute directly to the survival or reproduction of the organism.

An organism may also establish a relationship with another animal and influence its behaviour, which implies in this case that there is a form of communication between the individuals present. This is the case of mating or territorial defence. These second-order behaviours thus contribute to:

- the synchronization of individual activity cycles;
- the selection of partner activities;
- the regulation of partner activities and distances;
- the physiological adjustment of interacting individuals;
- psychological or ontogenetic adjustment. The quality of information and the manner in which it circulates in social groups lead to individual differentiation of hierarchies and behavioural styles that prove useful for the smooth function of social structures.

There are obviously relationships between the two types of actions, and it is sometimes difficult to differentiate them, especially since the organs used in these two behavioural categories are often the same. For instance, electrical signals allow Mormyridae to locate themselves in the environment and detect an obstacle or prey (electrolocation), but they are also communication signals between individuals.

Structure of behaviour

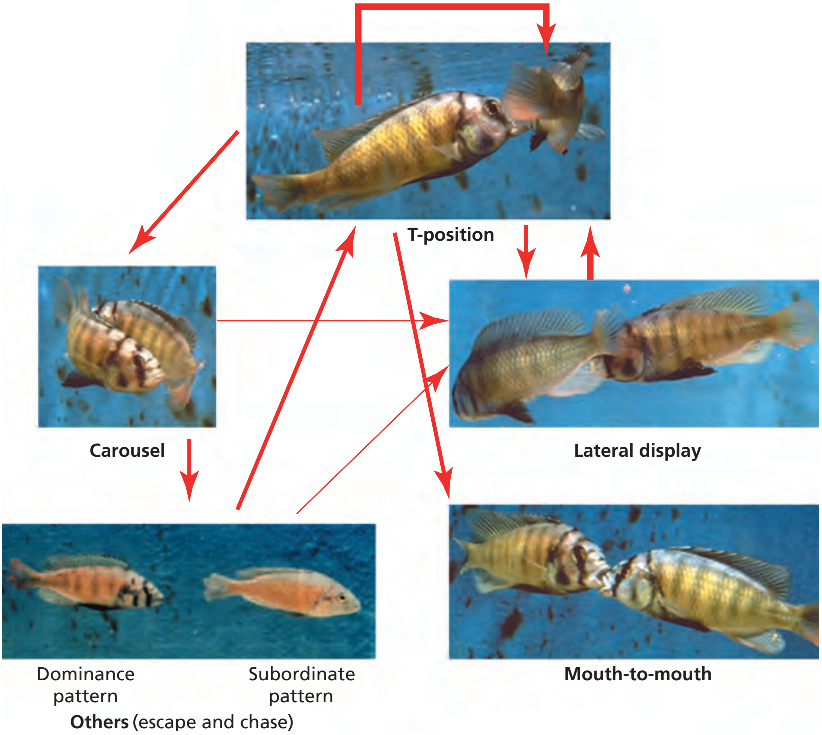
Behaviours have a structure that has well-defined properties and characteristics:

- They are organized in systems: a behaviour is composed of a set of events that are arranged in a gradual or fragmented manner. For a given signal (colour, sound, etc.), a species has one or several structured signalling systems ("repertoires"). For example, in *Haplochromis brownae*, a Cichlidae species endemic to Lake Victoria, fights are ritualized and a given position will be followed by another one in a relatively consistent manner (figure 14.1). A "T-position" will often precede a "carousel" position, which is then often followed by the flight of one of the protagonists, with the loss of its aggressive colouring pattern (Fermon & Voss, 1990).

- They are multimodal: a message may be sent using different types of signals that reinforce or complement each other. For example, in *Haplochromis burtoni*, the aggressiveness of a male is expressed by the association of two components, one locomotor (vertical position) and the other pigmentary (slope of the lachrymal stripe) during fights (Heiligenberg, 1974). This is also the case during the mating ritual in *Maylandia zebra* (Escobar-Camacho & Carleton, 2015) (figure 14.2).

- The structure of behaviour is, in general, highly specific given the intra-specific functional framework. In fights between congeners among Cichlidae, the lateral position is followed by a carousel in *H. brownae*, whereas in *Neolamprologus fasciatus*, it is mainly followed by a face-to-face phase (figure 14.1) (Fermon & Voss, 1990; Busson, 1996).

FIGURE 14.1.
Fight habits between males of *Haplochromis brownae* (from Fermon & Voss, 1990).



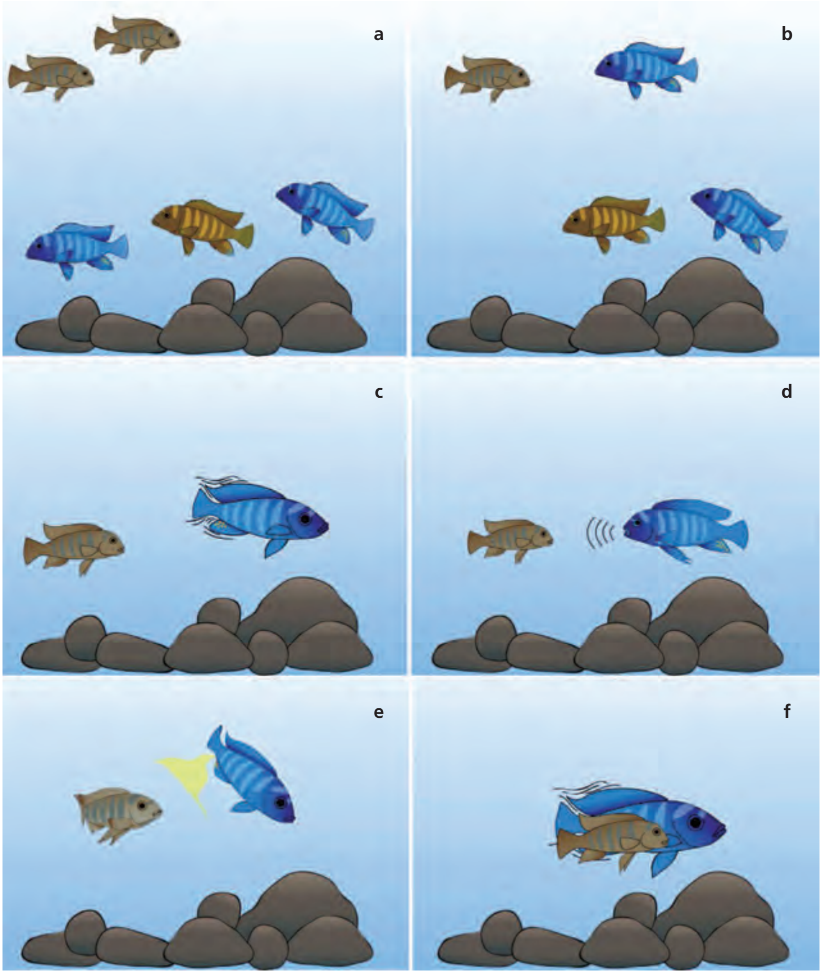


FIGURE 14.2.
Behaviours associated with multimodal courtship in cichlids. We show an ethogram for the Malawi species *Maylandia zebra*.
(a) Females swim freely above the lek and view males on their territories. Females may first use visual cues to detect conspecifics or dominant individuals looking for their pigmentation colour patterns.
(b) Males approach the females to attract them to their territory. Males may also use visual cues to select which females to approach.
(c) Males extend their fins and display in front of the females, quivering their fins and body.
(d) Males produce vocalizations toward the female which may be coincident with their quivering.
(e) Males exhibit several urine pulses in the presence of females to stimulate egg maturation and to indicate their social reproductive status.
(f) Males quiver close to the female potentially stimulating superficial neuromasts of the lateral line.

- They vary gradually. Within a species, the general expression of a behaviour may vary from one individual to another according to age and sex, but also social rank or physiological state. For instance, female *Neochromis greenwoodi* in Lake Victoria take the aggressive colour pattern of males and become territorial during incubation (Witte pers. com.; Fermon, pers. obs.).

Different behavioural signals – communication

Communication is the transmission of signals and information between a sender and a receiver. It takes very diverse sensory channels in the animal kingdom, and we now know that a fish species may use various modes of communication. This is a means of reducing the risks of misinterpreting messages from a single sensory channel, but it also allows better targeting of the receiver. In aquatic systems that are inhabited by numerous species, it may be indispensable to remain recognizable to one's congeners, if only for reproduction. To the extent that vision is limited at night-time and in murky or plant-rich waters, it is even more necessary to develop other specific modes of communication that can transmit rapid, precise messages. This is the case with electrical signals, sounds, and the olfactory or gustatory perception of chemical messages.

Visual signals

Many fishes communicate visually through body movements and/or colour patterns. These visual cues are favoured in certain families such as the Cichlidae or the Cyprinodontiformes.

The position of the body is a signal perceived by other fishes. This mode of communication is used especially during mating rituals or encounters between rivals. Baerends & Baerends van Roon (1950) were the first to propose a nomenclature of positions, for Cichlidae. Some are common to numerous species. For instance, in "lateral" position, a threatened Cichlidae may appear larger if its pelvic and median fins are extended (figure 14.1). Likewise, in "face-to-face" position, the threatened fish turns its head towards the attacker while puffing out its opercles and branchiostegal membranes. Conversely, frightened fish try to make themselves as small as possible by drawing in their fins close to the body. Nonetheless, when drawing up the catalogue of positions, their order of appearance, combination, and length for a given family, specific differences can be noted and may play an important role, in particular as reproductive barriers during mating rituals.

Noble & Curtis were the first to posit in 1939 that the mating ritual of *Hemichromis bimaculatus* did not have a solely ornamental purpose. It was not until the 1960s that scientists truly found evidence of the role of coloured structures in communications between individuals. They found that the colour pattern at a given moment could play an important role in social and/or sexual behaviour. Generally speaking, each fish has a range of predetermined and specific colouring composed of various coloured structures whose overall configuration is characteristic of the species. However, under the effect of internal emotional or physiological factors (such as changes in serum hormone levels) or external environmental factors (presence of a congener, temperature changes, etc.), many species can change their colour pattern (figure 14.3). Pigments are grouped in special cells called chromatophores, which can aggregate or disperse them to the point of changing the animal's appearance almost instantaneously. The characters of the pigmentation and colouring range vary in Cichlidae in close conjunction with reproductive behaviour and parental care (Voss, 1983). In species such as *Tilapia* which are substrate spawners, where partners remain together for a long time and both play a role in defending territory and protecting eggs, colouring range is complex but nonetheless remain very similar in the male and the female. Meanwhile, in Cichlidae where couples only exist during spawning and only one of the two partners cares for the fry (*Oreochromis, Haplochromis, Labeotropheus*, *Pseudotropheus*, etc.), the range of colour patterns is limited but with marked sexual dimorphism. Marks and colouring play an important role

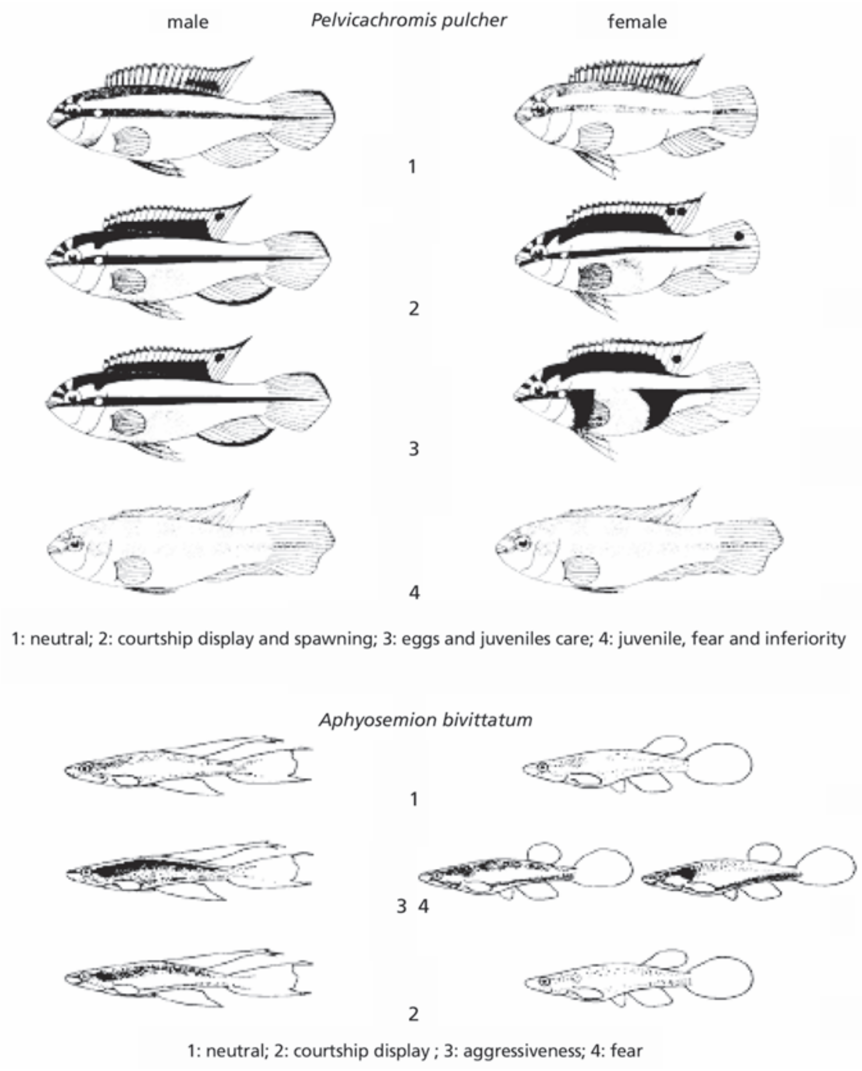


FIGURE 14.3.
Colour patterns of *Pelvicachromis pulcher* (simplified from Voss, 1977) and *Aphyosemion bivittatum* (from Ewing & Evans, 1972).

in the social status of Cichlidae. The intensity of the colour red during the mating ritual of *Pundamilia nyerer*ei in Lake Victoria is correlated with the individual's social status in the group (Dijkstra *et al.,* 2007). In *Neolamprologus pulcher*, results of experiments using familiar and unfamiliar images indicate that individuals are capable of distinguishing familiar from unfamiliar individuals using facial colour patterns (Kohda *et al.*, 2015).

Touch signals

Physical contact may also be a mode of communication. During mating rituals, contact is established between the two partners. In *O. mossambicus*, the male touches the genital papilla of the female to determine the sexual state of the latter. Similarly, in *Haplochromis* spp., contact with the anal fin of the male by the female is a decisive factor in ejaculation and the fertilisation of eggs in the female's mouth (Wickler, 1962; Hert, 1986; Fermon, 1997). In many Mormyridae it can be observed that manual stimulation leads to a flexion of the anal fin (Kirschbaum, 1987). This reflex may facilitate the fertilisation of eggs by forming a canal for sperm flow.

That said, the line between a communicative act and a fight is often difficult to establish, especially in agonistic situations. For example, in mouth-to-mouth positions in Cichlidae, the two individuals seize and push each other by the jaw. In T-position, one of the protagonists moves its tail to send water towards the head of the other (Baerends & Baerends von Roon, 1950; Fermon & Voss, 1990) (figure 14.1).

Chemical signals

Chemical communication plays an especially important role in the aquatic environment, as water can transmit chemical messages over long distances (Saglio, 1992). Depending on the type of end neurological connections of receptors, there are two major categories of chemical communication: olfaction and taste. Olfactory receptors are located in the nasal cavities. Taste receptors can be found throughout the body, but are generally concentrated in the barbels, filamentary fins, the gill zone and the mouth (Nelissen, 1991).

Fishes are able to react selectively to the perception of substances produced by their congeners, prey, or predators. A substance produced by an animal and perceived by an individual that reacts immediately to it is called a pheromone. Its duration of action is generally transient. We can distinguish *releaser pheromones* that induce an immediate change in the receptor's behaviour from *primer pheromones* that trigger a change in the physiological state of the individual that receives them. The latter category includes the sex pheromones, which influence the appearance and synchronization of male and female reproductive activities. It has thus been shown that female *Haplochromis burtoni* cichlids that are ready to spawn produce chemical signals that stimulate sexual activity in males of their species (Crapon de Crapona, 1980). In experimental conditions, it has been shown that ovulating female *Clarias gariepinus* preferred the waters of male-occupied basins rather than female-occupied ones because of the pheromones produced by the males (Resink *et al.*, 1989). These substances also play an important role in parental care. Experimentally, it has been shown that parents of *Hemichromis bimaculatus* recognize their own young but not those of a heterospecific spawn. Likewise, young are attracted by chemical substances produced by their congeners (Kühme, 1963; 1964). In *Oreochromis mossambicus* (Barata *et al.*, 2007) and *Haplochromis burtoni* (Maruska & Fernald, 2012), the urine of males plays a role in social interrelations.

Chemical substances can also play a role in the detection of prey or congeners. The electric fish *Malapterurus electricus* reacts when it is placed in contact with the mucous of prey or a conspecific. This reaction disappears when taste receptors are severed (Bauer, 1968).

Sound signals

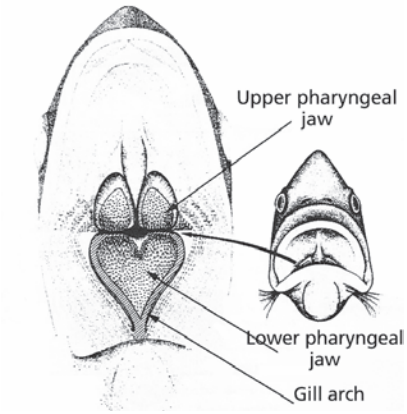


FIGURE 14.4.
Pharyngeal jaws of *Oreochromis mossambicus* (from Lanzing, 1974). The friction of the jaws produces a sound.

The aquatic system is far from being the "silent world". Fishes are not mute, as people sometimes think, and many species produce sounds. Those produced by catfish of the genus *Synodontis* are familiar to African fisherfolk, who refer to them as "konkon" in certain countries, in reference to the grunts they produce when they are taken out of the water.

There are three broad categories of sound signals:

- strident sounds produced by the friction of teeth (figure 14.4) or fin rays;
- sounds resulting from swimming movements;
- sounds from the swim bladder which acts as a resonating chamber when it is moved by certain muscles.

Sound communication in African fish is still poorly understood, but a number of works tend to show that it plays an important role in social relations. For Cichlidae, investigations have been carried out on some 30 species. Cichlidae produce more than one type of sound and use them for social interactions and reproduction. For example, *Hemichromis bimaculatus* can produce and receive sound signals (Rowland, 1978). Nelissen (1978) was able to show in various closely related Cichlidae species in Lake Tanganyika that the use of sound communication varied depending on lifestyle. *Simochromis diagramma* and *S. babaulti*, diurnal fish, had several colour patterns but mostly similar acoustic signals. The exact opposite holds true for *Tropheus moorii*, *T. brichardi* and *T. duboisi* which are nocturnal species. Sound communication may play a role in the recognition of individuals during the mating ritual. Sounds produced by three closely related species in Lake Malawi (*Maylandia zebra*, *M. callainos* and *M.* sp. "zebra gold") differ during mating (Simoes *et al.*, 2006). Meanwhile, it appears that in Cichlidae living in social groups, such as *Neolamprologus pulcher*, there is no sound communication (Pisanski *et al.*, 2015). Some Mormyridae can also produce and detect sound signals whose biological significance is still unclear. It is probable that these signals come from the swim bladder. We have discovered that they play an important role in the reproductive behaviour of *Pollimyrus isidori* and a nomenclature of these signals has been established for this species (Crawford *et al.*, 1986). Territorial males produce grunts, whines, and growls during sexual activity, whereas snapping and hooting sounds are produced during attacking behaviour. The acoustic signals of territorial males may be warning signs for congeners to inform them of the presence and location of reproductive sites. In *Marcusenius macrolepidotus*, it appears that these sounds differ depending on the populations (Lamml & Kramer, 2007).

Electrical signals

Many organisms are sensitive to electrical field deformations (including *Xenomystus nigri* and *Papyrocranus afer,* in African fishes), but few are capable of generating electricity themselves. Yet in African fresh waters, certain fish families have developed an electro-sensorial system that is complex enough to play an

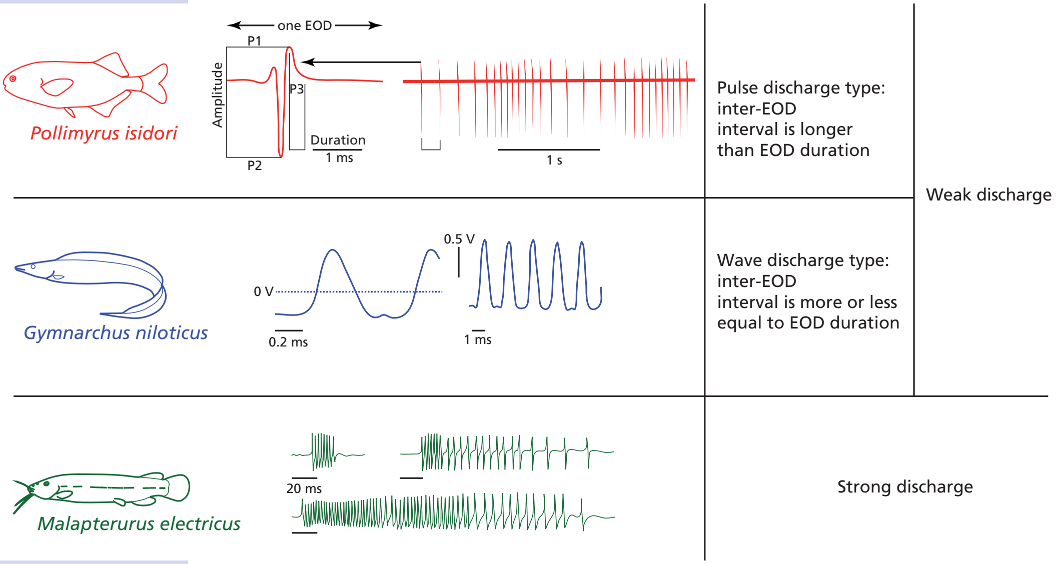
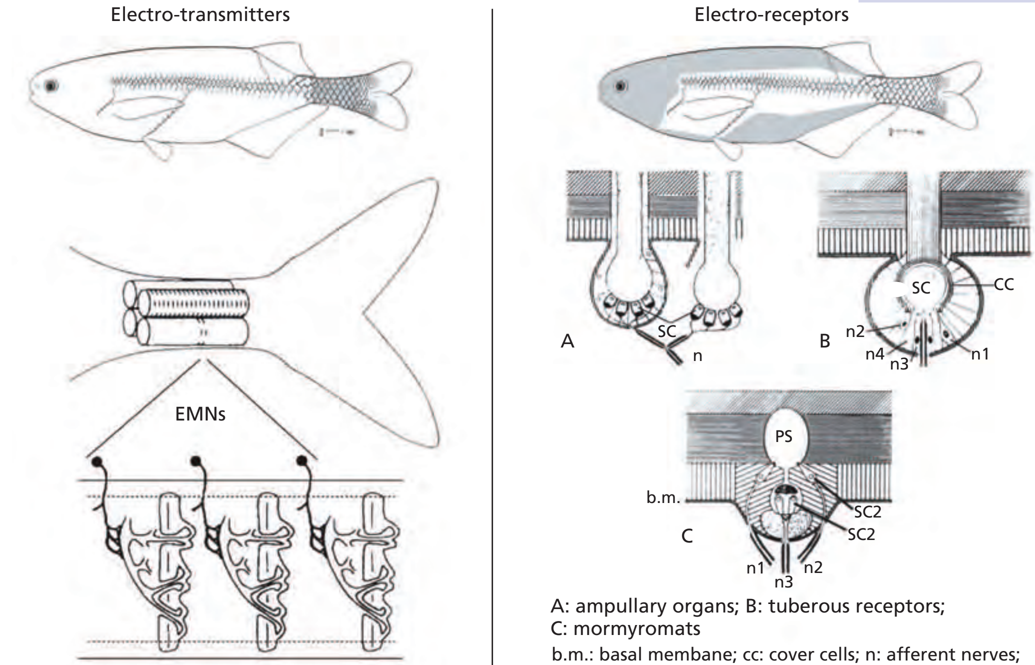


FIGURE 14.5.

The major types of electric discharges in African electric fish (from Crawford, 1991; Bennet, 1971 and Belbenoit *et al.*, 1979). To study electrical signals, different characteristics are taken into account. For fish with weak discharge, the signal is based on properties of the waveform of a single discharge which remains almost constant over time (left), and on trains of EOD (Electrical Organ Discharge) pulses (right). For *Malapterurus electricus*, the signal is based on the global structure of the train of EOD pulse (total duration, number of electric discharges series and number of EOD series, etc.).

essential behavioural role and be a favoured means of communication. This is the case of so-called weakly electric fish that emit, almost constantly, discharges of several tenths of a volt to one volt. Depending on the rhythm of the discharges, we can distinguish species that emit pulses (Mormyridae, around 250 species) or waves (Gymnarchidae, a single species, *Gymnarchus niloticus*) (figure 14.5). In both cases, modified muscle cells (electrocytes), found in the caudal peduncle in Mormyridae or spreading from it in Gymnarchidae, are responsible for producing electricity (figure 14.6). The resulting electric field is directed from the tail to the head. Electrical signals are received and analysed by a highly sensitive receptor system. These electroreceptors, innervated by nerve fibres from the lateral line, can be found on the peripheral parts of the body (stomach and back), but are more numerous in the head (figure 14.6).

One of the functions of this electro-sensorial system is to allow the animal to orient itself in its environment. The fish is informed of an obstacle's existence by the deformation it induces in the electric field. This electrolocation can be used to advantage in hunting and detecting prey (von der Emde, 1990). The system also plays an important social role, particularly in Mormyridae. The fish's discharges are imperceptible to humans, but they can be recorded and visualised using an oscilloscope. This allowed researchers to discover the enormous range of electrical signals, in form as well as frequency and rhythm. The characteristics of the electrical discharge may form a veritable specific signature allowing congeners



EMNs: electromotor neurons

A: ampullary organs; B: tuberous receptors;
C: mormyromats

b.m.: basal membane; cc: cover cells; n: afferent nerves;
PS: perisensory space; SC: sensory cells

FIGURE 14.6.
Electro-transmitters and electro-receptors of mormyrids (example of *Brevimyrus niger*) (from Szabo,1974 and Westby, 1984).

to recognize each other. This may be used in systematics to distinguish morphologically similar species (Hopkins, 1981; Crawford & Hopkins, 1989; and chapter *Taxonomy and Systematics*). The characteristics of signals may also vary according to sex or the physiological state of individuals within the same species. Fishes can thus transmit information on their aggressiveness, sexual maturity, or their respective hierarchical rank. Interruptions in the discharge rhythm most often indicate a sign of submission. Meanwhile, accelerations in rhythm are often correlated with attacking behaviour, and dominant individuals often emit discharges more rapidly (Kramer, 1974; 1978; Kramer & Bauer, 1986). Many Mormyridae live periodically or constantly in shoals, and continuously exchange information to maintain the spatial and social structure of the group (Moller, 1976; Squire, 1981; Serrier, 1986; Graff, 1986, 1989; Moller *et al.*, 1989). One can imagine that when hundreds of individuals from different species of electric fish cohabit, there must undoubtedly be a genuine electrical "cacophony". In these conditions, how can one perceive the messages of a congener without any risk of transmission jams? Electroreceptors in fact have filtering capabilities that are comparable to those of auditory receptors. Moreover, they have maximal sensitivity for electrical stimulations whose components, in frequency and phase, correspond precisely to those of the species's discharges. It was recently discovered (Hagedorn *et al.*, 1990; Baron *et al.*, 1994) that fishes other than Mormyridae and Gymnarchidae were capable of emitting weak electrical discharges. This is the case of several catfish of the genera *Clarias* or *Synodontis* (figure 14.7). The range for discovery undoubtedly still remains open in this field (see also box "Electrical fish history").

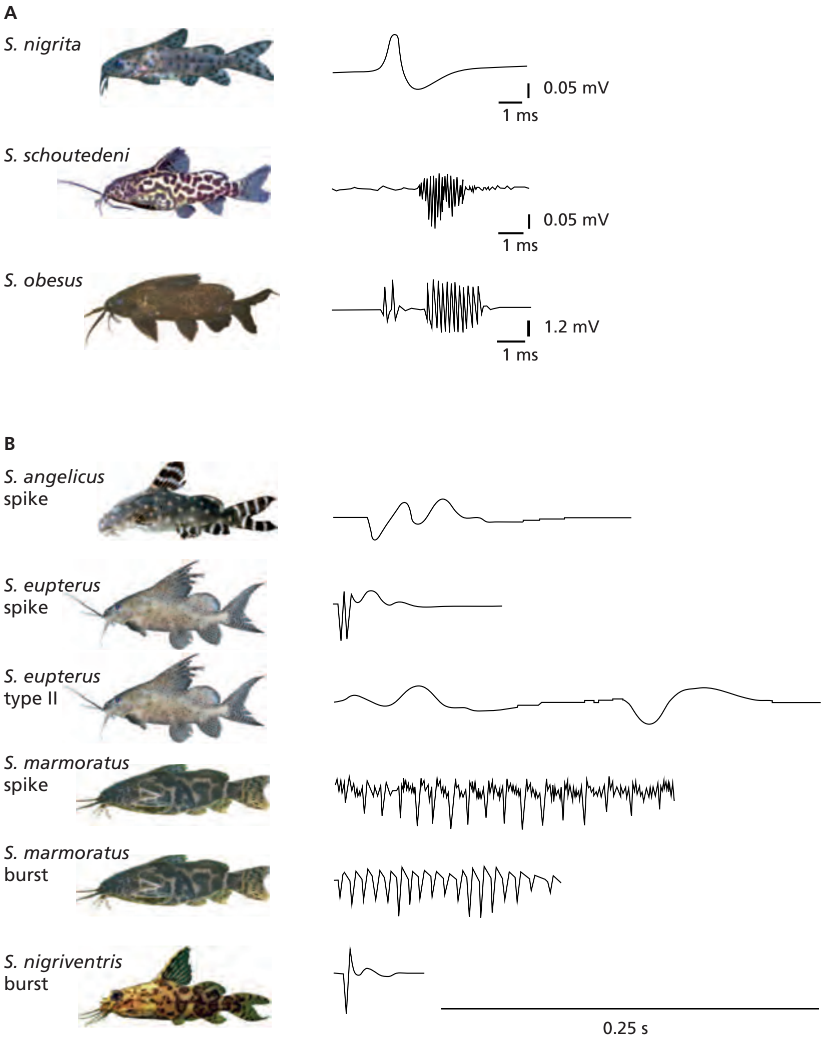


FIGURE 14.7.

In synodontid catfishes, the electricy appears to have originated from a sonic muscle. The organ lies dorsal to the swim bladder, and contains modified muscle tissue. Distinctiveness of *Synodontis* spp. EODs. A: EODs from three *Synodontis*: *S. nigrita* has a weak (50 µV/cm) biphasic, pulse-like EOD; *S. schoutedeni* produces bursts of weak (50 µV/cm), biphasic, pulse-like only when it swims; *S. obesus* also produces bursts of biphasic, pulse-like discharges but of greater intensity (2-4 mV/cm) (redrawn from Hagedorn *et al.*, 1990); B: Four tested species emit EODs of different types (redrawn from Boyle *et al.*, 2014).

Alongside these weakly electric fish, there are others that can generate high-intensity discharges. They are represented in Africa by the family Malapteruridae, which has 18 species. In *Malapterurus*, electrocytes develop from the pectoral muscles and are found over nearly the entire body surface. Production of electricity is intermittent and in salvos (figure 14.5) that include one or several bursts of discharges. A salvo can thus last up to 30 seconds and contain over 1,000 discharges. The amplitude of the latter varies with the size of the fish and can reach 350 volts in an individual measuring 50 centimetres in length. It is a fearsome weapon, but *Malapterurus* does not appear to limit the use of its electric potential to attacking prey or defending itself. A typology of discharge salvos emitted by *Malapterurus* classifies them into five categories (Moller, 1995). Four are directly linked to predatory or protective activities. A fifth

ELECTRIC FISH HISTORY

Highly electric fish have fascinated humans since ancient times. Representations of *Malapterurus electricus* are painted on Egyptian tombs in Saqqara. It was considered the "protector of fish" and any fisherman that felt its discharge was supposed to free his entire catch. Ancient Arabs called it "thunder fish" or "trembler fish".
Closer to Europe, the Jesuit Nicolao Godigno recounted in wonder in 1615 how dead fish were brought back to life when they were placed in contact with a freshly caught *Malapterurus*. Depictions of Mormyridae (*Petrocephalus*, *Mormyrus* and *Marcusenius*) have also been identified in fishing scenes on the bas-reliefs of tombs in Giza and Saqqara (figure 14.8). There was even a cult devoted to *Mormyrus*. However, as the fish emits discharges that are imperceptible to humans, one would be hard-pressed to attribute this veneration to the fish's electric characteristics.

In the early 1950s, H. Lissmann paved the way for the study of weakly electric fish. During an expedition in Ghana, he noticed that the rivers were teeming with "live" electricity (Lissmann, 1951). Ample proof was provided by dipping two copper wires connected to an amplifier, and hearing the crackling sound that testified to the electric activity of fishes.

FIGURE 14.8.

Amulet of *Oxyrhynchus* (bronze), Graeco-Roman period (332 B.C. -337 A.D.), Egypt (© Musée des Confluences, Lyon/P. Ageneau).

is only used during confrontations with congeners (Rankin & Moller, 1992). But to the extent that this type of discharge only concerns one of the congeners (be it the dominant or the dominated), it is difficult to determine if it has any real value as an element of communication, or if it only reflects the individual's degree of agitation. Yet observations in laboratory conditions (Kastoun, 1971, 1972; Rankin, 1984; Rankin & Moller, 1986, 1992, among others) suggest that when they are associated with other sensory systems (gustatory, olfactory, and chemical), the electrical discharges of *Malapterurus* play a role in inter- and intraspecies relationships.

Ecology and behaviour

Reproductive, social, and feeding behaviours cover the active attitudes of fishes and their adaptation to external constraints in order to ensure their survival and propagation.

Reproductive behaviour

To ensure the best possible reproductive success, fishes employ diverse strategies that are coded genetically. These are expressed as often complex sexual and reproductive behaviour.

Sexual selections and competitions

Most fishes do not actively seek out sexual partners. However, in species where such a choice is made, it is generally the female who does the choosing, and it may be based on a quest for immediate or material benefit in order to increase the chances of gene dispersion and preservation. This generally manifests as active selection based for instance on the best builders or protectors (selecting the male with the largest nest, in *Mchenga eucinostomus* (McKaye, 1983); selecting a large partner, in *Sarotherodon* (see box, "Small females for large males")).

In the search for benefits tied to the genetic potential of the partner ("choosing good genes"), males generally sport brilliant colours that are designed to attract females. The most colourful ones have greater success, as in mouth brooding Cichlidae, especially in lakes Malawi and Victoria (McKaye, 1991). The same dimorphism is seen in Nothobranchiidae (figure 14.9). In Cichlidae, some secondary sex characteristics play a very important attractive role during the mating ritual. These are decoys such as the ocellae on the anal fin of Haplochromines, or spots on the pelvic fins of *Cyatopharynx* or *Ophthalmotilapia* (figure 14.10). In *Pelvicachromis taeniatus*, the length of the pelvic fin and the colour pattern in females could play a role in the choice of male (Baldauf *et al.,* 2010; Baldauf *et al.,* 2011). An investigation of the genetic analysis of male colour patterns and the choice of females in the Cichlidae of Lake Malawi, *Maylandia zebra* and *M. benetos*, suggests that (i) several non-additive genetic factors influence melanistic factors; (ii) the choice of sexual partner can be controlled by at least 1 or 2 non-additive genetic factors; the choice of the female from the second generation of hybrids is not influenced by the male's efforts to court her (Ding *et al.*, 2014). An analysis of the colour pattern and the female's choice indicates that these two traits are physically linked. The electrical signals in Mormyridae may play a similar role as that of colouring. A study of two closely related sympatric species of *Campylomormyrus*, *C. rhynchophorus* and *C. compressirostris*, showed that the length of the EOD could be one of the elements of reproductive isolation (Feulner *et al.*, 2009).

Aphyosemion coeleste

Fundulopanchax sjostedti

FIGURE 14.9.
Examples of sexual dimorphism in the colour pattern in two species of Nothobranchiidae (Photo M. Chauche, Revue française d'Aquariologie).

SMALL FEMALES FOR LARGE MALES

In mouth brooders, the number of eggs that can be incubated depends on the size of the oral cavity, and thus the size of the parent providing this form of care. In *Sarotherodon melanotheron*, a paternal incubator, small males cannot efficiently incubate all the eggs laid by a female of similar size, as these would occupy 90% of their oral cavity. During growth, the volume of the oral cavity increases more rapidly in males than the spawn volume does in females. Hence it is only after a given size that the male can care for all the eggs laid by a female, even a small one (Legendre & Trébaol, 1997). Females that pair off with larger males thus ensure the efficacy of incubation.

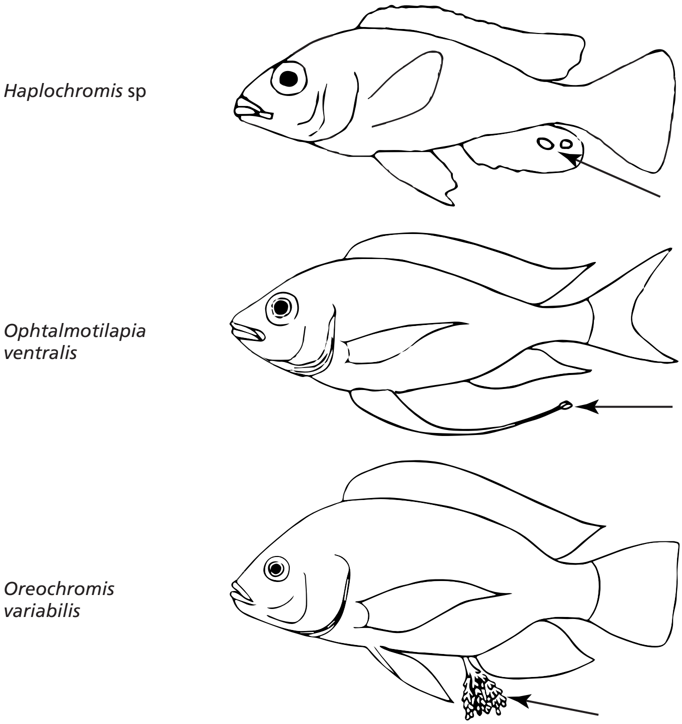


FIGURE 14.10. Different kinds of egg dummies in cichlids. *Haplochromis* sp.: anal fin spread to display egg dummies; *Ophthalmotilpia ventralis*: tips of pelvic fin are swollen and coloured to simulate eggs; *Oreochromis ventralis*: male which bears a genital tassel (synthesised from Fryer & Iles, 1972; Goldschmidt, 1991).

As they make their choice, females must also consider other constraints, such as the risk of forced fasting, or competition for food at the very least. In *Tropheus moorii,* an endemic Cichlidae in Lake Tanganyika, the female will feed in the male's territory a few days prior to reproduction (Yanagisawa & Nishida, 1991). The wealth of resources in the male's territory can thus become an important factor. That said, the female's desire for good-quality territory reinforces competition between males and male reproductive success (Hermann *et al.,* 2015). The choice is also limited by the attitude of the members of the opposite sex. A territorial male can spend time chasing off intruders, and other individuals can sneak in and fertilize the eggs already laid by the female present in the territory, as occurs in *Pseudocrenilabrus philander* (Ribbink & Chan, 1989). Among the Cichlidae '*Lamprologus' lemairii*, the females enter nests formed by crevices in the rocks, and the male passes in front of the opening to fertilize the eggs. Parasite males attempt to fertilize the eggs. But males that reproduce in nests with smaller openings have greater reproductive success (Ota *et al.,* 2014). In species that have harem structures, a single male monopolises all the females, as is the case with *Ctenochromis horei* in Lake Tanganyika (Ochi, 1993a). The choice of females is thus very limited and can lead to significant competition. In some colonies of shell-dwelling fishes, nearly all aggressive interactions between females are regulated by the male. This is the case in *Neolamprologus ocellatus*, where the polygamous male guards the snail shells that will serve as shelter and spawning sites for females (Walter & Trillmich, 1994). The most common intraspecific reproductive competition between males involves conflicts related to the defence of territories (see section below, "Social life, Conflict, and Cooperation").

From reproduction to parental care

The majority of reproductive systems, from monogamy to polygamy, can be found in African fresh water fishes (see box, "Different reproductive systems").

Many species select a spawning site either directly on the substrate – the most usual case – or in the water, with no visible barriers, for a number of pelagic species. In the former case, on or around the spawning site, some species build nests. They have a twofold role: to attract females by their shape, size, and arrangement (figure 14.11), and to protect eggs and larvae. They can be guarded by the parents.

There is a wide variety of nests in fishes. Some are constructed depressions as with *Heterotis niloticus* or consist of burrows, as with *Protopterus annectens*. Floating nests are a fairly common form in physical systems presenting a risk

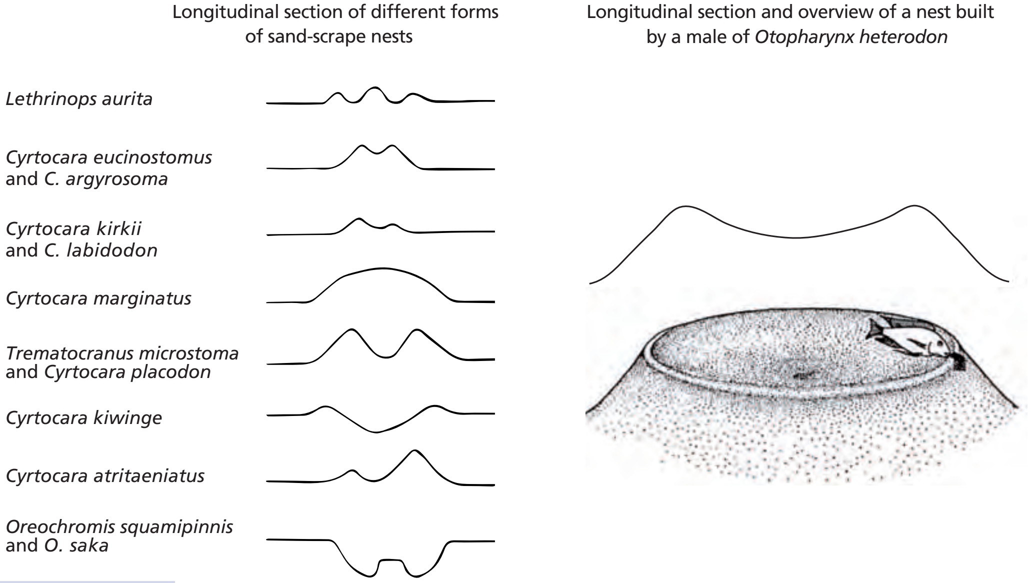


FIGURE 14.11.
Major forms of sand-scrape nests in Cichlids of Lake Malawi (from Fryer & Iles, 1972; McKaye, 1983 and McKaye & Stauffer, 1988).

DIFFERENT REPRODUCTIVE SYSTEMS

Polygamy

As males are capable of producing enough gametes for reproduction more often than females are, polygyny is frequent. While males do not provide parental care, a territorial structure is often found in polygamous males. This is the case of fishes living in harems (such as *Neolamprologus pulcher (= brichardi*) (von Siemens, 1990). When males protect the eggs, they can take care of several broods and thus reproduce with several females. This appears to be the case in the Mormyridae *Pollymirus isidori*. In Cichlidae maternal mouth brooders, the females can simultaneously incubate eggs fertilized by several partners (*Mchenga eucinostomus* of Lake Malawi) (Mc Kaye, 1983).

Monogamy

Monogamous species generally practice biparental care. After the spawning event, both parents remain associated throughout the period when the young need to be cared for. A good number of Cichlidae species, including the Tilapia (except *Oreochromis* and *Sarotherodon*), the Lamprologini, are monogamous and in some cases fishes mate for life. A study of *Neolamprologus caudopunctatus* has shown that genetically, the young come from the same couple (Schaedelin *et al.*, 2015). This is also the case for other species such as *Bagrus meridionalis* in Lake Malawi (Mc Kaye *et al.*, 1994).

Alternative strategies of males: satellite males or dominant males

Strategies can vary depending on the age of the individual: for instance, a large male of a species can stake out a reproductive territory to attract females. Meanwhile, a smaller male of the same species can adopt another tactic by taking on the colour pattern of a female and attempting to fertilize eggs during the mating ritual between a female and a territorial male.
There is an intermediate stage with semi-territorial fishes that attempt to attract females, but in an occasional manner.
Their territory is hence located outside the customary substrate for the species.
This strategy has been observed in mouth brooding Cichlidae species such as *Pseudosimochromis curvifrons* and *Pseudocrenilabrus philander* (Kuwamura, 1987; Ribbink & Chan, 1989).

Other strategies

There are only a few known examples of sex change in African fishes.
Cases of male-to-female sexual inversion have been observed in a brackish water fish, *Polydactylus quadrifilis* (Loubens, 1966).
The converse may happen occasionally in some Cichlidae.
In certain Cichlidae of Lake Victoria and particularly in *Neochromis greenwoodi*, some individuals possess functional gonads of both sexes while exhibiting the full set of external male characteristics (Fermon, pers. obs.).
Simultaneous hermaphroditism (where male and female gonads are functional at the same time), known only in reef fishes, and sexual and asexual reproduction, observed in *Rivulus* and the Poeciliidae, have not been seen in African fishes.

of anoxia. This is the case for nests of *Gymnarchus niloticus* built using plants. Mormyridae nests are also built using plant matter. In *Pollimyrus petricolus*, a species endemic to Niger, males actively guard the nest built from decomposing roots and branches of *Echinocloa stagnina*, which allows development of micro-invertebrates that serve as food for their young. Floating foam nests are also built by *Hepsetus odoe*. In some Cichlidae such as *Cyatopharynx furcifer* of Lake Tanganyika and *Mchenga eucinostomus* of Lake Malawi, structures similar to bird "leks" are observed. These are large surfaces or arenas where territorial males are found, and where they build their nests according to the hierarchy of the individuals, from the edges towards the centre (McKaye, 1983; Rossiter & Yamagishi, 1997).

On the spawning site, many species engage in a mating ritual (figures 14.12 to 14.14) whose specificity serves as a reproductive barrier and the role of which is to optimize egg fertilisation. These rituals, often highly complex, call several types of signals into play. Their structure and duration depend on the type of parental care provided by the species, as well as external factors to which the partners are subjected. For example, in mouth brooding Cichlidae such as Haplochromines, the females lay a small series of eggs (3 to 6) that they immediately take into their mouths, where fertilisation takes place; in *Oreochromis*, the female lays a large number of eggs that will be fertilized in part onsite, then, later, in the female's mouth. It is thought that, for Haplochromines, the speed at which eggs are taken into the mouth is essential because of the number of potential predators that may eat the eggs (Trewavas, 1993). They may also be the victim of "cuckoo" fish (see box, "Cuckoo fish"). In the Gobiidae *Glossogobius callidus*, the male prepares the nest and is joined by the female after a few days. The sticky eggs are adhered to the roof. After spawning, the male enlarges the opening and chases away the female. The male does not feed himself throughout the entire period of caring for the young (Wasserman *et al.*, 2015).

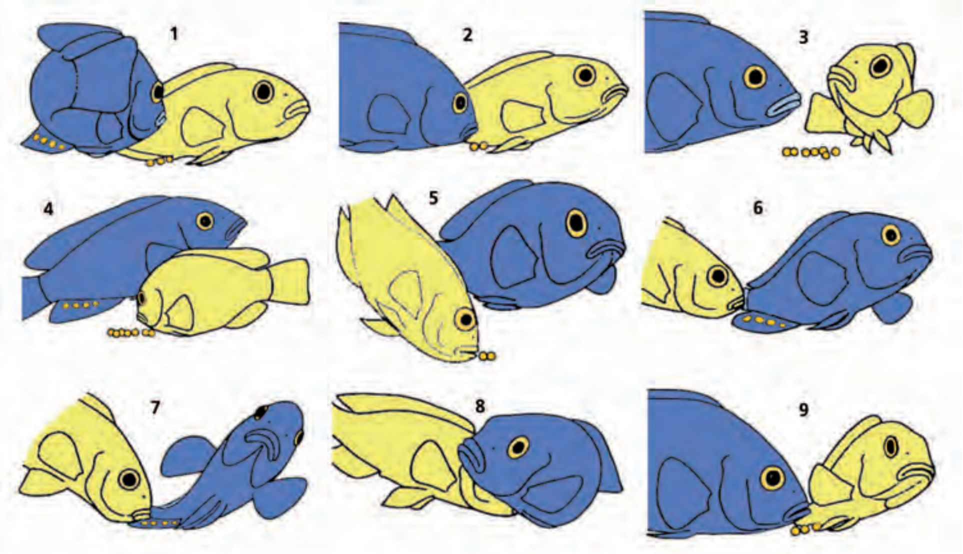


FIGURE 14.12.

Courtship and spawning in *Haplochromis burtoni*, a Lake Tanganyika cichlid.
The male is in blue and the female in yellow. 1: At the culmination of courtship the female begins to extrude eggs and the male is in close attendance; 2: egg laying continues; 3: A small batch of eggs having been laid, the female quickly turns; 4: the female prepares to take the newly laid eggs into her mouth, before the male has fertilized them; 5: the female quickly collects the eggs into her mouth; 6: the male extends his anal fin to reveal the eggs dummies "painted" on it and displays it before the female; 7: attracted and deceived by the egg dummies the female attempts to collect them and thereby brings her mouth, now containing eggs, into close proximity with the genital aperture of the male, which discharges sperm;
8: attempted collection of the egg dummies and fertilisation continue; 9: the female begins to lay another batch of eggs. The whole sequence is repeated several times until the mouth is filled with fertilized eggs (redrawn from Fryer & Iles, 1972).

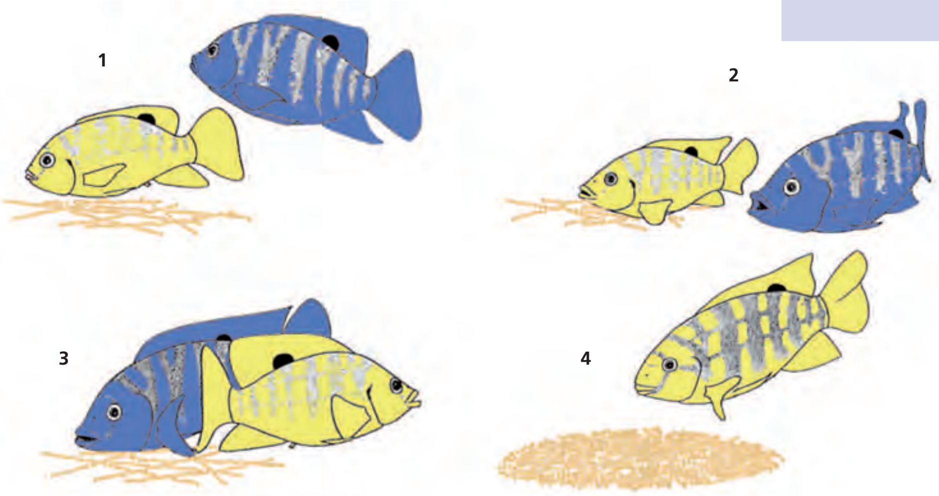


FIGURE 14.13.

Courtship and spawning in *Coptodon zillii*, cichlid from West Africa.
The male is in blue and the female in yellow.
1: the female prepares to deposit a row of eggs on the cleaned surface where spawning has already begun. The male stands by;
2. the female begins to lay. The male prepares to follow;
3: the female leaves the site, after spawning and the male, following the same course across, fertilizes the newly laid eggs;
4: the female, now darker than when spawning, guards and aerates eggs
(redrawn from Fryer & Iles, 1972).

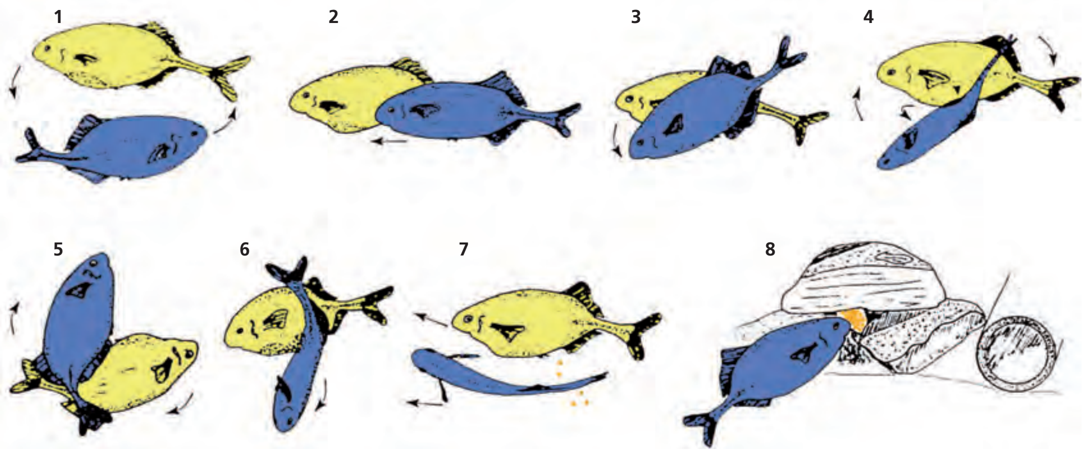
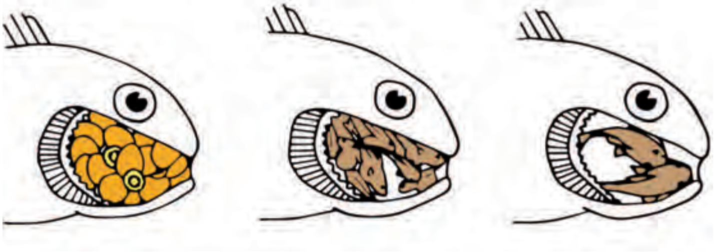


FIGURE 14.14.

Courtship and spawning in *Pollimyrus isidori*, mormyrid from West Africa.
The male is in blue and the female in yellow. 1: the female advances into the male's region;
2: the male arrives alongside of the stationary female; 3: the male becomes coupled Vent-to-Vent;
4: then the male turns laterally; 5: as both fish pivot around each other; 6: in one complete rotation;
7: during spawning the rotation is deleted and the sequence runs from (4) to (7) when the eggs are laid;
8: the male then quickly picks up the eggs in his mouth and places them into the nest
(redrawn from Bratton & Kramer, 1989).

CUCKOO FISH

FIGURE 14.15.
Development of a brood parasitic squeaker (*Synodontis multipunctatus*) in mouth-brooding cichlid fishes in Lake Tanganyika



The behaviour of certain fishes recalls that of the cuckoo, which places its eggs in the nest of another species that will take care of them as it does its own eggs.

The catfish *Synodontis multipunctatus*, endemic to Lake Tanganyika, is a parasite to several mouth brooding Cichlidae species (Sato, 1986) (figure 14.15). This *Synodontis* spawns while a Cichlidae couple are engaged in their mating ritual. The eggs, which are of the same size as the host's eggs, are then taken by the female at the same time as its own eggs, and incubated in the same way.
However, the eggs of *S. multipunctatus* develop faster and the yolk sac is resorbed three days after hatching. The hungry larvae begin to feed on the embryos and larvae of its host.
This particular strategy allows the "cuckoo" fish to exploit its host twice over, by using the parent as shelter and the larvae as a food source.

This type of behaviour has also been observed in the Cichlidae of Lake Malawi (Ribbink, 1977) where *Nimbochromis polystigma* and *Serranochromis robustus* incubate eggs of another species, *Copadichromis chrysonotus*.
At least 15 species of Cichlidae in Lake Malawi incubate the embryos of other species in their mouths, and it has been observed that "broods" can contain juveniles of 2 or 3 other species (Ribbink *et al.*, 1980).

The direct or indirect risks of predation can be reduced by caring for the young. Such behaviour is not very widespread in African freshwater fishes. When it exists, it can take various forms, including:

- constructing and maintaining a nest,
- guarding eggs and larvae,
- incubating eggs and larvae in the mouth or gill cavity,
- fanning eggs with fins to ensure better oxygenation and remove deposited sediments,
- feeding the young.

Such care is most often provided by the male, then, in decreasing order of frequency, by both parents, then by the female.

In the Cichlidae, there are two large groups of fishes that provide care to their young (see box, "Different reproductive styles in cichlids"):

- substrate spawners keep their eggs on a surface and watch over the young until they are self-sufficient;
- mouth brooders transport their offspring in the mouth, from the time of spawning until they are self-sufficient. There are paternal, maternal, and biparental brooders. Intermediate cases also exist, wherein the female carries the eggs in the mouth then the male protects the fry along with the female. This is the case of the Cichlidae *Perissodus microlepis* (Yanagisawa & Nshombo, 1983).

The distribution of tasks between the two parents is sometimes well-established. In shell-dwelling Cichlidae, the male defends the territory while the female watches over the young. *Neolamprologus mondabu* feeds on benthic animals on the sandy surface, but also unearths prey by moving its body and fins vigorously. The young also feed on the benthos on the substrate surface, but only using the first technique. Feeding by digging represented 30% of feeding activity in adult females. That said, parental females fed less frequently than non-parental females. The young are gathered together in the pit and feed intensively, which suggests that parental females dig for their young (Ota & Kohda, 2014). In *Pelvicachromis taeniatus*, parents adjust the care according to the vulnerability of the young. However, parents with a poor quality brood showed a more significant reduction in care than parents with good quality broods. The result suggests that parents adjust their care to the quality of the brood, and takes into account the theory of parental investment. Moreover, mothers of high quality fry were much more aggressive towards their partners than mothers of low quality ones (Thünken *et al.*, 2010). In *Bagrus meridionalis*, the parents share the task of feeding the young; the female gives them eggs and the male collects small benthic invertebrates. When fighting off predators, the female attacks the intruder while the male stays with the young. As they grow, the risk of predation decreases and parents spend more effort in feeding them (McKaye *et al.*, 1994).

Social life, conflict and cooperation

A fish comes into contact with congeners and heterospecifics in its physical system. Such contact creates relationships that are often conflictual in nature and related to defending space. This territoriality may be temporary or lifelong (lithophilic Cichlidae of Lake Malawi). There are different types of territories (breeding or home range) that may overlap. In *Tropheus duboisi*, the male defends a large area against males of the same species (reproductive territory) while tolerating other species (Yanagisawa & Nishida, 1991; Yanagisawa, 1993). Within that area, it also defends a smaller space where it feeds (home range), and finally, a small surface which serves as a spawning site. In *Gnathochromis pfefferi*, a Cichlidae of Lake Tanganyika, the home range is different from the breeding territory. Males occupy their reproductive territory in the morning and feed in the living area in the afternoon (Ochi, 1993b) (figure 14.18).

In the goby Cichlidae of Lake Tanganyika that lives in rocks in shallow depths, *Eretmodus cyanostictus*, individuals with the poorest competitive capacity ignore the high quality habitats which are also most in demand. Habitat quality and individual size are correlated. Rockier territories are preferred by both sexes in the absence of competition, and smaller fishes prudently occupy vacant territories of lesser quality (Taborsky *et al.*, 2014).

Conflicts can lead to actual fights that nonetheless remain highly ritualized to avoid killing one of the protagonists, at least in a specific framework. In schooling fish, a hierarchy emerges. For example, in the "leks" of *Mchenga eucinostomus*, subordinate males are found in the periphery while dominant ones are in the centre (McKaye, 1983).

DIFFERENT REPRODUCTIVE STYLES IN CICHLIDS

Substrate spawners

The sticky eggs are deposited on a hard surface. Depending on the species, this may be hidden (crevices in rocks, snail shells) or an open substrate (pits in the sand or in the mud) (figure 14.16).
The eggs are then fertilized and hatched after a few days, during which both parents generally guard the eggs attentively.
When the fry can swim freely, they remain grouped closed to the substrate as the parents watch over them.

Mouth brooders

The eggs of mouth brooders are larger but less numerous than that of substrate spawners. In most cases, eggs are deposited on a substrate, often prepared by the male.
In some pelagic species, eggs may be released directly into the water. There are three broad categories of mouth brooders (figure 14.17):

- *maternal mouth brooders* constitute the most common system. Spawning takes place on a substrate, and the non-sticky eggs, released individually or in small batches, are rapidly taken into the mouth by the female. The male releases its sperm as the female collects the eggs, or fertilizes them in the mouth. Incubation lasts until the young are fully independent. In some cases, the female abandons them from time to time in order to feed, then takes them back again into the mouth.

- *paternal mouth brooders* are found in only a few species. This is the case for *Sarotherodon melanotheron*.

- *biparental mouth brooders* are also a rare case in Cichlidae. In most of the *Chromidotilapia* the two parents split the fry.
There are also species wherein the female begins incubation, which is later taken up by the male. This is the case for the goby Cichlidae of Lake Tanganyika, *Tanganicodus irsacae* and *Eretmodus cyanostictus*.

FIGURE 14.16.

A pair of *Coptodon zilli* guarding a clutch of eggs which the female (in yellow) is cleaning (from Fryer & Iles, 1972).

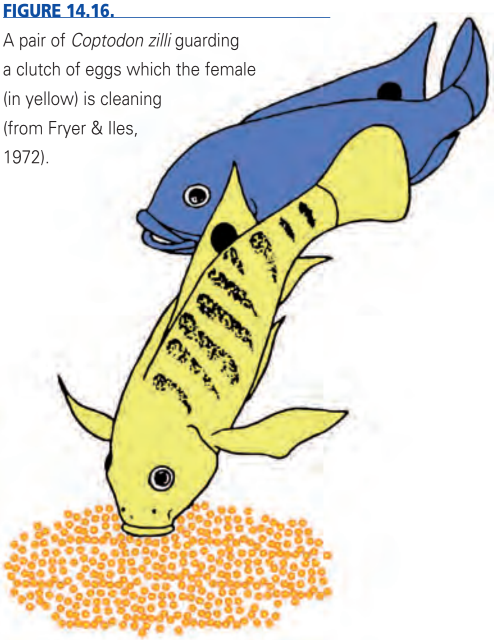
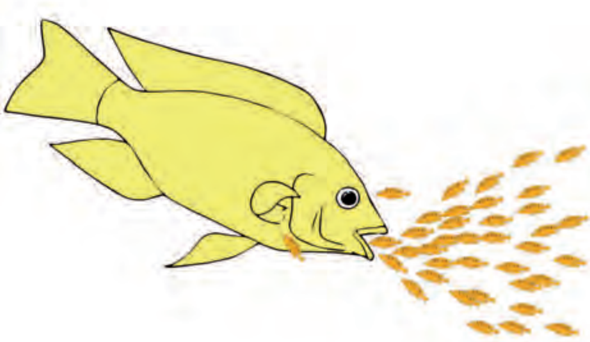
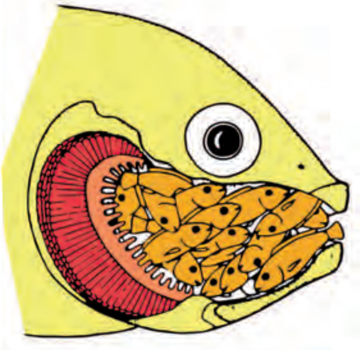
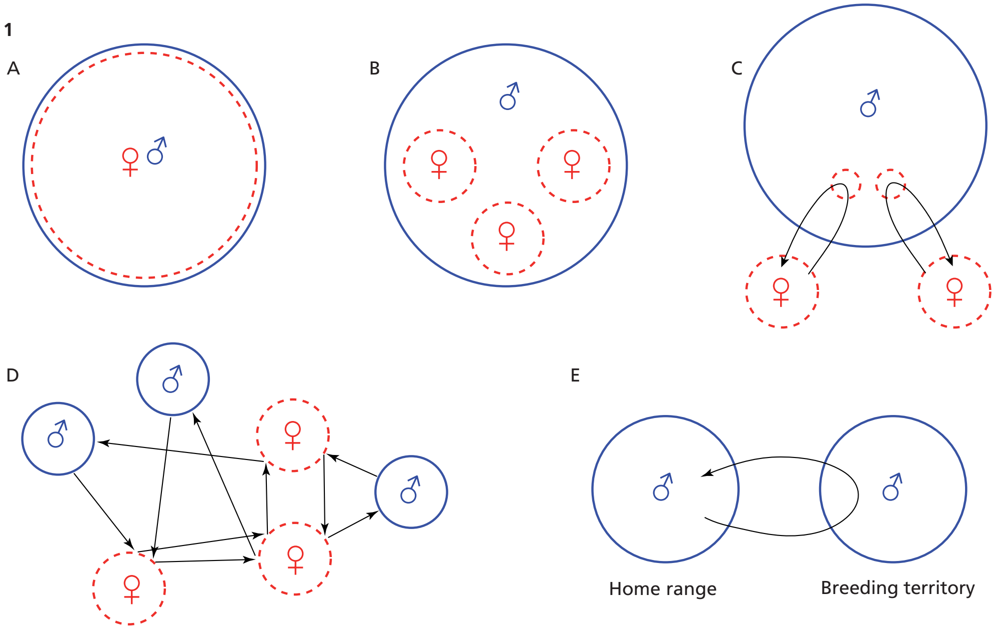


FIGURE 14.17.

To any alert, young cichlids rush into the mouth of their mother (redrawn from Fryer & Iles, 1972).







2

Species		male			female	
	H R	B T	C T	H R	B T	C T
monogamous						
Neolamprologus toae	● ?	●	●	● ?	●	●
Neolamprologus tretocephalus	● ?	● ?	●	● ?	● ?	●
Xenotilapia flavipinnis	●	●	●	●	●	●
polygamous						
Neolamprologus furcifer	○			●		●
Neolamprologus mondabu	●	●		●		●
Neolamprologus savoryi	●	●		●		●
Altolamprologus compressiceps	● ?	●		○		○
Lamprologus callipterus		○				○
Gnathochromis pfefferi	○	○				
Lobochilotes labiatus	○			○		

FIGURE 14.18.

Types and arrangement of the territories of benthic cichlids of Lake Tanganyika (redrawn from Yuma & Kondo, 1997).

1. A: monogamous species. Male and female protect a multifunctional territory (home range and breeding territory); B: species in harem-like social structure. The male protects a breeding territory which includes several females; C: Polygamous species. The male protects a breeding territory which includes several breeding sites. The females have home ranges outside of the male territory. Females meet the male only during the reproduction period; D: polygamous species. Each male or female has a small territory. Males visit only neighbouring females; E: polygamous species. The male has two multifunctional territories; a breeding territory where it lives during the morning and a home range where it feeds during afternoon. Females, non-territorial, meet the male only during the mating. Then they go away with eggs in their mouth.
2. open circles: monofunctional territory; filled circle: multifunctional territory; HR: home range; BT: breeding territory; CT: young care territory.

Forms of cooperation can exist alongside these conflictual situations. This is the case in some colony-forming Cichlidae which accept young from other broods. In *Neolamprologus pulcher (= brichardi),* the young are monitored by their parents and young subdominants. These "helpers" clean the clutches while the dominants feed on eggs. The behaviour of these helpers normally shifts towards a dominant model as they grow. This change may be slowed down or even prevented if the continued presence of eggs requires them to continue providing care (Siemens von, 1990). If a male breeder is removed, it is replaced by a male from outside the group in 71% of cases. Meanwhile, a female breeder will only be replaced by an outsider female in 15% of cases. The helpers increase the frequency of cooperative behaviour when a female is removed, but not when a male breeder is removed (Stiver *et al.*, 2006). This system exists in other Cichlidae hidden substrate spawners. The care provided by helpers can however be completely different. There have even been cases of symbiosis and/or mutualism between heterospecifics, as in lithophilic Cichlidae communities in Lake Tanganyika. The home ranges of *Tropheus moorii*, a grazer of filamentous algae, and *Petrochromis polyodon*, which feeds on unicellular algae, overlap. It appears that the latter species, when grazing, levels out obstacles by removing sand. It is followed by *T. moorii* which has been observed removing ectoparasites from the body of *P. polyodon*. (Takamura, 1983) (figure 14.19).

There are also associations between species based on their diet. For example, researchers have observed *Tropheus moorii* individuals grazing on algae being closely followed by carnivorous *Neolamprologus leleupi* (Takamura, 1984). The

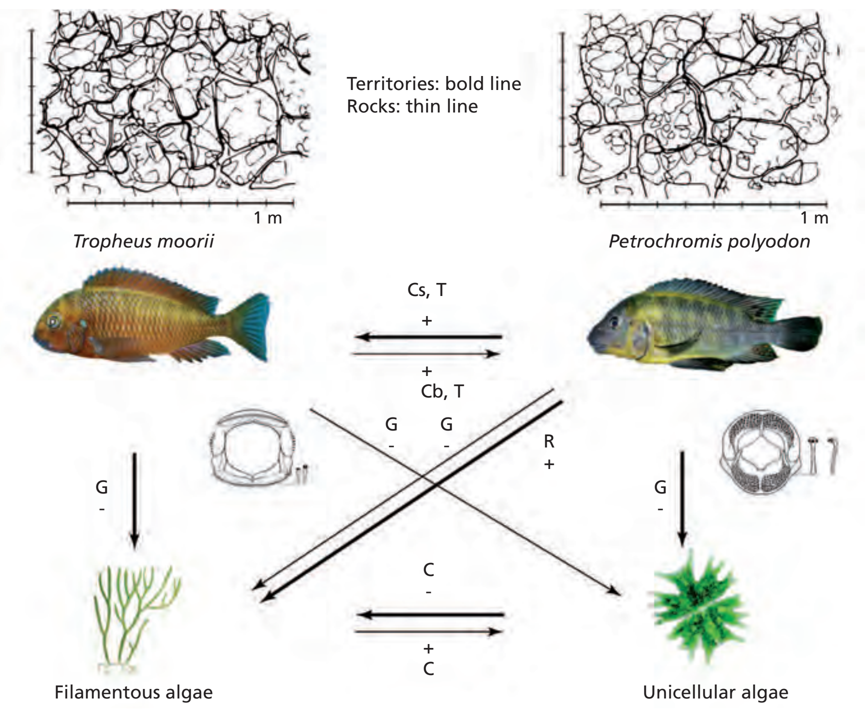


FIGURE 14.19.
Interaction between two rock-dwelling cichlids of Lake Tanganyika, *Tropheus moorii* and *Petrochromis polyodon* (from Takamura, 1997). +: positive action; -: négative action; Cs: cleaning of debris deposited on the grazing surface; Cb: cleaning of the body; T: protection against intruders of the common territory area; G: grazing; R: protection against competitors; C = competition. By grazing unicellular algae, *P. polyodon* promotes the development of the filamentous algae which feed *T. moori*. The thickness of arrows is proportional to the action's intensity.

latter appear to take advantage of *T. moorii*'s grazing to capture the shrimp that have been disturbed by such activity. In these cases, only one of the species benefits from the association, while the other enjoys no advantage. There are also mutually beneficial situations, as in the scale-eating fishes of genus *Perissodus*. An individual is more successful in its attacks in the close presence of a congener using a different hunting strategy (Hori, 1997), as the prey's attention is focused on the presence of the other predator. Such situations have also been observed in piscivores (Hori, 1987).

Survival: eat or be eaten

Among the many examples of trophic adaptations that we might name, the most remarkable are those observed in the Cichlidae of the African great lakes. All food types found in the lakes have been used by these fishes, often with the needed morphological and behavioural adaptations. For instance, in molluscivorous fishes, there are oral shellers/crusher species and pharyngeal crusher species. Meanwhile, epilithic algae grazers employ different strategies. Some rip the algae from the rocks, while others crop them (figure 14.20). There are also special adaptations, such as scale eaters and cleaner fishes that feed on the parasites found on other fishes.

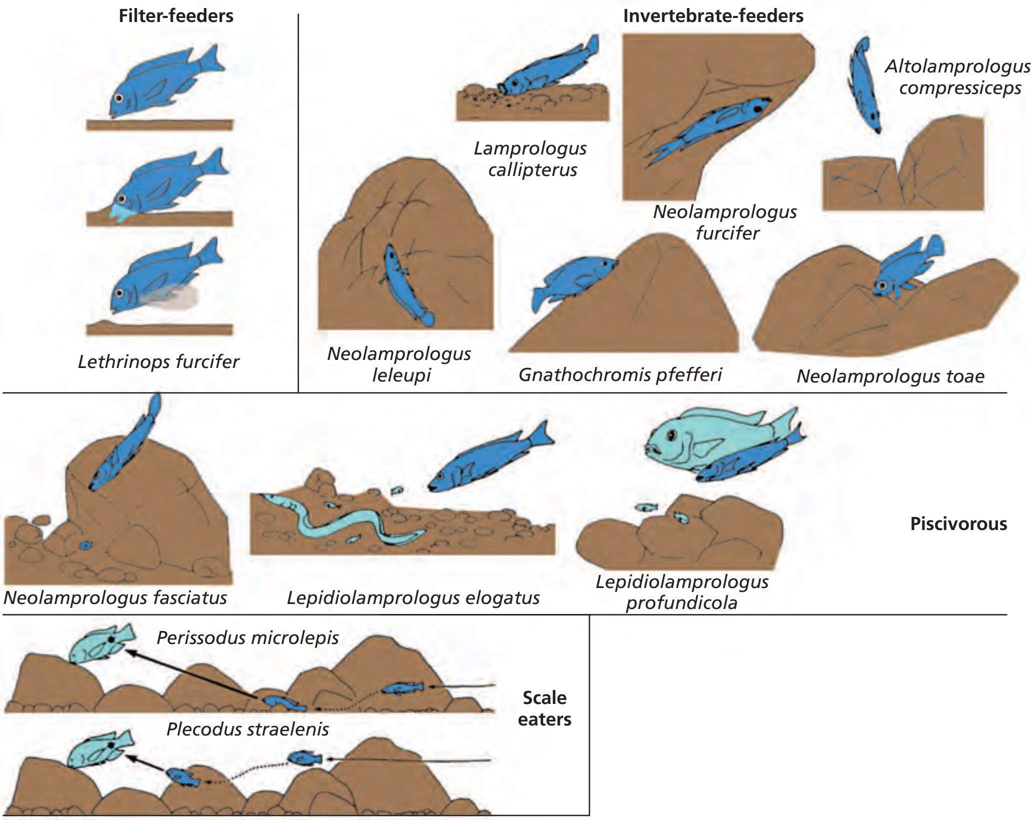


FIGURE 14.20.
Feeding behaviour in some cichlids from the Great Lakes of East Africa (from Fryer & Iles, 1972 and Kawanabe *et al.*, 1997).

Fishes often organize in groups for more efficient access to resources. This is the case for daily migrations (see chapter *Diversity of fish habitats*). Such groupings may also underlie more aggressive strategies. For example, they allow fishes to feed in zones that are already occupied as territories by congeners or other species. As the resident fish cannot chase off all the intruders, the others have access to the resource. This holds true for the young and females of many epilithic algae grazers.

Hunting strategies are varied in predators. The electric fish *Malapterurus electricus* uses the discharges it can produce to attack prey. *Nimbochromis livingstonii* "plays dead" to attract prey. Mimetism allows some fishes to approach prey more easily (McKaye, 1981). The scale-eating Cichlidae *Corematodus taeniatus* and *C. shiranus* of Lake Malawi have the same colouring as their prey (Fryer & Iles, 1972), a tactic also used by *Lepidiolamprologus mimicus* in Lake Tanganyika (Schelly *et al.,* 2007). Fin-eating Distichodidae (Roberts, 1990), *Eugnathichthys eetveldii* and *E. macroterolepis*, have the same caudal colour pattern as their preys (*Synodontis decorus* and *Mesoborus crocodilus*). The Clariidae *Channallabes apus*, which lives in muddly bottoms, can feed on dry ground (van Wassenbergh *et al.,* 2006).

External factors also have a large influence on species behaviour. In the Cichlidae *Astatoreochromis alluaudi*, there is a relationship between gill surface area and morphological changes in jaws depending on the amount of dissolved oxygen in the habitat (Binning *et al.*, 2010). The two Haplochromines *Haplochromis pyrrhocephalus* and *H. tanaos*, whose populations were drastically cut owing to the ecological changes in Lake Victoria, showed visual adaptations in relation to these changes but also adaptations in the size of prey (van der Meer *et al.,* 2012; van Rijssel *et al.*, 2015). In the Cyprinidae *Barbus neumayeri*, there does not seem to be an adaptation to the anoxia in the physical system, but there has been a drop in energy-intensive activities such as the feeding rate (Barrow & Chapman, 2006).

Ontogenetic development of behaviour

The previous paragraphs have shown us that an animal possesses a whole range of behaviours, very often specific, that address various types of situations. Very little research has been devoted to determine the true extent of learning. That said, several hypotheses have been proffered on the appearance and expression of behavioural patterns throughout a fish's life. They depend in part on the nature and development of sensory (recognising and analysing a message) and motor (responding to a message) organs used. In this sense, the chronology of development is more important than age. In Cichlidae, the faster transition to free swimming allows the young of substrate spawners to develop behaviours earlier than their mouth brooder counterparts. However, acquiring an organ's functions is not sufficient for achieving the final expression of some behaviours. Behavioural patterns change throughout the development of the young fish, and interactions between parents and juveniles play a primordial role. Initially, the young of *Pseudocrenilabrus multicolor* tend to stay close to the mother hide in her mouth in case of danger, even when they can swim freely. As they grow older, they become capable of actively avoiding larger fishes (Mrowka, 1987).

Parent-offspring interactions can be varied. The hypothesis of imprinting (Barlow, 1983; Colgan, 1983) designates the process of the same name that can take place between young of the same brood and their parents. Several authors (Kop & Heuts, 1973; Russock & Schein, 1977, 1978) have shown that young and their parents are capable of recognizing each other, at the very least as a species but perhaps also as individuals, as a result of their association when parental care was being provided. When young *Haplochromis burtoni* raised with other Cichlidae reach maturity, they initially ignore their conspecifics whereas they develop sexual behaviours towards members of their entourage of adoption (Sjolander & Ferno, 1973; Crapon de Crapona, 1982).

Relationships with parents often end with signal interruptions or changes at the end of the development of young. In the Mormyridae *Pollymirus isidori* where only the male provides parental care, it has been observed that young remain close to the nest until the electric signals they discharge match those of adults (see box, "Existence of a juvenile discharge in *Pollimyrus isidori* and acquisition of a second adult discharge"). At that point, the father chases them from the nest.

EXISTENCE OF A JUVENILE DISCHARGE IN *POLLIMYRUS ISIDORI* AND ACQUISITION OF A SECOND ADULT DISCHARGE

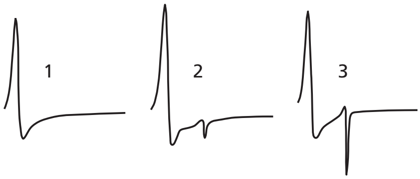


FIGURE 14.21.

Development of EOD in *Pollimyrus isidori*.
Examples of waveforms to illustrate the gradual transition from larval to adult EOD.
1. EOD in larva;
2: in juvenile a second "adult" EOD appears;
3: in adult EOD the second discharge persists and the amplitude increases.

It appears that all Mormyridae species possess a larval electric organ that is then replaced by the adult organ located in the caudal peduncle (figure 14.21).
In *Pollymirus isidori*, the larval organ is located on the trunk and the electrocytes forming it extend from the opercles to the posterior part of the dorsal and anal fins.

Larval electrical discharge

The larval discharge appears eight days after eggs are fertilized. Its amplitude grows rapidly during the first 10-15 days until it reaches a plateau (approximately 10 mV).
It remains at this amplitude for about sixty days.

Appearance of the adult electric discharge

Meanwhile, in general after the forty-eighth day, the adult discharge appears with a lag of 0.7 ms to the larval discharge.

Persistence of two types of electric discharges

The two discharges will coexist for some forty days.
During this period, the amplitude of the larval discharge decreases gradually, while that of the adult discharge increases rapidly until it reaches about a hundred mV somewhere around the sixty-eighth day.

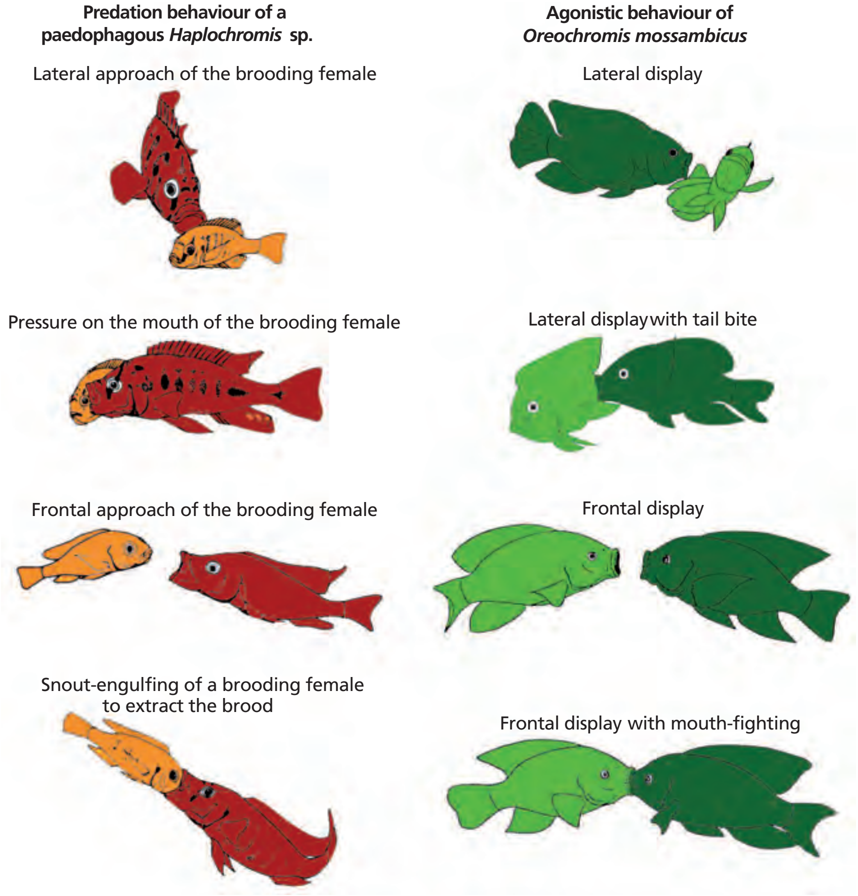
(from Westby & Kirschbaum, 1978)

Evolution and behaviour

The variation of a behaviour type can change the selective value of a species and lead to a phylogenetic development. Below we analyse examples of evolution in which behavioural changes played a major role.

Evolution of feeding mechanisms

The hundreds of Cichlidae species in the Lake Victoria basin all came from a single ancestral form that probably had a generalist diet. Since that time, eleven trophic groups diversified, each of which has a distinct bucco-pharyngeal morphology and a set feeding behaviour. Did changes in feeding behaviours lead to morphological changes, or the contrary? The first hypothesis is generally supported, when taking into account the disparity between morphological appearance and genetics, as well as the presumed speed of speciation (Sage *et al.*, 1984). Morphological differentiations may not be related to speciation events, but occur after them. According to this model, morphological differentiation would result from a behavioural mechanism that would involve the



Predation behaviour of a paedophagous *Haplochromis* sp.

Lateral approach of the brooding female

Pressure on the mouth of the brooding female

Frontal approach of the brooding female

Snout-engulfing of a brooding female to extract the brood

Agonistic behaviour of *Oreochromis mossambicus*

Lateral display

Lateral displaywith tail bite

Frontal display

Frontal display with mouth-fighting

FIGURE 14.22.
Comparison between the predation behaviour of a paedophagous *Haplochromis* sp. and the fight behaviour between males of *Oreochromis macrochir* (based on Ruwet & Voss, 1966 and Wilhelm, 1980).

intra-population spread of a new feeding behaviour, via social learning, that appeared in some members of the population. If this type of behavioural transmission exists, it is possible that it could be transmitted to other species. There are also convergent morphological adaptations tied to a specific behaviour. For instance, in the three African great lakes, certain species have hypertrophied lips that allow them to feed more easily in crevices.

Certain feeding strategies could have evolved from a social component. We can cite the case of paedophagous fishes in Lake Victoria (figure 14.22) whose method is to force open the mouths of incubating female Cichlidae in order to extract the brood.

Phylogeny of parental care behaviour

It has been suggested that parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990).

Fishes that do not provide parental care lay a large number of small eggs that are dispersed in the pelagic system. This is the case for many species belonging to the Clupeidae, Alestidae, and Cypriniformes families. This mode of reproduction could represent ancestral conditions, since one increases the chances of survival in an unstable environment by favouring dispersion. However, there is higher pressure from predators. In fact, many species that do not practice parental care do not lay their eggs at random, but deposit them in plants, gravel, or holes. It is indeed advantageous to recognise and select sites that are favourable to the brood. When the favourable habitat is identified and used regularly, there may be an adaptive advantage to staying there, which is the decisive stage for the appearance of site preparation and defence behaviour, in order to monopolise those that are most favourable to reproduction.

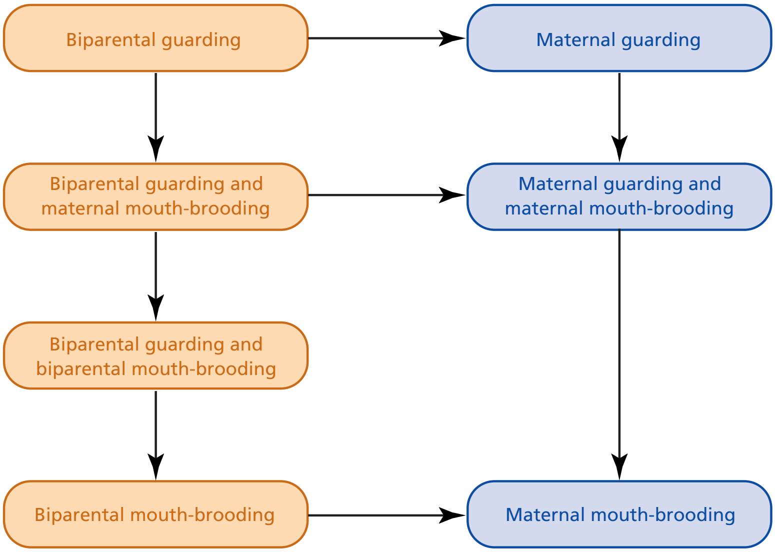


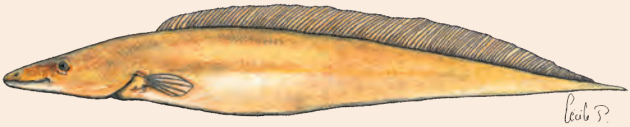
FIGURE 14.23.
Most likely steps of parental care systems of cichlid fishes in Lake Tanganyika (redrawn from Kuwamura, 1997).

Of the freshwater species practicing parental care, the habits observed in Cichlidae are among the best known. From parental care on the substrate, considered an ancestral behaviour (Stiassny & Gerstner, 1992), several possibilities can lead to mouth brooding, a more recent behaviour. Taking eggs into the mouth to transport them from one site to another could have become a permanent component of reproductive behaviour (figure 14.23). The adaptive advantage is in keeping embryos safe from predators and limiting competition for reproductive sites. One may also see there a means of freeing oneself from the need for a substrate, when there is intense competition for available benthic space (Balon, 1978).

In the beginning, among substrate brooders, parental care was probably provided by both parents. Mouth brooding evolved independently in phylogenically distant groups such as Ariidae, various Anabantidae, Arapaimidae, and Cichlidae.

Species richness of fish communities

BERNARD HUGUENY



Introduction

Freshwater habitats from Africa and Madagascar harbour about 3,255 fish species (Lévêque *et al.*, 2008). This is of course not a definitive figure because new species are still described and taxonomic revisions occur regularly. That means that about a quarter of all known freshwater fishes live in Africa, an expected pattern considering that biodiversity peaks in tropical biomes for most taxonomic groups. Indeed, other biogeographic realms with a large extent of tropical climate (Neotropical and Oriental) also display great freshwater fish diversity (3,000-4,000 species) in comparison with more temperate ones (about 2,000 species in Nearctic and Palaearctic). However, high biodiversity at a continental scale does not necessarily translate to high biodiversity at a smaller, regional, scale, a pattern clearly shown by the number of species recorded per 300*300 km quadrat in the FAUNAFRI database (an updated storage of fish distribution in Africa) which exhibits a high spatial variability with both "cold" (e.g. Maghreb) and "hot" (e.g. Congo) spots of diversity (figure 15.1). Similarly, the number of fishes encountered in rivers of comparable catchment area may differ greatly if we compare for instance the Nile (fewer than 200 species, Witte *et al.*, 2009) and the Congo (more than 700 species, Teugels & Thieme, 2005). At a smaller scale, species richness in similarly sized river sections may differ within the same drainage. This chapter is about how and, possibly, why species richness differs among localities, rivers or provinces, whether it scales down or scales up between different hierarchical spatial levels, and whether past climatic or orogenic events have left an imprint on present fish assemblages. Provided sufficient information, other components of biodiversity such as biological traits will be considered as well. Before describing the conceptual framework used to organize the existing knowledge about fish biodiversity in Africa, a description is given of the broad patterns obtained by analysing the FAUNAFRI database.

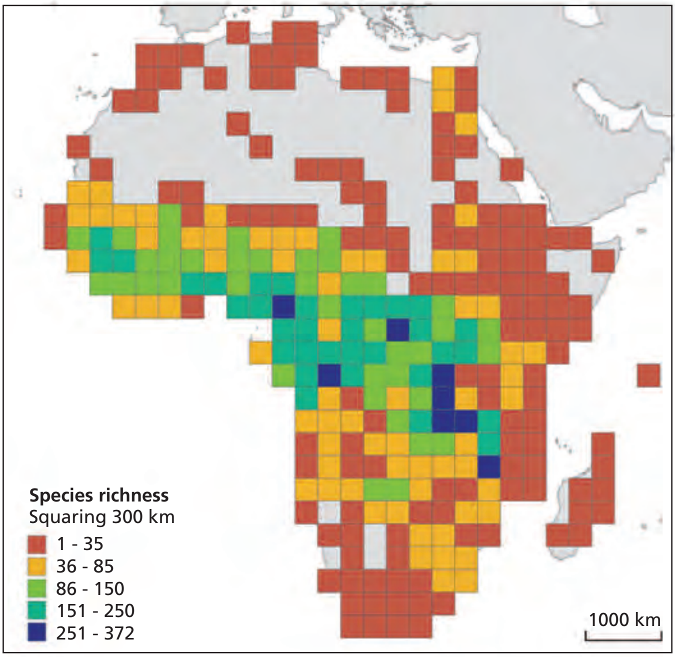


FIGURE 15.1.
Fish species richness per 300x300 km quadrat in Africa (FAUNAFRI database).

Broad patterns in fish diversity

Geographically Madagascar is included in Africa, but with regard to faunal affinities, and particularly considering freshwater fishes, this island clearly stands apart, reflecting its complex biogeographical history. In particular, none of the fish families endemic to continental Africa occur there, and most of the species belong to widespread families that can stand saline water and could have colonized the island on several occasions. Considering that it has been isolated for a long time, it is not surprising that relatively few freshwater species (135) have been recorded in this island despite its large size, many of them being endemics (Lévêque *et al.*, 2008). Other islands occur off the African coast, all are small and have not been colonized by strictly freshwater fishes due to a lack of connection with the continent in the past. As a result they harbour only a reduced number of brackish or migratory species. One notable exception is Bioko Island (off the coast of Cameroon) which was connected to the continent thanks to a lower sea level during the Quaternary and is now inhabited by 43 species, including strictly freshwater species (Castelo, 1994).

From a biogeographic point of view, continental Africa is generally divided into two realms. The Maghreb belongs to the Palearctic realm and is very depauperate, inhabited by only 47 species. The remaining part of continental Africa constitutes a biogeographic realm on its own, the Afrotropical realm, and takes the lion's share of fish biodiversity. This realm has been broken down into several ichthyological provinces of different shapes and numbers depending on the authors. Here we will use the provinces recognized in the FAUNAFRI database:

Nilo-Sudan, Upper Guinea, Lower Guinea, Congolese, Angolan, Zambezi, East Coast, Ethiopian, Cape and Karoo. To reduce the number of small provinces, we included the Ethiopian province into the Nilo-Sudan one and regrouped the Cape and Karoo regions into a Sourthern province (as in Lévêque *et al.*, 2008).

In addition, due to their specific evolutionary history dominated by adaptive radiations, we considered the lakes and their tributaries of the rift valleys as a separate entity, despite the fact that some of them are hydrologically connected to one of the abovementioned provinces. Strictly freshwater fish species richness per province span a range of one order of magnitude (from 70 species for the Southern province to 947 species for the Congo basin, according to the FAUNAFRI database), reflecting a diverse array of evolutionary histories shaped by past climates, orogenic and tectonic events, hydrological connections, extensions and retractions of active catchments, and sea level changes. It is worth noting however that these provinces also differ greatly with regard to our knowledge about fish distribution. Considering that regions for which identification guides exist are the best known, then the most reliable biodiversity patterns probably came from West Africa (Paugy *et al.*, 2003a, b), Lower Guinea (Stiassny *et al.*, 2007a, b), and South Africa (Skelton, 1993).

Not surprisingly, the great majority of African fish species are encountered in permanent rivers and lakes, but even temporary water bodies are not entirely devoid of fishes (inhabited by more than 500 species) as some species evolved specific life history strategies to cope with these extreme habitats. Fishes can also be encountered in deserts conditioned upon the existence of permanent water pockets that have been connected in the past to neighbour river basins. Due to the high seasonality of many African rivers, estuaries could be highly dynamic with regard to salinity and, depending on the season, are inhabited by strictly freshwater or marine species that add to a pool of brackish species. This explains the great number of species (about 600 are known to occur – sometimes temporarily – in African estuaries).

The African fish fauna is well-known for the multiple adaptive radiations that took place in lakes of the rift valleys (e. g. Victoria Lake), particularly within the Cichlidae family, leading to high species richness and endemism and motivating numerous studies to elucidate the factors underlying such outstanding biodiversity. About 1,850 fish species have been recorded so far in lakes and their tributaries within this part of Africa, but many more await scientific description (table 15.I). A large part of these species are not encountered outside the rift valley. Other cases of lacustrine adaptive radiation are known in Africa outside this region; among the most notable are Tana Lake (Ethiopia) with its cyprinid species flock and some small crater lakes in Cameroon (Barombi Mbo, Bermin) that provide some of the strongest support of sympatric speciation ever reported (Schliewen *et al.*, 1994).

Differences among biogeographic provinces suggest that biodiversity of freshwater fish is not distributed at random over Africa, a pattern also shown by the number of species recorded per 300*300 km quadrats in the FAUNAFRI database (figure 15.1). Depauperate regions are those with very low drainage density (Maghreb, Sahara, Sahel, Kalahari) while hot spots of diversity tend to

TABLE 15.I.
Composition of the ichthyofauna of the East African Great Lakes

Lakes	Tanganyika	Malawi	Victoria	Kivu
Non cichlids	124	53	63	10
Cichlids	250 +	800 +	500 +	17
Total	374 +	853 +	563 +	27

occur in regions with very high rainfall and co-occur with rain forest. One hotspot, in the rift valleys, is not related to the presence of rain forest and reflects the high number of endemic lacustrine species encountered there.

A conceptual framework

In this framework a pivotal role is given to the river basin mainly because it can be treated as a biogeographical island. From this level, scaling down to the local community requires the concept of ecological filter, and for scaling up to the biogeographical province the concept of spatial turnover is needed. These three important concepts: biogeographical island; ecological filter; and spatial turnover are introduced in the following.

River basins draining into the ocean and endorheic basins are isolated units for strictly freshwater fishes within an ecological time frame as no dispersal occurs between them due to impassable barriers (sea water or dry land). Within a geological timeframe, events such as river capture or overflow from one basin to another may allow faunal exchange, but these events are rare and primarily depend on major climatic or geological changes (Craw *et al.*, 2006). Consequently, most coastal rivers probably have been isolated since at least the end of the Pleistocene, the last period of great geological and climatic changes. River basins, as defined in this chapter, are biogeographical islands (Hugueny,1989), but they do not conform to the dynamic equilibrium hypothesis of MacArthur and Wilson (1967) because extinctions cannot be balanced by a continuous colonization within an ecological time scale. Without *in situ* cladogenetic speciation (a species splitting into two or more daughter species), the fate of species richness is to decrease in a river basin as long as no connection exists with a neighbour. *In situ* speciation may slow down this process or even take over.

Over an ecological time scale (10-1000 years) a river is a closed system (no immigration, no emigration) and over such a narrow time window speciation could be neglected. Consequently, the species richness of a locality cannot be higher than the total number of species encountered in the river catchment it belongs to. From this pool of species available for colonization, only a fraction will be encountered in a given locality because some species may fail to pass through one of a series of filters (Poff, 1997). First the species should have the opportunity to disperse from a source to the locality, then to find there environmental conditions that fit its niche requirements, then to cope successfully with competitors, pathogens and predators already present. In rivers, a major factor modulating the strength of these different filters is the position along the upstream-downstream gradient.

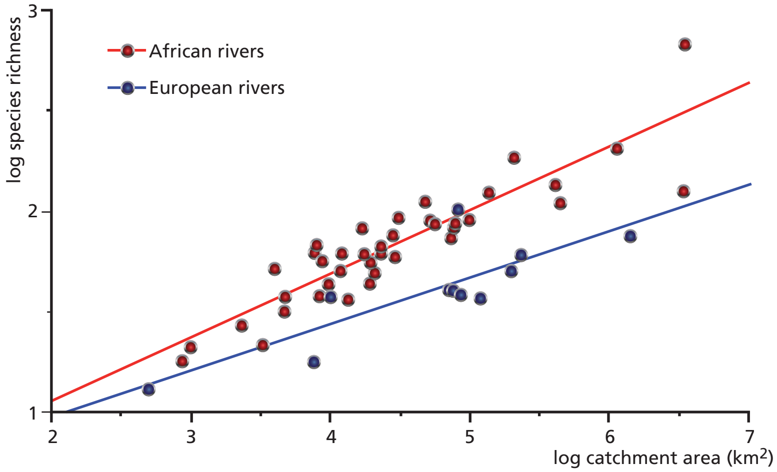
The species richness of a province cannot be lower than the one of its most speciose river basin. So this lower bound in species is set by the factors that contribute to the richness of a river basin, for instance its area. From this starting point, regional species richness increases as new river basins are added, up to the final list of rivers constituting the province. The increase in total species richness as new spatial units are added is known as spatial turnover (or spatial beta diversity). A rapid increase corresponds to a high turnover. Spatial turnover occurs mainly because most of the time basins are isolated and their faunal composition changes with the accumulation of extinction and speciation events occurring independently in each of them. When basins get connected again, faunal exchange will partly – rarely totally – erase spatial turnover.

Patterns among rivers

Species-area relationship

One of the few quasi-universal laws of ecology is the so-called species-area relationship (SAR) describing an increase of the number of species of a community or a fauna/flora with the surface area it occupies, and its quantitative modelling as a power relationship goes back to Arrhenius (1921). Daget & Iltis (1965) pioneered its use for riverine organisms by relating species richness of fish communities to the catchment area in a sample of 13 rivers, mostly from Côte d'Ivoire. More comprehensive studies by Welcomme (1979) and Hugueny (1989) estimated SAR over Africa as a whole and confirmed that a power relationship accounted for a great variability in species richness among rivers (table 15.II; figure 15.2).

FIGURE 15.2.
Relationships between the number of fish species and the catchment area (in km^2). A comparison is made between African and European rivers.



Rivers	Species richness	Surface (km^2)	Mean annual discharge (m^{3}s-^{1})
Congo	1068	3 457 000	40 487
Nile	156	3 349 000	2 640
Niger	335	1 125 000	6 100
Senegal	195	441 000	687
Volta	199	398 371	1 260
Bandama	123	97 000	392
Comoé	130	78 000	206
Gambia	135	77 000	170
Sassandra	95	75 000	513
Ouémé	157	50 000	220
Cross	223	48 000	
Cavally	88	28 850	384
Tominé	75	23 200	
Ogun	110	22 370	
Mono	87	22 000	104
Sewa	75	19 050	
Moa	93	18 760	
St Paul	96	18 180	
Konkouré	99	16 470	353
Loffa	78	13 190	
Cess	76	11 920	
Bia	64	9 730	81
Agnébi	81	8 520	50
Mano	53	8 260	
Jong	114	7 750	
Kolenté	102	7 540	
Boubo	48	4 690	32
Mé	50	3 920	32
San Pedro	46	3 310	31
Néro	25	985	16
Dodo	18	850	
Mungo	38	4 570	
Wouri	157	11 500	308
Sanaga	224	135 000	2 060
Nyong	145	27 800	443
Lobé	52	2 305	102
Ntem	194	31 000	348
Ogowe	344	205 000	4 758
Niari	200	56 000	913

TABLE 15.II.
Species richness, area and mean annual discharge for different African river basins.

Three nonexclusive explanations have been put forward to explain the species-area relationship: (1) area-dependent extinction rate (MacArthur & Wilson, 1967), (2) the area-dependent speciation rate (Losos & Schluter, 2000), and (3) the influence of habitat diversity (Williamson 1988). Area-dependent extinction assumes that probability of extinction of a species increases with a reduction of its population size, which in turn is a function of the surface area of the catchment. The fact that the lifetime of a population increases with its size has been supported by numerous empirical studies. In particular, an empirical relationship between population extinction rate and surface area has been established for Holarctic fishes (Hugueny *et al.*, 2011) and there is no reason to suspect African fishes differ in this regard. According to this relationship, population lifetime in a huge river basin such as the Congo is predicted to be about a few million years, a value not different from the average lifetime of a fish species evaluated on a global scale. Such a comparison suggests that very large river basins are biogeographically more like continents. Besides harbouring large populations, a large basin is probably able to maintain more persistent populations by being buffered against climatic variability. Conversely, small basins are expected to react quickly to environmental changes and a good example is provided by the Casamance, a small coastal river in West Africa. Following a period of drought, the salinity of the Casamance River in 1984-85 was higher than in the open ocean for the first time since the beginning of the century. Salinity followed an increasing upstream gradient at the end of the rainy season, and values above 90‰ were observed in the upper reaches (Albaret, 1987). Along this gradient, the total fish species richness, estimated from commercial and experimental catches, decreased dramatically and only the two brackish water cichlids *Sarotherodon melanotheron* and *Tilapia guineensis*, were recorded in the most extreme environmental conditions. A dramatic impact of this new ecological situation is the assumed disappearance from the Casamance River of many freshwater species which were previously recorded. That is the case for *Hepsetus odoe*, a few cyprinids including *Labeo* and *Barbus*, mormyrids, characids (*Alestes* and *Brycinus*), citharinids, *Malapterurus electricus*, etc. which were recorded by Pellegrin (1904), and still observed by fishermen in the river before the drought (Albaret, 1987). It is unlikely that those species were able to survive in refuge zones, given that most of the upper reaches dried out during the dry season. Only a few species such as *Hemichromis bimaculatus*, some Cyprinodonts and *Clarias,* were sampled in the upper reaches.

Area-dependent speciation assumes a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers (Rosenzweig, 1995). This hypothesis is quite old but received empirical support only recently thanks to phylogenetic studies of insular biotas (e.g. Losos & Schulter, 2000). Similarly, there is phylogenetic evidence that many endemic species of some large river basins originated by *in situ* cladogenesis (a species splitting into two or more species). For instance, entire clades of *Synodontis* species probably originated in the Congo basin as revealed by phylogenetic studies of this specious genus distributed all over tropical Africa (Day *et al.*, 2013, Pinton *et al.*, 2013). However, for most river systems and taxa such phylogenetic information is lacking and we have to rely on the taxonomic hierarchy to assess the likelihood of *in situ* cladogenesis. As a first approximation let us assume, following Tedesco *et al.* (2012), that the existence in a river basin of two or more endemic species within the same genus could be the result of a cladogenetic event. In figure 15.3 the proportion of such species is plotted against catchment area and this value is quasi-null up to an area of about 8,000 km^2. That means that species extinction could be balanced by *in situ* speciation only in large or very large basins such that they can maintain or possibly increase their species richness even in complete isolation. In contrast, small rivers are in a disequilibrium state, losing species through time because of species extinctions that are not balanced by speciation or immigration. It is worth noting that catchment area is not sufficient to explain the observed pattern, as for the same area the percentage of endemism depends on the biogeographic provinces (see below for the possible contribution of drainage density to this pattern).

The habitat diversity explanation suggests that habitat heterogeneity and diversity of available trophic resources increase with area, thus offering more available niches and consequently favouring the existence of a large number of species. For instance Hugueny (1989) attempted to test this hypothesis in a sample of African rivers by considering the diversity of terrestrial vegetation over the river catchment, based on the observation made by Daget & Iltis

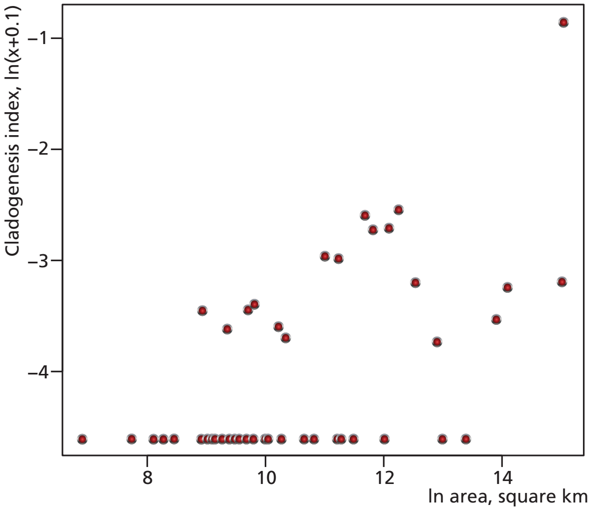
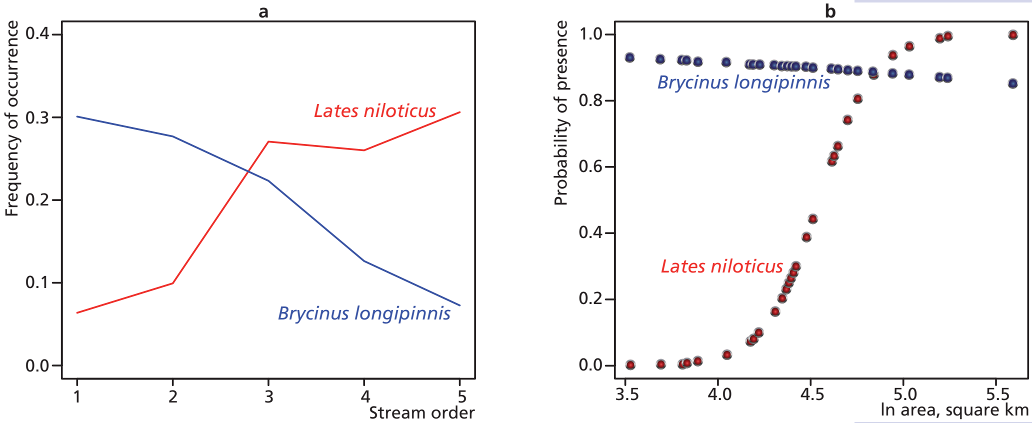


FIGURE 15.3.
Relationship between an index of *in situ* cladogenesis (see text) and the area of the river basin catchment for freshwater fish assemblages in 49 African rivers (FAUNAFRI database).

(1965) that some species were associated with forested areas and others with savannah. No clear signature of vegetation diversity on species richness was observed, suggesting a loose relationship between terrestrial landscape and fish distribution. Another important pattern in this context is that hydrological and geomorphic features of a river change along the upstream-downstream gradient in a more or less predictable way and species are not distributed at random along this gradient. The consequence is that some habitats encountered in the lower courses of a large river may be absent from small river basins. Thus, a positive species-area relationship may be observed just because habitat diversity is truncated in small rivers in comparison with larger ones. To illustrate this hypothesis let us consider two species with contrasting distribution along the upstream-downstream gradient. As shown in figure 15.4, *Brycinus longipinnis* occurs preferentially in low order streams (small tributaries) while *Lates niloticus* is more likely to be observed in high order streams (downstream sections of the river). In a small river basin, high order river sections are

FIGURE 15.4.
Frequency of local occurrence as a function of stream order (B1) and the probability of presence in a river basin as a function of its area (B2) for two fish species in 30 rivers in the Nilo-Sudan region (FAUNAFRI database).

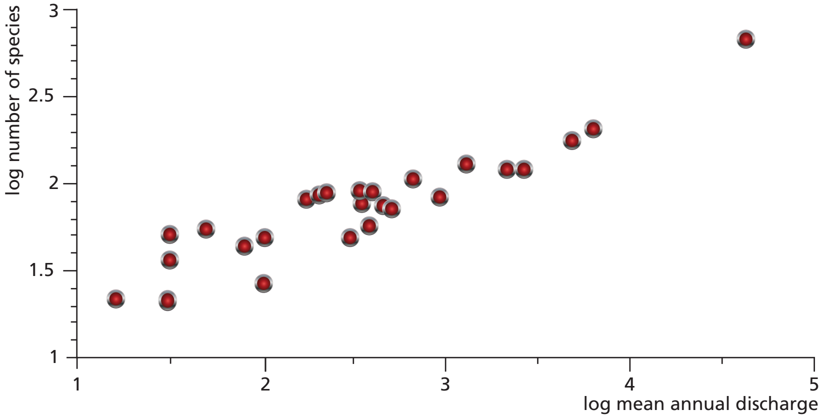


not encountered while both low and high order streams occur in a large one. On this basis we expect *B. longipinnis* to be present in both small and large river basins, while the probability of presence of *L. niloticus* should be very low in small rivers due to the absence of high order streams. The distribution patterns of these two species in West Africa fit this expectation (figure 15.4), suggesting that the dendritic structure of river networks could be an important component of SAR among river basins.

The role of discharge

Once the important role of area is controlled for, the action of other factors underlying species diversity may appear more clearly. For instance the Nile River, as already pointed out by Greenwood (1976), has considerably fewer fish species than the Congo (128 against more than 700; see section 2, "Broad patterns in fish diversity") despite very comparable catchment areas. To explain this pattern, Livingstone *et al.* (1982) suggested that discharge at a river's mouth could be a better predictor of species richness than catchment surface area. This was confirmed in their study of the fish fauna from some African rivers and by subsequent works in West Africa (Hugueny, 1989; figure 15.5). Models including both surface area and discharge are better predictors of species richness than models using one of these variables alone. At least two explanations could account for this successful use of discharge as a predictor variable. First, discharge is a better surrogate for the total surface area of habitat available for fishes than catchment area since drainage density varies with precipitation (de Wit & Stankiewicz, 2006). For the same catchment area, a river with a high discharge will have a higher number of perennial streams than a river with a lower discharge. This is particularly striking when maps of the Nile and Congo river networks are compared. Another explanation for the association between discharge and species richness, formulated by Livingstone *et al.* (1982), was that discharge also reflects productivity of the terrestrial vegetation within the river basin. This is a variation of the so-called species-energy hypothesis that we will discuss below.

FIGURE 15.5.
Relationship between the number of freshwater fish species recorded in one river catchment and the corresponding mean annual discharge at the river mouth (in $m^3 s^{-1}$) (from Hugueny, 1989).



Species-energy relationship

The species-energy hypothesis (Wright, 1983) predicts a positive correlation between species richness and the energy available within an island, or in our case a river catchment. The rationale is that a river catchment with great energy output (primary productivity) should sustain more dense animal populations than those located on a river catchment of the same but less productive area. As a result, population sizes are higher, extinction rates lower and species richness higher in the more productive river basin. The species-energy hypothesis has been supported by studies that used terrestrial net primary productivity (NPP) as a surrogate for the available energy for fish (Oberdorff *et al.*, 1995). It is worth noting that these studies conducted at a global scale included African rivers and that the effect of NPP was significant even when discharge had been accounted for, suggesting that the discharge does not act only through the available energy. The species-energy theory as originally developed by Wright (1983) has been modified by postulating that diversity is controlled directly by the effect of climate on organism energetics and its consequences on individual performances (growth, reproduction, etc.). The recent "metabolic theory of ecology" (Brown *et al.,* 2004) predicts, for ectotherms, a positive association between speciation rate and ambient temperature (Allen *et al.*, 2006). When the sample size is restricted to African rivers, NPP does not add much to discharge in explaining species richness and therefore it is difficult to disentangle the effect of available habitat (river network density) from the energy contribution in this part of the world, and *a fortiori* to test competitive hypotheses dealing with the species-energy relationship.

Historical factors

Considering the low dispersal ability of obligate freshwater fishes, it seems logical that the influence of historical events should be detectable for riverine fish assemblages in terms of species richness. African river discharge was greatly affected by dramatic climatic changes during the Quaternary, and during dry periods a number of fish species, unable to survive extreme conditions or face habitat shrinkage, could have disappeared in the rivers most affected by drought. Recovery of the presumed original richness needs either time for speciation, or reshaping of the hydrological network to permit immigration from other river basins. For most rivers the elapsed time since the last dry period (Last Glacial Maximum, LGM) has been too short to allow speciation and, to a lesser extent, colonization and therefore extinction rates should have been higher for river basins affected by drought (through a decrease in discharge and available habitat) than for river basins located within one of the rain forest refuges that persisted during the LGM. Currently, presence of rain forest refuges during the LGM is associated with high contemporary species richness in African rivers (Tedesco *et al.*, 2005). Past configurations of hydrological networks, when they are known, may shed light on present fish distributional patterns. For instance, in Southern Africa the presence of a lake that vanished about 2,000 years ago probably explains the high diversity of Haplochromines (Cichlidae) presently observed in rivers formerly connected to the lake (Joyce *et al.*, 2005). The Haplochromines are well known for their propensity to diversify quickly within lacustrine habitats and the former lake may have acted as a regional cradle for this group.

Global gradients

It is usually assumed that species diversity increases from high to low latitudes for most of the major groups of plants and animals and that biodiversity peaks in tropical and equatorial Africa, South America and Asia. This pattern holds true for freshwater fishes. For instance a comparison between species richness in African and European rivers shows that the fish species richness is significantly lower for the same catchment area in European than in African rivers (figure 15.1). Among the numerous hypotheses that have been proposed to explain the latitudinal gradient, only a few have been tested and received empirical support from studies comparing fish species richness in rivers distributed all over the globe. One is the species-energy hypothesis stating that rivers receiving higher energy input per unit area (tropics) should sustain richer communities than rivers with low input (temperate). The same data are also compatible with the metabolic theory postulating higher speciation rate for poikilotherms in warmer habitats and hence a positive relationship between temperature and species richness. The relationship between “energy” (NPP or temperature) and fish diversity per river basin is empirically established but the underlying mechanisms are still poorly known. The species-energy theory as originally developed by Wright (1983) posits a positive relationship between species richness and energy availability because of a reduction in population extinctions due to higher population densities. This hypothesis could be further tested if population density data were available along an energy gradient, or along a crude surrogate such as a latitudinal gradient. According to the few studies available for fishes (Knouft, 2002; Randall *et al.*, 1995; Mazzoni & Lobón-Cerviá, 2000), average density per species is not related to latitude. Similarly the relationship between temperature and speciation rate which underlies the metabolic theory still lacks empirical support for freshwater fishes. Moreover, among tropical biomes differences persist that cannot be attributed to differences in available energy, and for instance rivers in South America harbour more fish species than in Africa for the same area and energy input. The existence of a continental effect not explained by present features of rivers leads to the conclusion that unknown historical factors, maybe particular to each geographical region, are responsible for differences in fish diversity between Africa and South America and only palaeontological or phylogenetic data could provide some insights on these factors.

Biological traits

While major species richness patterns are well identified for African rivers, very little is known about the relationship between assemblage structure (quantified by using some biological traits) and river basin characteristics. For example, Tedesco *et al.* (2008) tested the hypothesis that hydrological regime within a river basin should be linked to life-history strategies of fish species. In particular, according to the scheme proposed by Winemiller & Rose (1992), species known as "periodic" (highly fecund, small eggs, no parental care) should have a higher probability of presence within river basins with marked seasonal floods. This hypothesis was confirmed for a set of West African rivers and by results obtained using river (seasonal) versus lake (stable) comparisons in the same biogeographic area (Bruton & Merron, 1990). In a global analysis Blanchet *et al.* (2010) observed that river basins with high species richness tend to be inhabited by a larger proportion of small species. For instance in Africa, the median body length of species inhabiting the Congo River is one of the lowest observed in African rivers. Many processes may explain such a pattern. First, speciation rate is expected to be higher for small, short-lived species than for large species with longer generation times. Second, large species with low population density and slow recovery after disturbance are likely to have high extinction rates. In support of these hypotheses, diversification rate (speciation minus extinction) tends to be inversely correlated to body size in fish families endemic to Africa (figure 15.6). Third, large species are expected to have better dispersal abilities than small ones. In support of this hypothesis, there is in West Africa a significantly positive correlation between fish body size and the geographic range of that species' distribution, estimated as the number of catchments where the species is present (Hugueny, 1990a). As a whole such processes should lead to an accumulation of small species in speciose river basins that experienced few population extinctions and many speciation events. It is also expected that single river endemic species should be of small size, a pattern that is observed for African fishes and at a global scale as well.

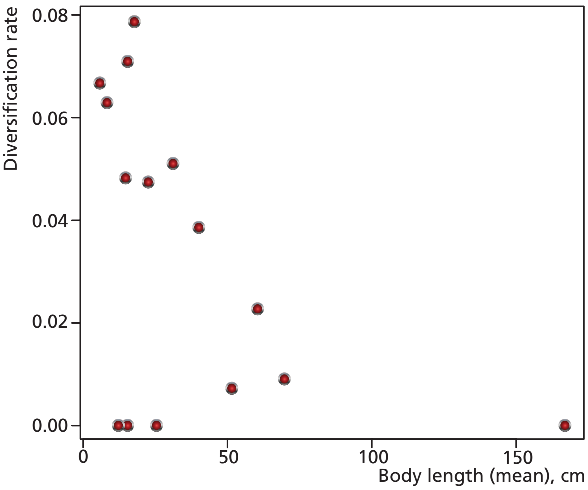


FIGURE 15.6.
Diversification rate (log number of species/age in million years) and average body size for 15 African endemic families (from Tedesco *et al.*, unpublished).

Patterns within rivers

Local-regional richness relationship

Most models integrating regional dispersal predict that local species richness directly depends on the number of species that are regionally available for colonization or, in other words, that the local features of the habitat (e.g., productivity and complexity) do not set a limit to the number of species that can coexist even if competition occurs, in contrast with what could have been anticipated from a strict interpretation of the niche theory. A positive relationship between local and regional richness is the rule more than the exception (Cornell & Karlson, 1997), provided that local communities occur in comparable habitats in terms of area, productivity and complexity. For riverine fishes, the number of species available for colonizing a local habitat is given, in first approximation, by the total number of species encountered within the catchment because there is no possible dispersal from adjacent river basins. Within this framework, Hugueny & Paugy (1995) tested for the existence of a local-regional species richness relationship by comparing local communities from similar habitat ("pool") in rivers from Côte d'Ivoire spanning a large gradient in their total species richness (20-90 species). As expected, the average local species richness is correlated with the river species richness, as shown in figure 15.7. Note that the proportional increase in local vs. regional species richness observed in this example was formerly interpreted as the signature of non-interactive communities, but the present wisdom is now to consider that the shape of the local-regional species richness conveys little information about the strength and nature of species interactions. The salient conclusion is that processes affecting species richness per basin and acting over large spatial and temporal scale such as extinction, speciation and dispersal among rivers, scale down to the local communities. In the present example, analysis of the data led to the conclusion that the area of the river catchment governs the

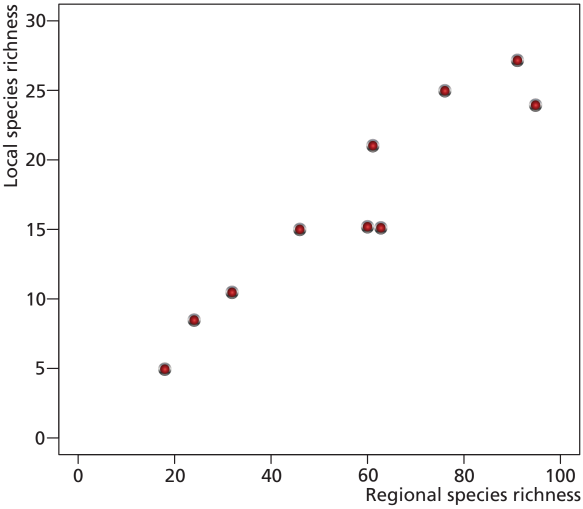


FIGURE 15.7.
Relationship between the average local fish species richness per basin and the total number of species encountered per basin (regional richness) for rivers in Côte d'Ivoire (From Hugueny & Paugy, 1995).

number of species present in the catchment which in turn governs the average local species richness of the pool assemblages. Interpreting how local species richness varies among basins should go hand in hand with finding out what mechanisms are responsible for the species-area relationships observed in aquatic systems.

Upstream-downstream gradient

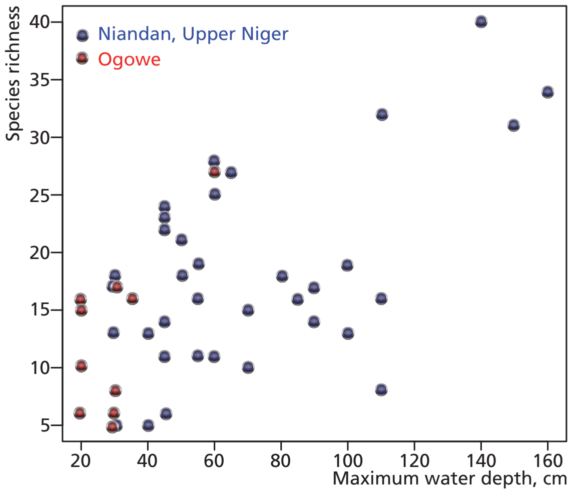
The previous section focused on local communities from the same habitat compared among different rivers to emphasize the role of regional factors on local community structure. The objective of the present section is to discuss the relationship between local communities and local habitat features within the same river basin, and in particular in light of a major structuring agent of river systems, namely the longitudinal gradient. Changes in physical conditions of streams and rivers from upstream to downstream reaches are generally assumed to favour an increase in species richness through increasing habitat heterogeneity and habitat volume (Schlosser, 1987; McGarvey & Hughes, 2008) or decreasing hydrological variability (Horwitz, 1978). An increase of fish richness along a longitudinal gradient has been reported in Africa from the Mono (Paugy & Bénech, 1989), the Ogun (Sydenham, 1977) and the Nyagui (Kadye & Marshall, 2006) rivers to provide selected examples. In the Mono, fish species richness increases rapidly with increasing distance from the source, and then becomes asymptotic. It is therefore important to carefully investigate the headwaters in order to show an upstream-downstream gradient. It is worth noting that the existence of a longitudinal gradient in species richness is not as frequent in Africa as in other parts of the world, because many rivers flow through very flat landscapes that do not generate great environmental dissimilarity along the river course, as observed for the Bandama for instance (Mérona, 1981).

There were different attempts to explain the above observations. Gorman & Karr (1978) explained the increasing richness with river size by increasing habitat diversity. It is a general observation in community ecology that habitat diversity or complexity is correlated with species richness because of more ecological niches and an easier coexistence of competitors, preys and predators. For stream ecosystems, the depth, current velocity, and the nature of substrate have been the most widely used to characterize habitat diversity (Gorman & Karr, 1978) to account for the major role of hydraulics in habitat selection by species, refuge from predation and distribution of food resources. As expected, a positive relationship between habitat diversity and species richness has been observed in some African rivers. For instance, the upstream-downstream gradient in species richness is explained by a parallel gradient in habitat diversity in the Nyagui River in the Zambezi catchment (Kadye & Marshall, 2006).

Schlosser (1982) pointed out that deep "pools" are absent or rare in the upper streams, and that explains the absence of the fish species inhabiting these deep and quiet habitats. In support of this hypothesis, a positive relationship between richness and maximum depth has been reported in the Niandan River and the Ogowe River (figure 15.8), suggesting that localities with both deep and shallow habitats are inhabited by more species. Note that at the same depth, species richness in the Ogowe is higher than in Niandan, as expected on the basis of the higher species richness of the Ogowe with respect to the Niger (figure 15.8).

FIGURE 15.8.

Relationship between local fish species richness and maximum water depth of the station in the Niandan River (Upper Niger) and the Ogowe River (from Hugueny, 1990a and Ibañez *et al.*, 2009)



Another hypothesis for explaining longitudinal gradients is that the greater hydrological variability upstream results in the extinction of populations and thus in a lower species richness (Horwitz, 1978). No study has explicitly tested this hypothesis in African rivers but the fact that in some rivers headwaters are temporary (e.g. Bandama) certainly contributes to reduce species richness upstream.

Besides species richness, other community descriptors may change along the longitudinal gradient such as the trophic structure. For instance in the Ogowe river Ibañez *et al.* (2009) observed an increase in the percentage of omnivores (both individuals and species) and a decrease in the percentage of invertivores (both individuals and species) as stream size increases. Observed trophic differences along the longitudinal gradient were also consistent with many other studies that described a longitudinal progression in fish trophic guilds that generally begins upstream with generalized invertivores and ends downstream with omnivores, detritivores, herbivores and piscivores (Angermeier & Karr, 1983; Schlosser, 1987; Oberdorff *et al.*, 1993; McGarvey & Hughes, 2008). Some of these trends are expected under the River Continuum Concept (Vannote *et al.*, 1980). The greater importance of herbivory/detritivory as a river becomes larger follows the prediction of increasing endogenous primary production and the accumulation of fine particulate detritus.

Mahon & Portt (1985) considered that each species, according to its size and behaviour, needed a minimal water depth to survive. As a result, the shallow waters could only be colonized by small species or juveniles of larger ones (Angermeier & Karr, 1983). This hypothesis was supported by a positive correlation between the length of the largest individual collected and maximal depth of the sampling station in the Niandan (Hugueny, 1990b).

Patterns among provinces

Distance species decay

From one river to another, fish species lists are rarely, if ever, identical, even within the same biogeographic region; some species are encountered in one river basin but not in the second and contribute to spatial turnover. Different indices exist to assess the similarity between two species lists, the most frequently used being Jaccard or Sorenson. Conversely, distances (according to axes of an ordination for instance) could also be used in this aim. A general pattern observed in community ecology and biogeography is the distance species decay (Soininen *et al.*, 2007) which describes a decrease in similarity between two communities with the geographical distance that separates them. Basically two processes may explain this pattern. The first is dispersal limitation. Two communities are increasingly unlikely to exchange individuals through dispersal as geographical distance increases between them. The second is a negative relationship between similarity in environmental features and geographical distance. If the environmental conditions that fit the requirement of a given species are present in a locality, then they are more likely to be found in close localities than in remote ones. For strictly freshwater fishes distributed in isolated river basins, dispersal took place mainly between adjacent basins when a freshwater connection is created by climatic changes (e.g. spillover due to high floods during the last humid period, 8,000 years ago) or orogenic or tectonic events (e.g. river capture). In this context of stepping stone colonization, a convenient way of expressing spatial distance between two river basins is to count the minimum number of river divides that should have been crossed by a species to go from one basin to the other. In West Africa, there is a clear increase in species dissimilarity between two river basins along such a stepping stone distance (figure 15.9). The relative contribution of dispersal and environmental heterogeneity to a species decay pattern is generally difficult to assess, but it can be expected that two recently connected basins should be more similar in species composition than an average pair of adjacent basins. In West Africa Hugueny & Lévêque (1994) listed four pairs of basins for which there is geographical evidence that they had been recently connected (Quaternary). These authors also listed river basins connected via coastal brackish creeks and lagoons. For species that can tolerate brackish water this is a possible dispersal route between river basins. For the other, less tolerant, species such exchanges could have been facilitated during past pluvial periods when high freshwater inputs may have diluted the brackish waters. For these pairs of basins that had been recently connected and maybe still are for some of them, the faunal similarity is higher than for other pairs of adjacent basins (figure 15.9). Finally, exchanges between rivers may have occurred during periods of lower sea level than at present. For instance, during the LGM drop in sea levels (up to 120 m), river mouths progressed through kilometres of exposed marine shelves before reaching the ocean, which sometimes resulted in a connection between previously isolated drainage basins. Dias *et al.* (2014) reconstructed such palaeo-connections at the global scale and compared pairs of river basins connected during the LGM with pairs that were not, to assess whether ancient connections left an imprint on present faunal similarities. At the global scale the response is yes, but restricting the analysis to African rivers leads to a statistically non-significant result despite the fact that, as expected, the existence of palaeo-connection results in higher faunal similarity. The narrow continental shelf of the Afrotropical realm resulted in a very limited number of palaeo-connected rivers under low-sea-level conditions and may explain, by lack of statistical power, the absence of a significant pattern. To conclude, when information is available it appears that recent connections between basins have favoured faunal exchanges that resulted in a greater faunal similarity between them. Such connections, by homogeneizing ichthyofaunas among basins, contributed to shaping biogeographical provinces. For instance all the connections through river capture, overflow, or brackish creeks listed by Hugueny & Lévêque (1994) occur between rivers located within the same province (Nilo-Sudan or Upper Guinea). The fact that the recent known connections occurred between basins that are considerably larger in the Nilo-Sudan than in the Upper Guinea resulted in provinces differing greatly in their spatial extent.

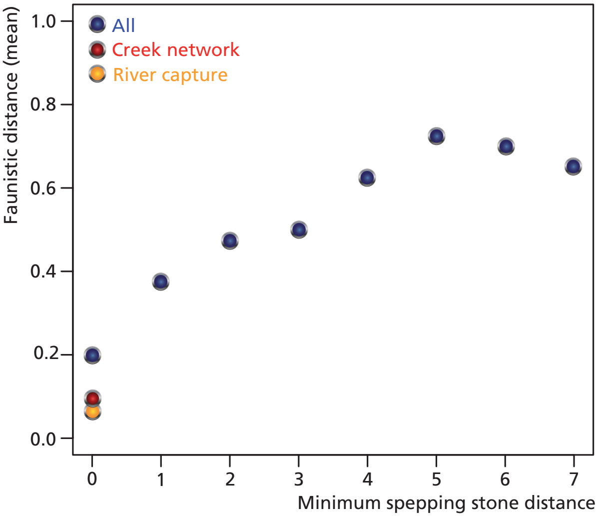


FIGURE 15.9.

Freshwater fish faunal dissimilarity between two rivers increases with the geographical distance separating them. A geographic distance of zero is for two contiguous river basins, one when they are separated by one river catchment and so on. For comparison, the faunal dissimilarities between pairs of rivers connected by a recent river capture or through a coastal creek network are shown (from Hugueny & Lévêque, 1994).

Provincial biodiversity

The species richness of a province is a combination of the richness of its most specious river basin and spatial turnover. To graphically represent these two components, species richness increments from the most specious river to the province is plotted as a function of area, the slope connecting the two points being an index of species turnover, the higher the slope the higher the turnover. Such river-to-province species-area relationships are depicted in figure 15.10 for all provinces but Congo (one river) and Maghreb (no reliable species richness estimates per river).

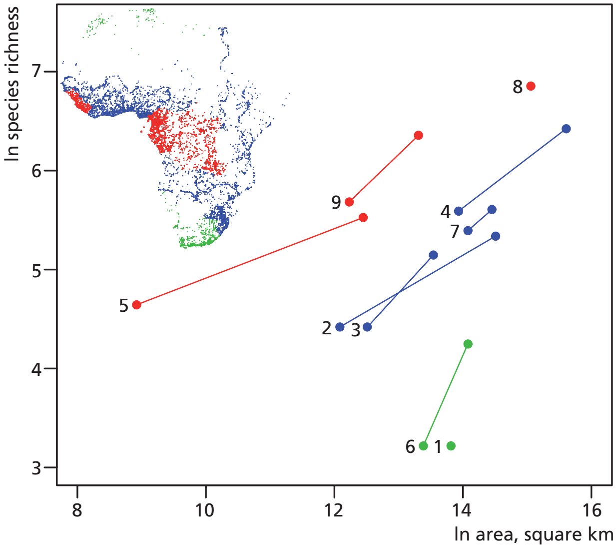
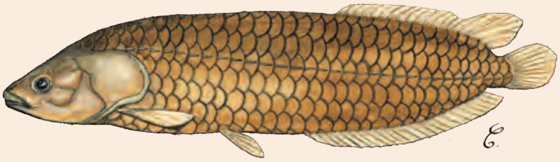


FIGURE 15.10.
Species-area relationships depicted by linking the most diverse river to the province it belongs to for 9 biogeographical provinces (1: Maghreb, 2: East Coast, 3: Angolan; 4: Nilo-Sudan; 5: Upper Guinea; 6: Southern; 7: Zambezian; 8: Congo; 9: Lower Guinea). Three groups of provinces are identified and their spatial extent is depicted in the inserted map (FAUNAFRI database).

The most salient result is that the species richness of a province is highly correlated to the richness of its most specious river (91% of the variability is explained in log-log space) so that spatial turnover has a very low contribution. We can distinguish three groups with regard to species area-relationships. The first includes the three regions (Upper Guinea, Lower Guinea, Congo) that are mostly located within the rain forest biome and have harboured one or several rain forest refuges during the Last Glacial Maximum. Rivers and regions belonging to this group have the highest richness for a given area. In contrast a group of two regions located in arid climatic zones display the lowest species richness for a given area. The remaining regions are intermediate. Grossly, the main factor explaining why a river basin harbours a rich fish fauna irrespective of its area, namely precipitations that remained high during the Quaternary despite the alternation of dry and humid phases, scales up and also explains biodiversity patterns at the regional scale. Species-rich provinces are rich just because of the aggregation of species-rich river basins. The disparity observed in spatial turnover among regions is not sufficient to blur this simple pattern. For instance the highest spatial turnover is observed for the Austral province, yet this region is very depauperate considering its area. Interpreting the differences in spatial turnover among provinces is a difficult task because the evolutionary histories of the lineages (speciation, extinction, dispersal) and past changes in the geographic and climatic setting may have been complex, and, unfortunately, frequently imperfectly known. According to an analysis conducted at the global scale (Leprieur *et al.*, 2011), basins located in mountainous areas are more likely to be dissimilar in species composition than when located within flat areas, probably because river capture and overflow are more likely to occur between catchments separated by low elevation river divide. However the observed pattern in Africa does not fit this expectation. For instance the Upper Guinea has a low spatial turnover while being in a high elevation region.

Diversity of fish habitats

CHRISTIAN LÉVÊQUE



Habitat is the place where a species lives and its surrounding biotic and abiotic environment. Ecologists seeking to develop explanatory and forecast models have long wondered about this fundamental question: how can the presence of an individual at a given place and time be explained? Indeed, the different fish species are not distributed at random in aquatic systems, but according to their biological and ecological requirements. The knowledge of factors governing the distribution of species could also improve our understanding of the structure of populations.

Habitat concept

When considering the many parameters that can characterize habitat, one must keep in mind that a fish, at each stage of its existence, is faced with three fundamental requirements (Lévêque, 1995):

- to protect itself from the limits set by the environment (current, oxygen, temperature, etc.) as well as predators and any competitors in order to ensure its survival;
- to feed in the best possible conditions to ensure its growth and maturity, given that nutritional requirements will vary as the fish develops;
- to reproduce once it reaches the adult state, in the most favourable conditions, in order to ensure survival of the species. The fish may thus need to move (migration) and potentially develop means of protecting its eggs (parental care).

Aquatic systems, particularly lotic ones, are characterized by high spatial and temporal variability because of fluctuations in water flow and level that considerably modify the nature and extent of the volumes that fishes can use. In reality, in such a highly variable environment, we can hypothesize that fishes will constantly seek compromises to address the three abovementioned requirements in the most optimal way. For instance, such compromises may take the form of leaving a shelter and risk exposure to predators in order to feed, or to migrate to areas that have poor food resources but are more suitable for egg and larva development. One of the major problems facing every fish is thus figuring out how to allocate its time and energy for feeding and/or reproducing in a way that maximizes its reproductive success. By minimizing the energy needed to find and capture prey, the fish will have more energy to devote to growth and metabolism (Hart, 1986). This quest for compromise aims to optimize "fitness", or the relative contribution of an individual to future generations. Faced with the different options in the natural environment, animals do not choose at random, but carry out activities that ensure higher reproductive success (Pulliam, 1989). These options may lead an individual to behave in ways that seem to require high levels of energy expenditure initially, but that pay off in the longer term for the survival of their young. This is the case of species that undertake long migrations to reproduce.

Throughout its life, and depending on its daily or seasonal activities, the same species may thus successively and temporarily occupy several types of biotope. Habitat, by definition the geographic physical system specific to an animal or plant species, shall thus be defined here as the set of biotopes necessary for the completion of a fish's biological cycle. It has a spatial and temporal dimension, partly related to the variability of the system and the biological and ecological needs of species.

Spatial and temporal scales and the hierarchical system concept

Aquatic environments are complex systems whose different abiotic and biotic components have highly varied spatial and temporal dynamics. In an attempt to untangle these complexities, ecologists often refer to concepts of scale, to better account for temporal variability and spatial heterogeneity in order to derive general laws that can help predict the evolution of ecosystems.

With regard to temporal scales, one generation for a bacterium (several hours) is very different from that of a planktonic crustacean (1 month), and that of a fish (1 to 10 years) is often much longer than for invertebrates. In terms of population dynamics, reaction times to disturbances vary according to the organisms in question. Environments that have been newly created or have just undergone a major upheaval will be colonized more rapidly by organisms with short generation times than by those with long ones.

Certain phenomena can also be present over shorter or longer periods. Hence long-term climatic trends can be superimposed on seasonal variations, in such a way that the slow evolution of a system may escape our notice as the phenomenon is difficult to identify in the absence of a long series of observations. The expression "invisible present" (Magnuson *et al.*, 1983) has been used to qualify these changes that are only identifiable with long observation series (table 16.I). On the scale of a decade, for example, a river slope may appear stable whereas on the millennial scale it is probably variable.

Years	Scale	Physical events (examples)	Biological phenomena (examples)
100 000	100 millenniums	orogeny; glaciations	evolution of species
10 000	10 millenniums	climate changes; drought-pluvial	species extinction; refuge zones
1 000	millennium	river catches	exchanges between watersheds
100	century	100-year flood	community changes
10	decade	anthropogenic impacts	fish lifetimes
1	year	flood cycle	reproduction cycle; migratory activity
0.1	'month'	lunar cycle	activity cycle
0.01	'day'	diel cycle	circadian cycle; feeding cycle
0.001	'hour'	accidental disturbances	physiological process

TABLE 16.I.
Theoretical relationships between time scales, physical events and biological phenomena (from Magnuson, 1990).

Similar problems crop up for spatial scales. For instance, fish species diversity in a drainage basin is a function of the surface under consideration (see chapter *Species richness of fish communities*). Moreover, many species have discontinuous distributions, and the probability of observing them depends on the scale at which one is working. Finally, given the variability and the heterogeneity of the environment, species can disappear in certain regions and thrive in others depending on the favourability of ecological conditions over time. As we can see in the previous example, there are obviously close interactions between the temporal and spatial scales. The presence of species in a region far removed from its current area of distribution is sometimes the heritage of an historical situation during which the species was much more widely distributed than today (see chapter *Biogeography and past history of the ichthyological faunas*).

The structure and composition of a fish community at a given time and spatial scale are thus the result of a set of phenomena that interact at different spatial and temporal scales for each of the populations that comprise the community. To better understand such situations, scientists often use the concept of hierarchic structure: in heterogeneous systems, it is possible to consider that the area under study is composed of sub-units that in turn can sometimes be broken down into even smaller units. An illustration of this notion of hierarchy in lotic systems was proposed by Frissell *et al.*, 1986 (figure 16.1) as a series of overlapping spatio-temporal scales. The principle behind these hierarchic organizations is that higher levels have slower dynamics and impose restrictions on the lower levels. As such, a watershed will be located in a biogeographical area, which explains the species composition of communities, and several watersheds may belong to an ecoregion whose abiotic characteristics are relatively homogeneous. Likewise, a river may contain different reaches that in turn have several types of microhabitats.

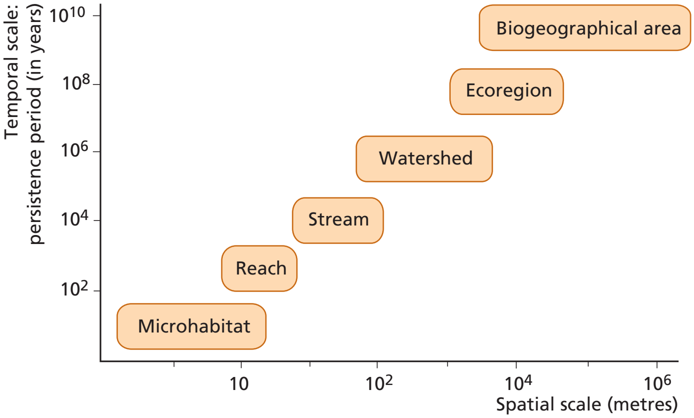


FIGURE 16.1.
Spatial and temporal scales, and hierarchies in lotic ecosystems.
The time scale corresponds to a theoretical period (persistence period) during which we may consider that the hierarchical level in question remains relatively stable (adapted from Frissell *et al.*, 1986).

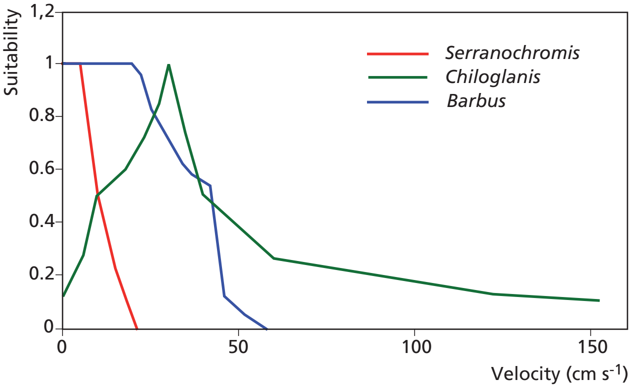
A fundamental question is tied to these notions of scales and hierarchy. Problems that we can consider resolving depend on the scale at which research is focused. Questions of biogeography cannot be tackled by considering a single watershed, nor can we work on migrations if we are only studying one reach. In reality, it is difficult to extrapolate results obtained at a given spatio-temporal scale to other hierarchic levels, given that parameters that are relevant at one level are not necessarily so in others. While biogeography can explain why a given species exists in a given basin, hydrology or the nature of the substrate will explain the presence of the species in a given reach. Much is at stake for environmental research in this question of changes of scale, as it is necessary to know the constraints posed by higher levels before scientists can accurately interpret observations made at a lower level.

Protect itself and rest: the microhabitat

In a river, the distribution of species according to different biotopes does not happen at random. Knowledge of the physical parameters of a biotope as well as the species pool, allows scientists to determine a species' preferences in terms of ecological factors. Microhabitat is defined as the site where a fish finds the most favourable temperature, current, depth, substrate, shelter, etc. conditions that minimize its current energy expenditure and allow it to rest while remaining as well-protected as possible from predators. Habitat changes during development are linked to changes in a fish's performance in terms of physical and physiological capacity. Microhabitat data are thus collected for specific stages of development by collecting enough information to describe the ecological preferences of a given stage.

In rivers, a distinction is usually made between rheophilic species that seek out running water and species that prefer still waters. These preferences should be viewed in relation to the more or less developed swimming capacities of different species, as well as physiological requirements, for instance in terms of the water's oxygen content. In line with this, preferential habitat curves have been created for several fish species in the Sabie River, a tributary of the Limpopo in Kruger Park (Gore *et al.*, 1992). Juvenile *Serranochromis meridianus* and *Barbus viviparus* inhabit stagnant ponds but *B. viviparus* is slightly tolerant to low velocities (up to 60 cm s^{-1}). Both species prefer relatively deep ponds (up to 2.5 m) with gravel or sandy bottoms. Meanwhile, *Chiloglanis swierstrai* prefer rapids in shallow waters (< 50 cm) with shingle bottoms, and water current velocities between 35 and 150 cm s^{-1} (figure 16.2).

FIGURE 16.2.
Habitat suitability in terms of mean water current velocity for three species from the Sabie River, Kruger National Park (from Gore *et al.*, 1992).

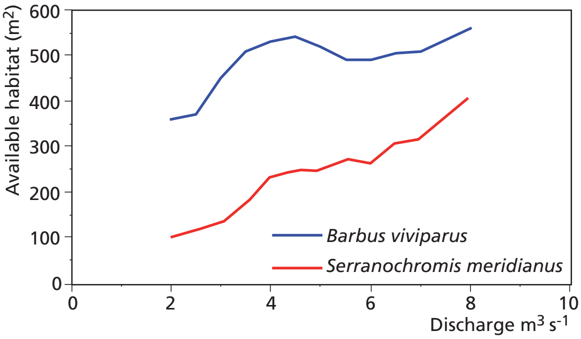


By considering habitat preferences in terms of current velocity, it is possible to predict the surface available for a species for different river discharges. Thus for a 300 m reach of the Sabie River, when the discharge increases from 2 to 8 m^3s^{-1}, the available surface for *C. swierstrai* and *S. meridianus* increases considerably (figure 16.3) whereas it remains constant beyond 3.5 m^3 s^{-1} for *B. viviparus*.

Pouilly (1993) also studied the organization of fish communities in three small watercourses in Guinea during the dry season, by identifying the ecological profile of species – that is, their preferences in terms of ecological factors such as current, depth, substrate type, etc.

A connection should also be made between the selection of certain habitat types and the need to find shelter from predators. In many African rivers, flooded zones are thought to provide juveniles of many species that reproduce during the flood

FIGURE 16.3.
Habitat available for *Serranochromis meridianus* and *Barbus viviparus* as a function of discharge at the Skukuza site on the Sabie River (from Gore *et al.*, 1992). Available habitat is expressed as usable area in m^2 for 300 m river length and discharge in m^3 s^{-1}.



with shelter from large fish-eating predators that have difficulty moving in heavily vegetated areas. It is true that such zones are also particularly favourable to the development of plankton species that meet the nutritional requirements of these juveniles.

In the East African great lakes, many endemic cichlid species sometimes have very specific requirements in terms of microhabitat. In particular, many species that are confined to rocky areas use crevices as both refuge and microhabitat. Other original microhabitats in Lake Tanganyika are the beds of empty gastropod shells that cover large surfaces at depths between 10 and 35 m on a sandy bottom, where the slope is gentle. Many cichlid species, mainly Lamprologines, use these shells as shelter but also as reproductive sites (Ribbink, 1991). The juvenile forms of *Chrysichthys* and *Mastacembelus* also find refuge in these empty shells.

Foraging

An essential reason for a fish to frequent certain types of physical systems is the opportunity of finding food that is adapted to its size and physiological requirements. This relationship between size-diet-ecological conditions is an important parameter for understanding why a species occupies a particular place.

Ontogenetic changes of the diet and habitat

In their lifetime, the size and the weight of fishes change considerably and it is customary to distinguish different periods of development (Balon, 1985, 1990):

- the embryonic period, which begins with fertilization and is characterized by purely endogenous nutrition from the egg yolk;
- the larval period begins with the progressive but rapid transition from endogenous to exogenous feeding. This larval period is characterized by the presence of temporary larval organs;
- the juvenile period begins when the fins are well-differentiated and all temporary organs have been replaced by permanent organs. It ends with the maturation of the first gametes. It is generally a period of rapid growth, sometimes characterized by a specific colour pattern;
- the adult period begins with the maturation of the first gametes. It is characterized by a decrease in the somatic growth rate.

The different phases of development correspond to different dietary requirements, feeding behaviours, and ecological, physiological, and biological needs, which implies in many cases the occupation of different biotopes (Lauzanne, 1975; Winemiller, 1989). Small-sized and poorly vagile juveniles are limited to using small-sized particles as well, such as phyto- or zooplankton. As fish size and vagility increase, the size and nature of prey also changes. In adult ichthyophagous fishes, morphological changes associated with greater specialization are accompanied by changes in prey size and type.

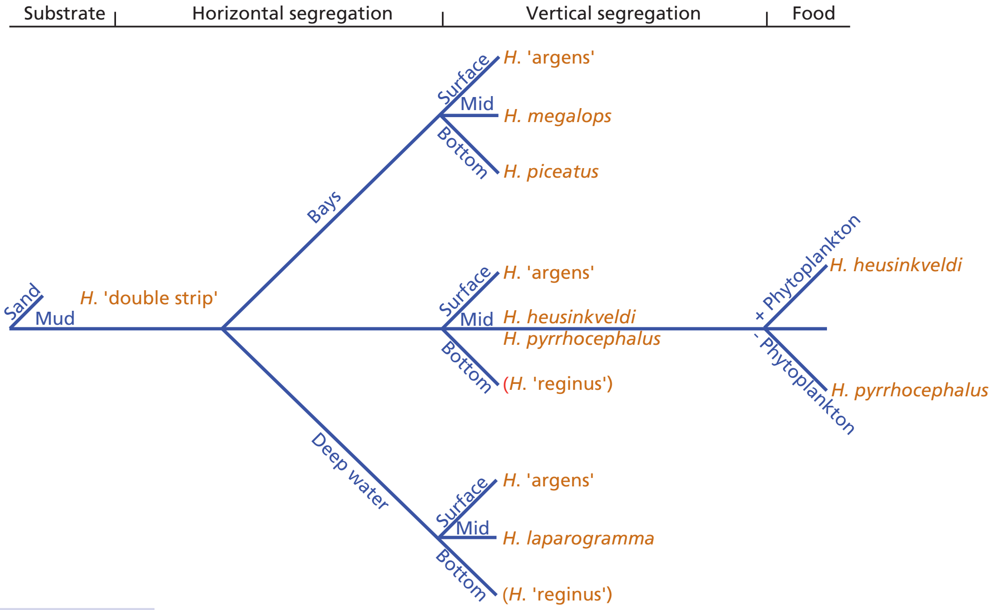
The consequences are significant in terms of habitat. Preys are not distributed at random in aquatic systems, and their availability can vary over the year. In riverine systems, for example, planktonic preys are essentially abundant in calm waters, that is, in riverine annexes where juveniles of many species find favourable conditions, both in terms of nutrition and in the physical conditions of the habitat. The existence and extent of these systems are highly dependent on hydrology, particularly water level. There thus needs to be good synchronization between the appearance of larvae and the existence of favourable prey in the corresponding habitat ("match-mismatch" hypothesis by Cushing, 1982).

Strategies of research and sharing of food, and spatial segregation of species

Food strategies can be viewed as decision-making systems to address questions such as: where should the individual feed, or what sort of prey should it seek out? (Cézilly *et al.*, 1991). The fish must decide when it will feed, where, for how long, the most suitable prey (in terms of size and nutritional value), the manner in which it will seek out and capture such prey, and so forth. It needs to be efficient in responding to environmental constraints such as competition, food scarcity, and unpredictable variations in the resource.

A fundamental axiom is that feeding strategies were shaped during natural selection, and that every decision tends to optimize certain variables such as the energy assimilation rate which is ultimately correlated to the concept of "fitness" (Pyke, 1984). But a number of results indicate that fishes also have the possibility of learning and engaging in alternative behaviours that allow them to seek out prey more effectively and live longer (Hart, 1986).

FIGURE 16.4.
Schematical representation of expected ecological segregation among zooplanktivore haplochromines in Lake Victoria (from Goldschmidt *et al.*, 1990).



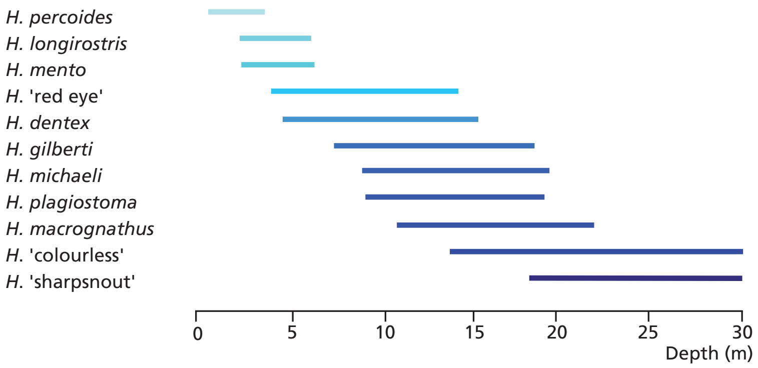


FIGURE 16.5.
Depth distribution of adults of some haplochromine piscivorous species from the Mwanza Gulf, Lake Victoria (from van Oijen, 1981).

In environments inhabited by numerous species belonging to the same trophic group and with relatively similar diets, strategies may be to occupy spatially different habitats in order to decrease interspecies competition. This is the case in Lake Victoria where spatial segregation phenomena were found among zooplanktophagic haplochromines, thus permitting the ecological isolation of species (Goldschmidt *et al.*, 1990). In addition to a horizontal distribution that is often well-differentiated for each of the species in the Gulf of Mwanza, the type of bottom, wind exposure, and depth of the water column are also important factors contributing to the segregation of species (figure 16.4). Most zooplanktivore juveniles are only seen in shallow waters (less than 9 m) where they find shelter from predators. For species with broad overlaps in their geographic areas of distribution, depth influences the manner in which they segregate themselves, sometimes taking into account the vertical migrations that follow different circadian rhythms.

While piscivorous haplochromines are present in all major habitat types in Lake Victoria, many of them have a distribution that is limited to certain types of substrates (van Oijen, 1981). Compared to their parents, juveniles are generally in shallower, less exposed zones. A few species only occupy sandy bottoms whose depth does not exceed 6 m. Moreover, adults of many species in the Gulf of Mwanza have a different depth distribution. Some are found only in the surface, while others in the deep (figure 16.5).

Trophic migrations

The search for feeding-friendly areas pushes species to engage in short-distance migrations to feed. In the deep lakes, species carry out nycthemeral migrations, spending most of the day in the depths and then swimming up close to the surface at night to feed. In Lake Malawi, the vertical distribution of species in pelagic systems depends on the daily cycle. During the day, most of the fishes are found at different depths: *Diplotaxodon* "big eye" and *Synodontis njassae* at the limit of the oxycline at around 200-220 m; *Diplotaxodon* "elongate" and *Rhamphochromis ferox* between 50 and 200 m; *Copadichromis quadrimaculatus*, *Engraulicypris sardella* and *Rhamphochromis longiceps* in the first 100 m. Most of these species migrate towards the surface at night. Species such as *S. njassae* and *Diplotaxodon* "big eye" carry out migrations of 200 m (Thompson *et al.*, 1995).

Reproduction strategies and breeding sites

The reproduction strategy of a fish species in a given environment is a set of biological traits such as age at first reproduction, the relationship between size (or age) and fecundity, parental behaviour, reproductive season, gamete size, and so forth. An individual may also develop tactics which are in fact variations of the typical reproduction schema to respond successfully to changes in environmental factors. It is thus an adaptive behaviour to specific ecological conditions and whose purpose is to ensure survival of the species.

Defining the habitat of a species requires taking into account the reproductive behaviour of that species and its need to find conditions that allow it to spawn in the best possible conditions. In particular, spawning generally occurs at a period when environmental conditions are, in theory, most favourable to the survival of eggs and larvae, and many species have a seasonal reproductive cycle. In large tropical rivers, the hydrological regime (that is, the set of climatic conditions prevailing at the start of the flood) appears to be the main regulator of reproduction. For many species, spawning coincides with the flood (see chapters *Variability of climate and hydrological systems* and *Life-history strategies*).

Balon (1985, 1990) distinguishes two broad types of ontogenic trajectories in biological cycle models.

In the indirect model, the eggs are generally small and produced in large numbers. They yield small, underdeveloped young larvae with only a small volume of yolk that is insufficient for producing the final phenotype. These young larvae must feed rapidly on small particles to complete their development and are highly vulnerable during this period.

In the direct development model, fishes produce a limited number of large eggs with a large amount of yolk, which allows the embryo to develop to an advanced stage. This shortens or eliminates the larval period, and juveniles are already well-formed and thus less vulnerable when they start shifting to an external diet. *Labeotropheus*, a cichlid mouth-brooder from Lake Malawi, is a good example of this type of fish that releases a large juvenile (14% of adult size) only 31 days after fertilization (Balon, 1977).

We thus have two main strategy types: indirect development consists of producing a large number of eggs that will suffer a high mortality rate, but which frees up the parents for other activities right after spawning, whereas direct development requires effort to be placed in the survival of a low number of individuals, which means parents must invest energy for a long period. In one case (direct development) fishes will have a sedentary and perhaps territorial behaviour. In the other case (indirect development), there will be nomad species who may cover large distances to reproduce.

Direct development and territorial behaviour

An example of highly sedentary behaviour connected to direct development is that of different cichlid species endemic to the East African great lakes. Fryer (1959) had already highlighted the fact that many littoral species were so confined to rocky zones that they had never been observed more than a metre from these systems. Mature individuals live, feed, and reproduce throughout the year within the strict limits of their habitat. Moreover, large yolk-rich eggs yield young that are large enough to use the same food as the parents, which means that there is no need for a pelagic planktonic stage such as that observed in coral fish (Lowe-McConnell, 1987), and the species can thus spend its entire life in the same biotope. The sedentary nature of these cichlids has been demonstrated experimentally by marking. Some species have an area of distribution limited to a few thousand m^2 (Ribbink *et al.*, 1983). In addition, species transferred from one area of the lake to another remain in the vicinity of the point of introduction and reproduce at that site.

As a general rule, direct development is most often accompanied by parental care, that is, assistance provided by parents to ensure better survival of the egg after its formation. This assistance may range from nest construction to guarding of eggs and fry. The practice of parental care is rather widespread in fishes, particularly in the Cichlidae family (Keenleyside, 1991) (see chapter *Diversity of responses to environmental constraints and extreme environmental conditions*). Its main function is to protect the young from predators. It has been suggested that the practice of parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990), in order to limit the dangers inherent to the latter. Nonetheless, it would do well for this theory to be verified by observations.

The practice of parental care can be accompanied by territorial behaviour linked to competition and the defence of a reproductive site. The territory in this case becomes an indispensable resource for spawning, and one whose availability may be limited. For 12 species of substrate-laying Cichlidae in Lake Tanganyika belonging to the genus *Lamprologus,* and which are very closely related to each other, Gashagaza (1991) has shown that they use the physical system in different ways to spawn and protect their young. Some spawn on block surfaces; others in crevices; still others in holes. This diversity of reproductive behaviour in a system where space is limited given the population density has the advantage of limiting interspecies competition for habitat use.

Territorial competition is often expressed in the defence of a territory from conspecific and heterospecific individuals (see chapter *Ethology*). By studying the behaviour of 6 herbivorous cichlid species that are maternal mouth-brooders, Kohda (1995) highlighted the existence of two types of territory:

- the males of six species studied have a restricted territory around the nest (20 to 40 cm in diameter) that they guard ferociously against intruders that are most often potential egg eaters. This nesting territory is used by the females who lay their eggs in the nest, after which they take the eggs in their mouth and leave the zone;

- there is also a larger territory of a few m^2 around the nest, where the males patrol at around 50 cm and 1 m from the bottom and where they feed. When a female enters this zone, the male courts her then brings her into the nest. On the other hand, a male will attack conspecific males and sexually inactive females that enter the zone.

The practice of mouth-brooding is more specialized and is more recent in origin. Its adaptive advantage is to shelter embryos from predators and limit competition for reproductive sites. It can also be viewed as a means of eliminating dependence on a substrate to reproduce when the available benthic space is in high demand (Balon, 1978). In substrate layers that practice mouth-brooding, the biotope occupation cycle can be relatively complex. Fryer & Iles (1972) so describe the reproductive cycle of *Oreochromis variabilis* in Lake Victoria (figure 16.6). On sandy bottoms, males build nests in which females spawn. The latter then take the eggs in their mouth and transport them to incubation areas where the young are released once the eggs have hatched. They first live in shoals in very shallow waters with rocky bottoms, and as they grow, they move to deeper areas. When they are bigger, they move in shoals to sandy shores or weed beds. They gradually acquire adult behaviour as they grow, living in the open water of exposed beaches. The males then build nests in their turn on sandy shores, and the cycle begins again.

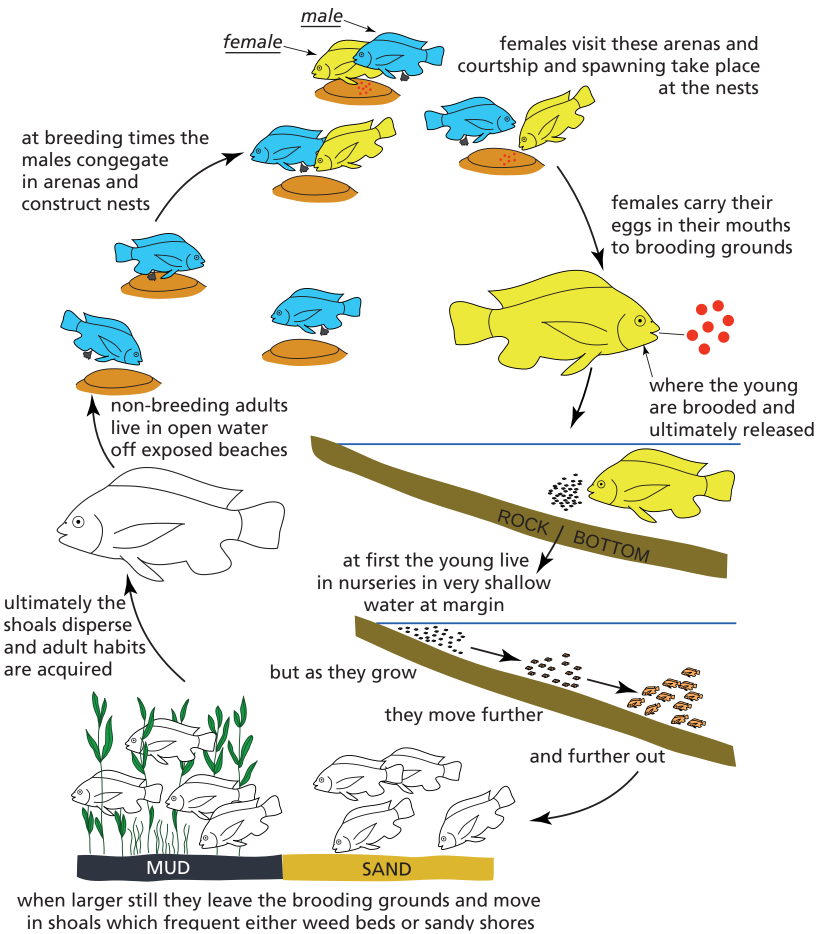


FIGURE 16.6.
The life cycle of *Oreochromis variabilis* in Lake Victoria. This diagram shows the different phases of the environment occupation in relation with ontogeny (redrawn from Fryer & Iles, 1972).

Indirect development and breeding migrations

In fishes with indirect development, the need to use distinct biotopes for the different stages of development, and in particular the search for sites that are suited to spawning, and then to good development of juveniles, forces the species to carry out migrations that may cover long distances. According to Northcote (1979), a migration is a transfer from one habitat to another that occurs regularly throughout the individual's lifetime, and which involves a large portion of the population.

TYPES OF MIGRATION

A distinction is usually made between diadromous migrations between the sea and continental aquatic zones, and potamodromous migrations which occur wholly within fresh water (Mc Dowall, 1987). Tropical river fishes that carry out long migrations to reproduce are thus potamodromous species.

Among the diadromous species, we can distinguish:

- anadromous fish that spend most of their life in the sea and migrate to fresh water to reproduce;
- catadromous fish that spend most of their life in fresh water and migrate to the sea to reproduce. The classic example is the eel;
- amphidromous species which divide their time between marine and continental waters, without these migrations being necessarily linked to reproduction.

More simply, we sometimes make a distinction between euryhaline fishes that move freely between fresh and sea water, and amphihaline species that only do so at certain stages of their life.

Fishes making anadromous or catadromous migrations are rare in tropical Africa, whereas plenty of potamodromous fishes can be found there. This type of migration provides an adaptive advantage in that its purpose is to reach sites that favour reproduction or feeding. Some authors believe that it is a mechanism that protects the young from predators, and Fryer (1965) considers it a means of ensuring the dispersion of young throughout the riverine system. The two hypotheses are probably complementary. Spawning in the tributaries of the upper courses allow larvae to be carried by floodwaters to all biotopes, over hundreds of kilometres downstream from the spawning site. Upstream or downstream migrations whose purpose is to bring parents close to floodplains so they can spawn there once water enters these systems also have the goal of allowing larvae to reach floodplains as rapidly as possible so they can find food and shelter there.

The sites most favourable to spawning are not necessarily the best ones for feeding, and some species must therefore migrate over long distances between the two. Daget (1960) and later Welcomme (1985) made the distinction between longitudinal migrations, often stimulated by reproduction and which occur in the riverbed, and lateral migrations, when fishes leave the main riverbed to go to the different habitats of the river flood bed. These lateral migrations are triggered both by the search for food and by reproduction.

MIGRATIONS OF 'TINÉNIS' IN THE NIGER RIVER
(SOURCE: DAGET, 1952)

Even the least-informed observer would agree that the phenomenon is absolutely spectacular.
These fishes (*Brycinus leuciscus*, Alestidae) go up the minor bed in successive waves related to lunar phases.
They all move in the same direction a few centimetres from each other, and parade for several hours with great regularity. Should a predator or fisherman disturb them, they scatter momentarily in all directions before reforming the school and moving on.

The average speed of the migration is not high – somewhere around 1 to 1.5 km per hour.
The extent of the displacement can nonetheless be significant, as Daget has estimated that some schools can cover, over several months, distances of close to 400 km. Generally, the main school itself is precedent beforehand by what local fishermen call "the head of tinénis" formed by a group of smaller individuals.

The migration of the "tinénis" begins when they leave the floodplains to join the minor bed. That said, the actual longitudinal migration only begins when this occurs during a full moon phase.
In the absence of the latter (the last few days of the lunar month), schools stop or disperse, only to reform in the early days of the new moon.

When they are prevented in their progress by a dam such as the Markala dam (Delta Central region of the Niger in Mali), the schools break up quite rapidly, and its elements then go downstream.
This essential fact shows that while the upstream phase is always done in tight groups, the opposite is carried out in a dispersed way, individually or in very small groups.
This school dispersion phase always corresponds to the darkness associated with the end of the lunar month.

In brief, let us revisit what Jacques Daget wrote: "To explain it, we believe there is reason to posit a group effect, as *Alestes* (henceforth *Brycinus*) *leuciscus* are only stimulated to go against the current when they are present in large numbers and packed against each other (…).
There is also probably a constant antagonism between the following phenomena: congregation on moonlit nights; scattering during dark nights.
At the end of the lunar month, scattering was predominant; schools stop and and break apart, whereas in the early days of the month, congregation takes precedence, leading to the formation of schools that keep moving owing to the group effect as long as the presence of moonlight prevents scattering from taking over."

The moon's influence is nonetheless not general and should be considered secondary compared with hydrology and the nycthemer for instance, and affecting only a few species in a stable, repeated manner (Bénech & Quensière, 1983).

The mechanisms that trigger migrations are still poorly known, especially for those that require movement over long distances. To the extent that species have different behaviours, there are probably several mechanisms that come into play, some of which are associated with the start of the flood (Welcomme, 1985). Scientists have also not yet identified the signals by which adult fishes know before the youngs that the time has come to leave the floodplains. It is true that these signals are not always very efficient and that large numbers of fishes are blocked every year in residual ponds that dry up during periods of low water flow. The depth and/or water oxygen concentration may be deciding factors.

BREEDING MIGRATIONS IN LAKE CHAD

In the Chad basin, several species carry out breeding migrations (Bénech & Quensière, 1989). In particular, many lacustrine species use the North Cameroon floodplain (Yaéré) as a nursery.

Some species carry out long-distance migrations when they are about to breed. These are primarily pelagic species – many of which are zooplanktivores – in Lake Chad, such as *Alestes baremoze*, *Synodontis batensoda*, *Schilbe intermedius*, *S. uranoscopus*, *S. mystus*, *Synodontis schall* or *Hyperopisus bebe*. A large part of lacustrine populations go up the Chari before the flood and reproduce close to the North Cameroon floodplain (Yaéré) in August and September, some 150 to 200 km upstream from the lake. Eggs and larvae are dispersed in flooded zones and spend several months there before joining the lake via the Chari or the El Beid, a major drainage channel that connects the Yaéré to Lake Chad during the flood. *Alestes dentex* appears to migrate for reproduction to other flood areas located even higher upstream (at least 250 to 300 km from the lake). This is also the case for other species such as *Synodontis membranaceus* and *Labeo senegalensis*. Other species such as *Polypterus bichir*, *Distichodus rostratus*, *Marcusenius cyprinoides*, also seem to possess characteristics of major migrators, but data collected thus far are insufficient to confirm this hypothesis.

Other species carry out shorter migrations. The lacustrine populations of *Hydrocynus forskalii* migrate in the Chari delta and lower reaches to reproduce when the flood subsides, from November to March, as well as at the start of the flood in July-August. *Bagrus bajad* also reproduces in the delta in May-June.

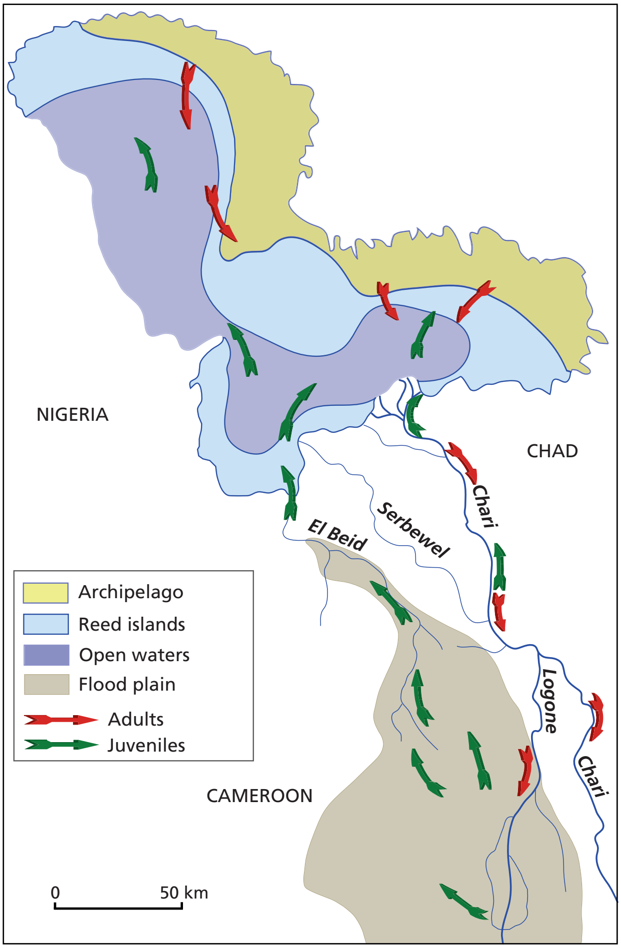
Finally, more or less sedentary species migrate from the main bed to flooded areas to find better feeding conditions, shelters, and conditions favouring reproduction. These species include *Brevimyrus niger*, *Petrocephalus bovei*, *Gymnarchus niloticus*, *Heterotis niloticus*, *Ichthyborus besse*, *Clarias gariepinus* and *Siluranodon auritus*.

The return migration of young fish to Lake Chad is an important phase in general migration patterns. A detailed study of downstream migrations of juveniles when the flood begins to subside was carried out in the El Beid, which connects the Yaéré in North Cameroon to the southern zone of Lake Chad (Durand, 1971; Bénech & Quensière, 1982 and 1983). A first group of juveniles composed of *Hyperopisus bebe*, *Marcusenius cyprinoides*, *Alestes dentex,* and *Labeo senegalensis* move in large numbers from mid-November to mid-December. It also includes other species such as *Alestes baremoze*, *Polypterus bichir*, *Hydrocynus brevis* and *Lates niloticus* which appear in early November, and *Heterotis niloticus*, *Distichodus rostratus*, and *Oreochromis aureus* which are present until January. *Mormyrus rume*, *Pollimyrus isidori,* and *Distichodus brevipinnis* are also present during the first two months of the flow.

A second group of species is found in large numbers in late January: *Sarotherodon galilaeus*, *Brevimyrus niger*, *Clarias* spp., *Barbus* spp., as well as *Oreochromis niloticus* and *Labeo coubie*. Finally, a third group can be observed at the very start of the El Beid flood. The fishes then disappear before coming back again in abundance in February: *Ichthyborus besse*, *Siluranodon auritus*, *Schilbe uranoscopus*, *Synodontis schall,* and *Synodontis nigrita*. The second and third group migrate to Lake Chad with the drainage of floodplain waters.

Migrations have been the subject of numerous investigations, most of which are nonetheless imprecise given the difficulty of tracking the movement of fishes in aquatic systems during the flood. In Nilo-Sudanian systems, research carried out in the Chad basin have highlighted very varied behaviours (see box "Breeding migrations in Lake Chad") (Bénech *et al.*, 1983; Bénech & Quensière, 1989) (figure 16.7). Similar groups of migrators have been observed in the Senegal River (Reizer, 1974).

FIGURE 16.7.
Ways of breeding migration of *Alestes baremoze* in the Chad basin (redrawn from Bénech & Quensière, 1987)



In the East African great lakes, many lacustrine species still carry out breeding migrations in the tributaries. In Lake Turkana for example, *Alestes baremoze*, *Citharinus citharus, Distichodus niloticus,* and *Barbus bynni* migrate in the Omo River, while *Brycinus nurse, Labeo horie, Clarias gariepinus,* and *Synodontis schall* migrate in small temporary tributaries (Hopson, 1982).

In Lake Victoria, Whitehead (1959) also identified major migrators such as *Barbus altianalis* that migrate 80 km in rivers, and migrators that cover shorter distances such as *Labeo victorianus* and *Schilbe mystus* that migrate up to 25 km upstream or in flooded zones along the banks to breed. Small Mormyridae (*Marcusenius victoriae, Gnathonemus longibarbis, Hippopotamyrus grahami, Pollimyrus nigricans, Petrocephalus catostoma*) go upstream on Lake Victoria's north tributaries. Mature fishes remain near the river mouths until the flood, then migrate upstream at night, with peaks at dawn and dusk (Okedi, 1969, 1970). They spawn in ponds located 8-24 km from the mouth, and the youngs stay for three to seven months in these ponds.

Generalisation of the habitat concept

Habitat is a notion that is essentially dynamic and involves spatial and temporal scales.

The habitat, consequence of a phylogenetic heritage and adaptive strategies

The place in which a species lives – its physical, chemical, and biological environment – is the result of a compromise between different constraints that, to a large extent, are related to the inheritance of vital traits selected by evolution. This, for instance, is the case for reproductive behaviour, for ecological or physiological requirements, for feeding habits and specializations. Phylogenetic heritage thus imposes a number of abiotic, biological, and behavioural constraints on a species that will determine its needs in terms of habitat.

Genome variability nonetheless allows species to develop tactics, which are adaptive responses to changes in the physical system inhabited by the fish. This flexibility can be vital for the survival of the species which can develop alternative behaviours, depending on the environmental conditions to which it is subjected.

Finally, research is beginning to uncover the possibility of a learning process which would expand the possibilities for fishes to occupy new environments.

This has important consequences in terms of habitat. If phylogenetic heritage limits the fish to a type of physical system, genetic variability would allow certain individuals to push the boundaries of the limits that the species can tolerate. Natural selection could then favour these genotypes and thereby modify species behaviour with regard to habitat.

Ontogenetic niche and its involvements

The species can only complete its biological cycle if the individual finds the conditions necessary for survival and growth at each stage of its development. The ontogenic niche is thus the set of habitats and resources that are needed for the smooth progress of the biological cycle. For species with indirect development in particular, there has to be excellent synchronization over time between ontogenesis and changes in the milieu. In other words, fishes have to be in the right place at the right time. This is the case for example of fishes in large tropical rivers that have flood zones, and which have different stages of reproduction and development that are closely bound to the cycle of hydrological events and the diverse habitat types that are associated with them (figure 16.8).

One of the practical applications of the ontogenic niche concept for the management of species and aquatic systems is that one has to consider all of the environments that the species may need during its development. It is not enough to preserve the biotopes required by adults to ensure the long-term survival of a species. The species must also be able to find conditions favourable to breeding and larval growth.

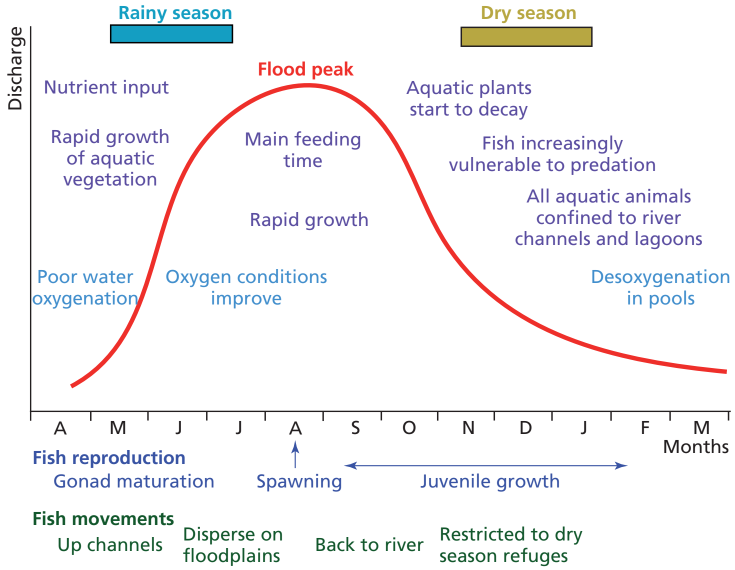


FIGURE 16.8.
The seasonal cycle of events in a floodplain river and their involvements towards the biology and ecology of fish (redrawn from Lowe-McConnell, 1985).

Typology of habitats

For practical and operational reasons, the need to identify a typology of habitats has led some authors to propose a conceptual framework based on physical and geomorphological characteristics (Frissell *et al.*, 1986). This hierarchic approach can serve as a reference for the study of fish communities at different spatial and temporal scales (Bayley & Li, 1992). Climate-related factors generally dominate at a large scale, whereas at the local scale biotic factors such as predation or competition can have a major influence. This classification has the disadvantage, however, of not putting enough emphasis on fish requirements in terms of habitat.

It can indeed prove useful in this space-time continuum to identify some entities of biological significance. Bayley & Li (1992) opened the way by distinguishing four main types of spatio-temporal organization. According to these authors, the microhabitat corresponds to the zone of daily activity: feeding, selection of the best abiotic conditions, social behaviour (gregariousness, territoriality). At the month-long scale, the area of activity covers the river (home range), whereas at the seasonal scale it can also include the drainage basin if the species carries out long-distance migrations. Finally, the regional scale covers evolution (speciation) and the establishment of fauna under the influence of climatic and geological events (extinction, colonization).

This typology proposed by Bayley & Li (1992) is worth noting for its emphasis on the relationship between the use of space and biological behaviour. This effort to provide a better definition of habitats based on the behaviour and needs of the fish nevertheless needs to be pursued, as the definition of the categories selected remains somewhat unclear. For this reason, Lévêque (1995) recognizes four main sets (figure 16.9):

- the resting area is the smallest scale at which a fish tackles a more or less complex set of biotic and abiotic stimuli. Most prevalent is the search for shelter

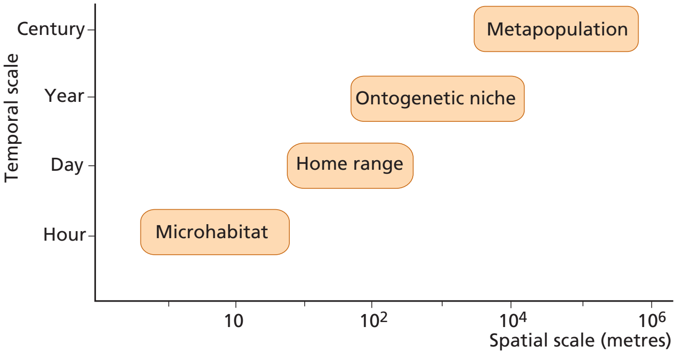


FIGURE 16.9.
The four main suggested patterns of spatial and temporal models of habitats used by fish (from Bayley & Li, 1992 and Lévêque, 1995a).

in relation to environmental conditions and/or predators. By staying in this resting area, the fish minimizes its energy use;

- the home range, within which biological and behavioural rhythms are conditioned by nycthemeral or lunar cycles. For territorial fishes, the territory can be the spatial scale of reference for this category. For others, it is the set of refuge or resting areas as well as the areas where the species will feed, which implies short migrations.

With the exception of accidents that compel them to move, many fish species complete their biological cycle in the spatio-temporal context of the activity area. This activity area can nevertheless change when the aquatic environment is modified;

- the ontogenic niche scale corresponds to the set of physical systems needed by a species to complete its biological cycle. The spatial limits are the geographic limits of different habitats occupied by the stages of development, including the spawning areas to which a species can migrate, sometimes over long distances, during reproduction. While the previous scales essentially concerned the individual, the ontogenic niche concerns the population as a whole;
- the regional scale, that of the metapopulation, corresponds to the different drainage basins in which the species is present. These basins are geographically isolated, except during periods that are exceptional from a geological perspective.

The four sets identified above correspond to a growing complexification in terms of the use of space for biological functions (figure 16.10).

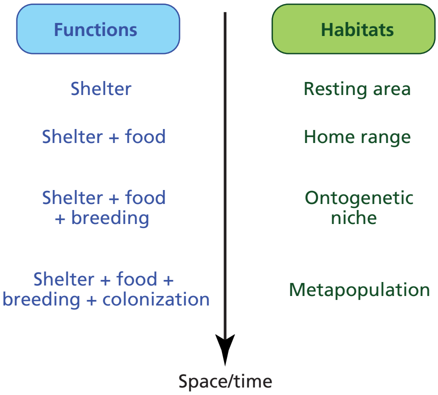


FIGURE 16.10.
The four spatiotemporal sets that define the correlation between habitat typology and biological functions (from Lévêque, 1995a).

Role of fish in ecosystem functioning

Christian Lévêque

The functional relationships between the species in an ecosystem are still poorly understood, but represent one of the main concerns of modern ecology. The role of biological diversity in the functioning of ecological systems is of particular interest. Are all the species found in an ecosystem truly needed to ensure its proper functioning? Do some species have redundant functions, and are there species with more important roles than others (keystone species)? Scientists also wonder about the role of biological diversity in the stability of ecosystems and their capacity to resist or adapt to disturbances, and study the relationships between specific richness and biological productivity.

The answers to these questions are important for the management of aquatic environments and the preservation of biodiversity. But their complexity makes it difficult to propose satisfactory hypotheses. It is nevertheless possible to analyse available data and attempt to find partial answers to the questions raised (Lévêque, 1995b and 1997).

Impact of fish predation on aquatic communities

Limnologists have long thought that the organization of ecological systems was essentially controlled by the nature and dynamics of the physico-chemical system in which the organisms live. In the standard view of bottom-up control, we look for example at the manner in which environmental factors or the availability of trophic resources influence fish biology and ecology, and the consequences in turn on the organization of fish communities. This deterministic approach regarding communities on the basis of abiotic characteristics remains relevant but needs to be refined. Indeed, several investigations have shown that fishes themselves can have a deciding influence on the ecological functioning of aquatic systems. The hypothesis of top-down control (Northcote, 1988) posits that the effects of predation by fishes cascade down the whole trophic chain and can control the state of the entire ecosystem. A number of studies on African fishes helps illustrate this hypothesis (Lévêque, 1995b).

Prey selection

Zooplanktivorous fishes visually select preys or use their gills for passive filtration of zooplankton (Lazzaro, 1987). In both cases, this leads to a decrease in the average size of organisms composing the zooplankton. In other words, large species disappear, to the advantage of smaller species, which modifies the specific composition of planktonic populations.

Thus, following the introduction of the planktivorous Clupeidae species *Limnothrissa miodon* in Lake Kariba in 1967-68, there was a marked reduction in the abundance of large planktonic crustaceans such as *Ceriodaphnia*, *Diaphanosoma*, and *Diaptomus* (Begg, 1974). Similarly, there was a disappearance of Cladocera and large Copepods from Lake Kivu after the introduction of *Limnothrissa* (Dumont, 1986).

Sympatric species can have a very specific impact on planktonic communities. In Lake Chad, for example, *Alestes baremoze* filters zooplankton through its gills, which starts retaining particles sized at least 400 µm. All particles larger than 880 µm are collected; in other words, large planktonic crustaceans are consumed whereas rotifers and nauplii are not (Lauzanne, 1970). Meanwhile, a micro-zooplanktivorous fish such as *Synodontis batensoda* captures prey with a length of at least 80 µm (Gras *et al*., 1981) (figure 17.1). Nauplii and rotifers are progressively retained depending on their size by the gill filter, and all particles larger than 260 µm are captured. The two species thus have a different impact on the zooplankton.

If fish predation leads to the reduction, if not the outright elimination, of large zooplankton, we can imagine that in the absence of predation, these large forms would develop. If so, the abundance of large zooplanktonic species in the open waters of Lake Naivasha would be due to the fact that the zooplanktivorous fish species, all introduced, remain in the coastal area and do not colonize the pelagic environment (Mavuti, 1990).

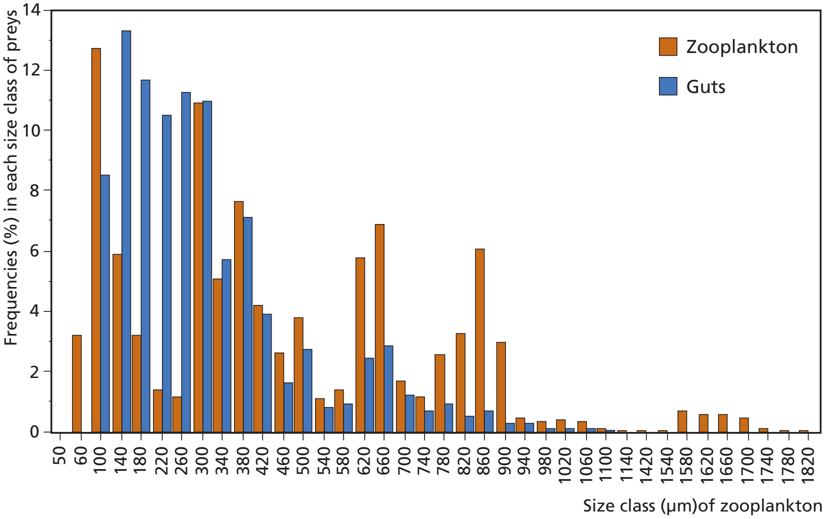


FIGURE 17.1.
Relative frequencies in each size class of preys (rotifers, nauplii, *Macrothrix, Moina, Diaphanosoma,* diaptomids and cyclopoids) in zooplankton and in stomachs of *Synodontis batensoda* in Lake Chad (from Gras *et al.*, 1981).

Similar observations have been made on benthic fauna. When fish predation selectively affects certain prey sizes, it can have a strong influence on the demography of a species. For example, molluscivorous fishes in Lake Chad such as *Synodontis clarias, S. schall* and *Hyperopisus bebe* mainly consume young individuals of benthic molluscs (*Cleopatra, Bellamya, Melania*) (figure 17.2). This strong selective predation explains why, despite nearly continuous reproduction throughout the year, benthic mollusc populations have a truncated size distribution, with a small proportion of juveniles and a large proportion of adults (Lauzanne, 1975 ; Lévêque, 1972).

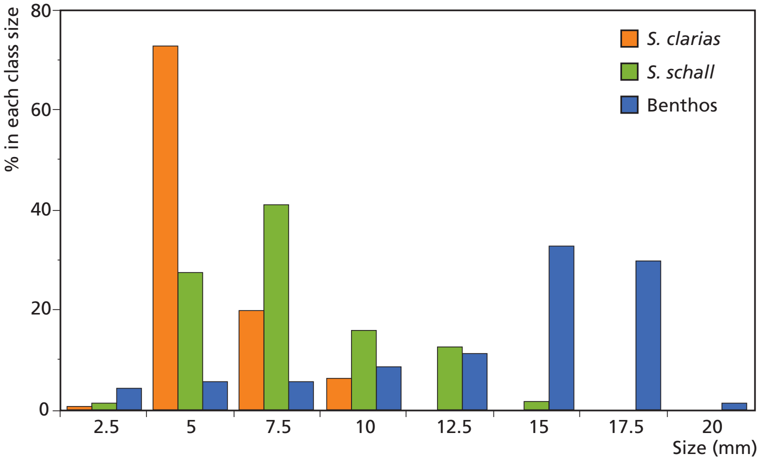


FIGURE 17.2.
Comparison of size distribution of benthic molluscs *Cleopatra bulimoides* in Lake Chad and in the gut of two malacophagous fish species *Synodontis schall* and *S. clarias* (from Lauzanne, 1975).

Changes in feeding habits during ontogeny

Fish size changes considerably during development and this has significant consequences on their ecology and feeding behaviour. Many fishes feed on plankton during their larval stage, then consume larger preys as they grow.

For *Hydrocynus forskalii*, in the Chari, juveniles up to 30 mm long are strict zooplanktivores (Lauzanne, 1975). Between 30 and 45 mm they eat both zooplankton and insects, and beyond 50 mm they are strictly piscivorous.

In Lake Victoria, *Bagrus docmak* juveniles of up to 15-20 cm long consume mainly invertebrates (insect larvae, shrimp). From 20 cm, they show a preference for fishes, and are strictly piscivorous beyond a size of 50 cm (Okach & Dadzie, 1988).

Cascading trophic interactions

The concept of the trophic cascade stems from a principle known to managers of lake fisheries. In a system with, for instance, four trophic levels (piscivorous fish – zooplanktivorous fish – herbivorous zooplankton – phytoplankton), an increase in the biomass of piscivores will have repercussions on all the lower levels of the trophic chain (Carpenter *et al.*, 1985). Increased predation by piscivores leads to a decrease in the biomass of zooplanktivorous fishes, which in turn allows an increase in the biomass of zooplankton that are subjected to less predation pressure. Meanwhile, this larger biomass of herbivorous zooplankton will lead to a direct increase in predation, and subsequent decrease in phytoplankton biomass.

It is difficult to identify trophic cascades in natural systems, but the introduction of new fish species in aquatic systems serve as large-scale experiments that allow for a number of observations. A spectacular example can be seen in the introduction of *Lates* in Lake Victoria. In the 1980s, predation by this piscivore led to the near-disappearance in some areas of the lake of Haplochromines (endemic Cichlidae) from the detritivorous/phytoplanktivorous group, as well as from the zooplanktivorous group, which represented 40% and 16% respectively of the biomass of demersal fishes. They were replaced by the indigenous detritivorous shrimp *Caridina nilotica* and the zooplanktivorous Cyprinidae species *Rastrineobola argentea* (Witte *et al.*, 1992a, b). These last two species are now the main food sources of *Lates* after the disappearance of the Haplochromines. Introduction of *Lates* thus led to a simplification of trophic chains, given that this predator also eats its own juveniles which, in a way, played the same zooplanktivorous role of the Haplochromines of the past (figure 17.3). Another consequence was the reduction in insectivorous Cichlidae and a significant increase in the larvae of aquatic insects whose adults form enormous swarms above the lake at certain periods.[1] This insect population in turn feeds the sand martin *Riparia riparia* which winters in Africa, and whose population massively increased (Sutherland, 1992). Meanwhile, the diet of the pied kingfisher *Ceryle rudis* has changed. It used to feed on Haplochromines but now feeds mainly on the pelagic Cyprinidae *Rastrineobola* (Wanink & Goudswaard, 1994). It seems that a similar change occurred in the diet of the great cormorant *Phalacrocorax carbo*.

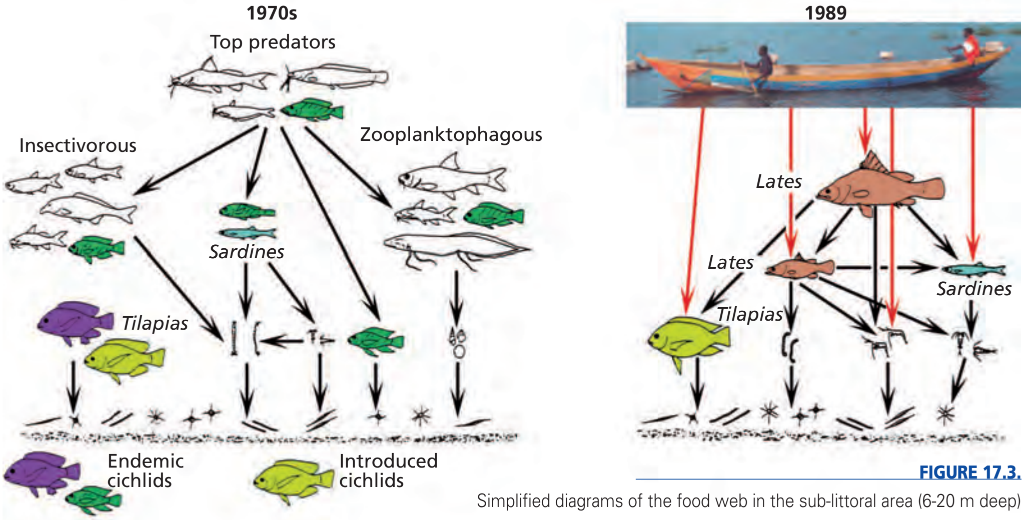


FIGURE 17.3.

Simplified diagrams of the food web in the sub-littoral area (6-20 m deep) of Lake Victoria in the 1970s and 1989, *i.e.*, before and after Nile perch introduction. Only organisms that are an important part of the diet of the main fish species have been mentioned. In the 1970s, *Haplochromis* were dominant in numbers and biomass in all trophic groups except the piscivorous. (modified from Ligvoet & Witte, 1991 and Witte *et al.*, 1992a).

NOTE 1

[1] At certain times, insect densities are so high that local people collect them and use them for food purposes.

We can compare the abovementioned trophic chains to the one suggested over 60 years ago by Worthington & Worthington (1933). An essential difference lies in the disappearance of crocodiles which used to be plentiful in Lake Victoria; their disappearance undoubtedly led to profound changes in the ecosystem's function, changes which were unfortunately not observed. It is worth asking if the introduction of *Lates* would have had the same consequences had the crocodiles not disappeared.

Some authors have suggested that the disappearance of Haplochromines from Lake Victoria could partly explain the increase in phytoplanktonic production, in line with the theory of trophic cascades. But this hypothesis has not been really confirmed, given the simultaneous eutrophication of the lake from urban and agricultural causes.

Another example of a trophic cascade concerns the introduction into Lake Nakuru (Kenya) of *Alcolapia grahami*, a species endemic to Lake Magadi (Kenya), to fight mosquito larvae. In this fish-free saltwater lake, the Cichlidae introduced in the late 1950s rapidly developed, feeding on the abundant populations of the cyanobacterium *Spirulina platensis* (Vareschi, 1978). The most marked effect was the development of a very large population of ichthyophagous birds including the white pelican which, by the late 1970s represented about 85% of ichthyophagous birds (Vareschi, 1979). Ichthyophagous birds began invading Lake Nakuru in 1963, only a few years after the introduction, and it has been estimated that pelicans consume 16 to 20 tonnes of fresh fish daily (Vareschi, 1979; Vareschi & Jacobs, 1984). Avifauna, which was essentially composed of pink flamingos prior to the introduction of Cichlidae, thus markedly diversified, and now counts over 50 aquatic bird species.

The concept of the trophic cascade was behind the idea of biologically manipulating aquatic systems. Indeed, if it is possible to modify trophic chains by controlling the biomass of consumers, one could then modify algal dynamics by selective fishing or stocking programmes. While the idea makes sense for combatting the eutrophication of aquatic systems, for instance, the interactions between trophic levels are much more complex in practice.

Role of species in ecosystem functioning

While the number of species makes it possible to characterize a fish community, each of the species within that community often plays a different role. Ecosystem functioning can thus vary depending on its specific composition. Ecologists have been investigating the functions of species in ecosystems, mainly by attempting to identify those that play a dominant role in trophic chains. But we have also realized that fishes can play an indirect role via the recycling of nutritional elements.

Keystone species

The concept of a keystone species applies to forms whose presence is crucial in maintaining the organization and diversity of ecological communities. Their disappearance can profoundly modify the ecological processes and specific composition of communities. Several broad sets can be distinguished:

- **key predators** are species whose presence strongly limits the presence of other groups. Thus, certain planktivorous fishes limit the abundance or even the presence of large zooplankton in the lakes (see above). Piscivorous predator fishes that play a role in the structuring of ecological systems through trophic cascades are thus often considered key species. Reduction in the biomass of piscivorous predators as an effect of fishing is probably a fairly frequent occurrence if we know that they are not only more vulnerable to gillnets (Bénech & Quensière, 1989), but are also in highest demand for consumption. Fishing thus probably has indirect consequences on the functioning of aquatic ecosystems, but there is generally a lack of precise information for African continental waters. What we know of the consequences of the introduction of *Lates* in Lake Victoria on trophic chains suggests, on the contrary, that the disappearance or reduction of members of this species can also have consequences on the ecology of aquatic environments. Hanna & Schiemer (1993a and b) also believe that the species *Alestes baremoze* and *Brycinus nurse*, which occupy the niche of zooplanktivorous fishes in the Jebel Aulia reservoir (Sudan) are keystone species that, owing to their abundance, exert a strong influence on zooplankton and hence on phythoplankton production in the lake;
- **key preys** represent resources that are critical for the survival of other populations, and are also considered keystone species. This can be illustrated by Lake Nakuru, where large ichthyophagous bird populations currently depend on the existence of *Alcolapia grahami*. The disappearance of this fish (epidemics, change in environmental conditions) would quite simply result in the disappearance of ichthyophagous birds.

Rare species

In systems that have undergone little disruption, ecologists are also interested in the role of rare species. As used in this context, "rare" is a qualifier that involves the abundance and distribution of a species. There are several possible interpretations. A species can have limited distribution but abundant populations; limited distribution with few individuals; or wide distribution with very few members. The diverse causes of rarity include the need to find highly specialized habitats, poor dispersion capacity, trophic position, etc. (Gaston & Lawton, 1990). The species could also have a special behaviour that makes it elusive to sampling techniques, but we could also consider it a relic of the past, one that is dying out.

What role do these rare species play in the functioning of ecological systems, given that in general, common forms fulfil the bulk of functions? It is clear that species could have differentiated according to highly particular local conditions. Their strong endemicity is, in that case, often associated with the occupation of a specific ecological niche. This holds true for many lacustrine species, especially those that are part of so-called species flocks. In this scenario, there was a co-evolution between biological species and ecological function.

How about groups with a wide distribution but few individuals? To some ecologists, these rare species – though they do not currently perform any major ecological functions – could represent a sort of insurance or guarantee of the stability of ecosystems, in the sense that they could replace currently abundant species should there be a significant change in ecological conditions. We know that aquatic ecosystems can change fairly rapidly depending on climatic conditions (see chapter *Variability of climate and hydrological systems*). To illustrate this hypothesis, we can look at how the composition of fish communities in Lake Chad evolved during a drying-out period (Bénech & Quensière, 1989). Species that were rare during the period of high waters (*Polypterus senegalus, Brevimyrus niger, Schilbe intermedius, Siluranodon auritus*, etc.) became dominant during the dry period, when lacustrine conditions shifted to a marshier system (see chapter *Fish communities in shallow lakes*). We thus saw the disappearance of lacustrine species to the advantage of palustrine ones, and this was only possible because the latter were already present, albeit in low quantities. More generally speaking, Nilo-Sudanian fauna inhabiting aquatic systems with high temporal and spatial variability would include numerous species that can replace ones that are currently more abundant should there be a change in the conditions of the habitat.

Recycling of nutrients

Limnologists long worked on the nutrient cycle by taking into account only the dissolved phase and the sediment storage phase. Scientists later realized that living organisms, particularly fish, were likely to play an important role in the storage, transport, and recycling of nutrients (Vanni, 1996). Most studies were conducted in temperate environments. This particular role of fish has hardly been investigated in African aquatic systems. Nonetheless, in Africa as elsewhere, there are fish species that may disturb the sediment layer in their search for food, allowing nutrients to re-enter a solution (bioturbation). Moreover, fishes can transport nutrients from one location to another, for instance when they feed in a littoral environment and excrete phosphorous in a pelagic one, which helps maintain primary production. Finally, detritivorous fishes contribute to recycling nutrients stored in organic debris.

The role of fishes in biogeochemical cycles in general remains a little-explored area of research in Africa. Yet results obtained in temperate systems show that this role can be very important, and should no longer be ignored by limnologists.

Fish biodiversity and responses of ecosystems to perturbations

A fundamental question for ecologists is whether or not all the species present in an environment are truly necessary for the smooth functioning of that same environment. Earlier, we saw that the concept of keystone species implicitly recognizes that some species play a more important role than others. Other hypotheses have been put forth in an attempt to justify the need for maintaining the greatest species diversity possible in ecosystems.

Nonetheless, ecologists are still debating whether the most complex systems – in terms of species composition and networks of interaction – are also the most stable in terms of adapting to perturbations from the outside. In reality, the degree of perturbation is an important aspect for aquatic systems, because extreme situations, such as drying out, lead to the elimination of species. In these conditions, the notion of refuge zones, where populations subsist that are capable of recolonizing the system once conditions are again favourable, is particularly important. This has been observed in Lake Chilwa and Lake Chad where fish populations can find refuge in tributaries when the lake dries up.

Experience from the introduction of *Lates* in Lake Victoria (see chapters *Diet and food webs* and *Species introductions*) tends to show that species diversity and the wide range of trophic specializations that existed in the lake were unable to support the resiliency of the ecological system which, on the whole, was significantly transformed and simplified.

A system's response to perturbations thus presumes, in the case of fishes, the simultaneous execution of multiple strategies: presence of refuge zones, development of biological strategies in order to address different types of stress (droughts, floods, etc.).

Specific richness and fisheries production

Ecological theories exist on the relationships between biological productivity and biodiversity, and there is considerable divergence in the different viewpoints. We might think that fisheries production in lakes with short trophic chains is greater than in systems with long trophic chains, where there is a concomitant significant loss of energy for each change in trophic level. In other words, given equivalent energy input, a lake composed mainly of phytophagous species should be more productive than one containing many ichthyophagous ones. This hypothesis supports an inverse relationship between specific richness and fisheries production, which can be empirically verified in areas with fisheries.

There is little data to help verify the above hypothesis. Nonetheless, it was possible to compare quantitative data on fish production estimated by fishery catches or estimated fish consumption by birds, in four shallow African intertropical lakes with very different fish communities (table 17.I). These data should be used very cautiously given the numerous sources of uncertainty in assessing catches. That said, we can note that fish production in Lake Nakuru, a saltwater lake with a single, introduced cichlid species, is higher than the other lakes. This species, whose production was estimated by the consumption of ichthyophagous birds (Vareschi & Jacobs, 1984), feeds on the cyanobacterium *Spirulina platensis* which has very high production in this type of environment. The short trophic chain can explain such high production in part. Meanwhile, in the other three lakes (Lake Chad, George, and Chilwa), fish production as estimated by fish catches appears to be equivalent despite their very different fish communities and the existence of short (Lake George) or complex (Lake Chad) trophic chains.

It is thus difficult to draw conclusions from these observations, as they do not seem to confirm the hypotheses made earlier but suggest no alternatives. It is possible that the great diversity of fishes observed in Lake Chad allows use of a wider range of resources, contrary to what occurs in Lake George phytoplanktophagous species are strongly dominant whereas the large zooplanktonic biomass. In these conditions, equivalent fish production (as measured) would in fact correspond to different use of trophic resources, only part of which are used by the fishes in Lake George. More precise data is needed to pursue these attempts to interpret information.

Lakes	**Nakuru**	**Chilwa**	**George**	**Chad**
Specific richness	1: *Oreochromis*	3: *Clarias*, *Barbus*, *Oreochromis*	30: including 21 Cichlidae	100: numerous families
Feeding	phytoplanktophagous	detritivorous, zooplanktophagous	biomass: 64% phytoplanctophagous, 20 % piscivores	every type
Fishery production (kg/ha/yr)	625-2436	80-160	100-200	100-150

TABLE 17.I
Fish diversity, feeding groups and fish production estimated by fishery catches (Lakes Chad, Chilwa and George) or by estimation of fish consumption by birds (Lake Nakuru) (from Lévêque, 1995b).

Fish predators

There is sometimes a tendency to act as though man is the only major predator of fish. In reality, in many water bodies, other vertebrates consume large quantities of fish. This is the case for various species of water birds with piscivorous diets, and whose presence in an aquatic environment depends on the availability of food. Their impact on fish communities, long underestimated, is sometimes considerable and can rival fishing, at least in appearance. In fact, piscivorous birds consume many diseased fishes that are incapable of escaping predators, and some scientists believe that they thus contribute to limiting the spread of certain epizootic diseases.

The white pelican (*Pelecanus onocrotalus*) has been found to consume 1.2 kg daily (Din & Eltringham, 1974). Other estimates range from 1.33 kg to 0.77 kg daily for breeding adults and immature birds respectively (Brown & Urban, 1969). These values correspond to fish consumption of approximately 10% of body weight. In areas with high concentrations of pelicans, such as Lake Nakuru (Vareschi & Jacobs, 1984), annual consumption can reach high values of between 650 and 2,400 kg (fresh weight) ha^{-1} yr^{-1}.

Hustler (1991) studied the consumption of the cormorant *Phalacrocorax africanus* and the darter *Anhinga melanogaster,* the most important piscivorous species on Lake Kariba. Daily, they respectively consume 20% and 11 % of their weight, the equivalent of 12% to 16% of artisanal coastal fishing. Their diet is mainly composed of small-sized fishes. The crocodile *Crocodylus niloticus* population, meanwhile, consumes 225 tonnes of fish a year, that is, 10% of the yield of artisanal coastal fishing (Games, 1990).

Fish communities in river systems and associated biotopes

CHRISTIAN LÉVÊQUE

DIDIER PAUGY

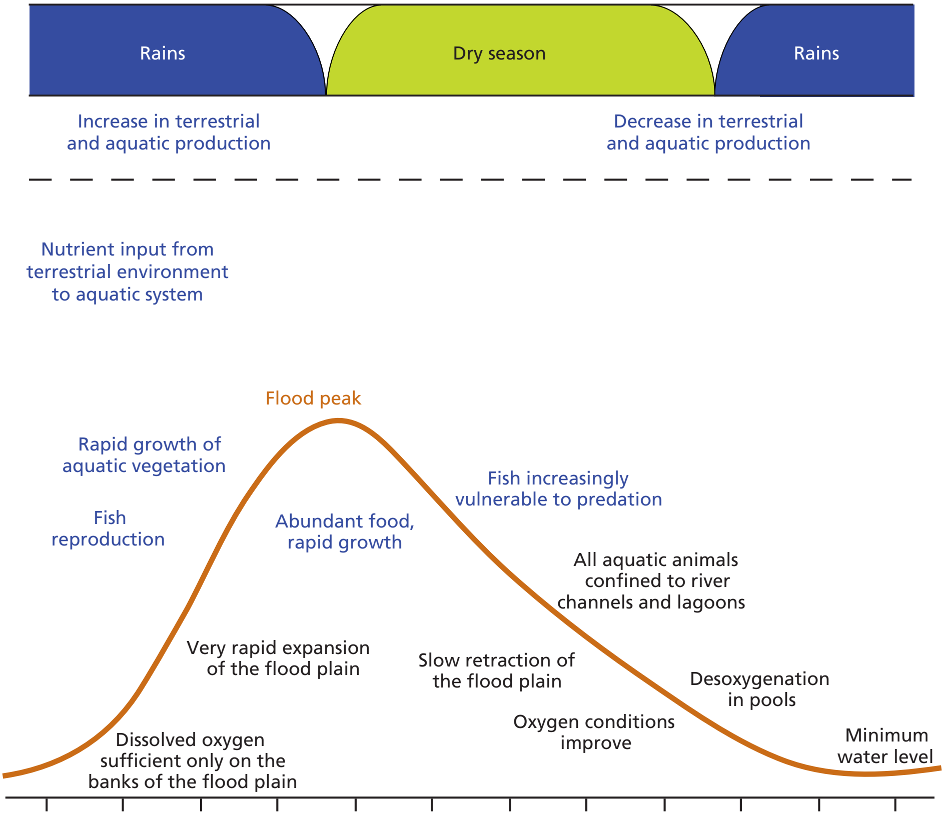
Except for the many lakes of East Africa, most African aquatic environments are formed by rivers whose total length is estimated at 13 million km (Welcomme & Mérona, 1988). Nevertheless, the communities, in these species-rich lotic environments, are far less well-known than those of lakes and reservoirs. Sampling difficulties in fluvial environments, particularly during flood periods, are one of the main reasons for the relative scarcity of information about riverine communities.

Dynamics of river systems and consequences for fish assemblages

Water flow varies according to seasons, as well as the morphology of the fluvial landscapes (see chapter *Variability of climate and hydrological systems*). The periodic shifts between floods and low water flows create a large diversity of habitats, of varying durations, that follow each other over time. For tropical rivers, changes in water level associated with the seasonal flooding of neighbouring floodplains are the main factors driving hydrosystem functioning (Welcomme, 1979; Lowe-McConnell, 1985; 1988).

In small watercourses, floods are often short-lived and unpredictable as they depend on the characteristics of local precipitation across the drainage basin. This is also the case for many rivers bordering the Sahara. During the dry season, these rivers dry up or are reduced to a series of residual pools. They are only inhabited by fishes that are able to adapt to extreme conditions, either through diapause or the ability to survive in environments that are sometimes relatively oxygen-poor.

Meanwhile, in large river systems, which are often associated with floodplains, floods are more regular and longer-lasting. Here, variations in the river's flow regulate the intensity and duration of exchanges between the different parts of the river-floodplain interactive system. When the level rises, the water enters part of the floodplain, creating connections and allowing exchanges with the minor river bed. When the level falls, some parts of the floodplain are isolated from the riverbed.



Fish movements	Up channels	Dispersion on flood plain	Back to river	Restricted to dry season refuges
Fishing activities	Anadromous migrators	Difficult to capture fish	Intensive fishing of migrators	Fishing in ponds and riverbed
Fish biomass	Recruitment of juveniles of most species	Rapid growth, important increase of biomass	Decrease of biomass (fishing and predation)	Restricted populations

FIGURE 18.1.
The seasonal cycle of events in a floodplain river (from Lowe-McConnell, 1985).

The river system thus functions by "flood pulses" (Junk *et al.*, 1989) whose rhythm is regulated by oscillations in the hydrological system, and whose impact depends on the degree, duration, frequency, and/or regularity of floods. Depending on the period at which high or low water levels occur, they exert a more or less strong influence on the life cycles of species and the productivity of hydrosystems. In particular, the period during which connections exist between the river and its annexes has significant consequences on the system's function and the biology of species. In relatively large rivers, a predictable flood of long duration favours development in organisms that survive by adaptation and opportunistic strategies that allow them to make efficient use of the transition zone between the aquatic and terrestrial environments, rather than depending solely on the resources of permanent aquatic environments. Some organisms, such as fishes, actually leave the main watercourse during the flood in order to use the habitats and resources available in the floodplain, and return to the main watercourse when the water level drops. If the flood is exceptionally too short, some organisms cannot complete their life cycle.

The seasonal cycle of events in a floodplain were summarized by Lowe-McConnell (1985) (figure 18.1). During the flood, floodplain waters are enriched in nutrients from the decomposition of organic matter and vegetation, as well as animal droppings (cattle, wild animals) grazing in the plains. This leads to the rapid development of bacteria, algae, zooplankton, and more generally speaking a rich fauna of aquatic invertebrates. At the same time, aquatic vegetation grows rapidly. Once the flood reaches its peak, the water begins to fall and leaves the floodplains through a series of channels to return to the river's main watercourse. Animals also leave the floodplains, but some are trapped in pools that are cut off, most of which will dry up before the next flood. Some of these pools remain throughout the year and serve as a refuge for aquatic fauna.

River zonation and fish assemblages

The gradient of physical conditions found throughout the watercourse, from upstream to downstream, induces a response from biological communities, with a progressive change according to the capacities of species to adapt to environmental constraints and available food resources. This longitudinal zonation is accompanied by an increase in species richness.

In temperate environments, there have been a number of attempts to establish the general principles of fish distribution throughout a longitudinal gradient, and several ecological zonations for watercourses have been put forth. One of the most well-known in Europe is the one proposed by Huet (1949), sometimes called the "slopes rule". It is based on the principle that for a given biogeographic territory, running waters of the same dimensions (width and depth) and with comparable slopes will have similar biological characteristics. By using simple parameters such as slope and watercourse width, we can thus predict the nature of dominant fish populations.

Little work has been done for Africa, and the initial attempts at characterization are based on the classification by Illies & Botosaneanu (1963) who recognize three main zones in a watercourse: the crenon (spring zone), the rhithron (middle course) with turbulent, oxygenated waters, and the potamon (lower course) which is the downstream section and corresponds to slow and turbid watercourses in the plains. This basic classification was applied to fish communities of the Luanga River, a higher-altitude river of the Congo basin (Malaisse, 1976).

A more elaborate form was applied to other West African rivers such as the Bandama (Côte d'Ivoire) which hosts about 90 fish species (figure 18.2). Its course is a succession of rapid areas (riffles) and calm areas (pools) wherein four main zones can be distinguished (Mérona, 1981):

- a short spring zone corresponding to narrow brooks, sometimes temporary, populated essentially by small species (*Barbus*, Cyprinodontiformes, small Alestidae);
- an upper course characterized by the presence of *Brycinus longipinnis*, *Hepsetus odoe* and *Schilbe intermedius*;
- a very extensive middle course with a relatively homogenous community, characterized by the presence of *Alestes baremoze*, *Brycinus nurse* and *B. macrolepidotus* in the deep biotopes and *Labeo parvus* in the riffles;
- downstream, the lower course, under marine influence, where estuary species can be found. This zone again contains *Brycinus longipinnis* and *Hepsetus odoe*.

The Ogun River in Nigeria (Sydenham, 1977) also has a very extensive middle course with a homogenous fish community. This situation is probably characteristic of rivers having a gradual slope over most of its course.

In the Mono (Togo), Paugy & Bénech (1989) showed that species diversity increased rapidly as one moves away from the source and then reached an asymptote. While their results for zonation are quite similar to the ones obtained for the Bandama, these authors have nonetheless noted that *Brycinus longipinnis* and *Hepsetus odoe* are frequently captured throughout the Mono, even though these species populate essentially the upper and lower courses of the Bandama. The much smaller size of the Mono drainage basin (22,000 km^2 versus 97,000 km^2 for the Bandama), probably accounts for the absence of a middle course similar to the Bandama's, especially given there are fewer species there (66 versus 90 for the Bandama), and that species such as *Hydrocynus forskalii,* which are characteristic of the middle course of the Bandama, are rarely found in the Mono basin.

The relationship between river size and species richness may be explained by the existence of a greater diversity of habitats when moving downstream. In a study of the longitudinal zonation of fishes in the Niandan River (upper basin of the Niger in Guinea), Hugueny (1990) highlighted a fairly strong relationship between species richness and the river's maximum depth, that is, a variable linked to river size. This relationship appears to be tied to the fact that shallow environments can only be colonized by small-sized species or individuals, and that there is a lower limit below which a fish, given its size, can no longer travel efficiently. Communities do not become complex in a random manner from upstream to downstream, but essentially by the addition of species, with few disappearances, at least for the portion of the Niandan River that was studied. In species-poor communities, there is a bias towards small species that feed near the surface, whereas more species-rich communities contain more large species that feed at the bottom.

The river zonation can be modified according to the river's shape. Balon & Stewart (1983) have described an unusual gradient in the Luongo River, a tributary of the Luapula River that flows into Lake Mweru. The upper and lower courses have steep slopes with riffles and falls, and are separated by a gradually-sloping middle course with a floodplain. The fish communities of the upper and lower courses contain species adapted to running waters, but the species composition is different in each one.

FIGURE 18.2.
Schematic longitudinal zonation of fishes in the Bandama basin (from Mérona, 1981).

Zonation	Habitat	Characteristic species
Spring zone	Brooks or pools	small *Barbus* small Alestidae Cyprinodontiformes *Neolebias* sp.
Upper course	Small pools	*Brycinus longipinis* *Hepsetus odoe* *Schilbe intermedius* *Synodontis schall*
Middle course	Alternating pools and riffles	**pools** *Alestes baremoze* *Brycinus nurse* *Brycinus macrolepidotus* *Hydrocynus forskalii* *Schilbe mandibularis* **riffles** *Labeo parvus* *Mastacembelus nigromarginatus* *Nannocharax* sp. *Brycinus imberi* *Tilapia* spp. *s. lat.*
Lower course	Large pools, salinity influence	**continental species** *Brycinus longipinnis* *Hepsetus odoe* *Schilbe intermedius* *Synodontis schall* **estuarine species** *Elops lacerta* *Awaous lateristriga*

In their upper course and occasionally a portion of their middle course, tropical rivers are seasonal. They flow during the rainy season and are interrupted part of the year during which the course dries up or is reduced to a string of residual pools. Most of the observations for fish communities are carried out during a period of water outflow, when sampling conditions are favourable, whereas it is much more difficult to carry out sampling during the flood, when some species carry out longitudinal migrations that allow them to recolonize and sometimes even reproduce in upper courses.

Changes in the structure of communities in the upper course of the Ogun River, which is seasonal, have been studied by Adebisi (1988). Piscivorous fishes (*Hydrocynus forskalii, Hepsetus odoe, Bagrus docmak, Mormyrops anguilloides*) are particularly abundant in captures using gillnets at the start and end of the flood. Some of them (*Hydrocynus* spp., *Mormyrops* spp.) probably migrate to the upper reaches to reproduce, then go down to lower reaches when the water level falls. Towards the end of the flood, omnivorous species (*Schilbe intermedius, Clarias gariepinus, Heterobranchus longifilis, Synodontis schall*) become preponderant until fragmentation into residual pools begins. In these pools, fish communities are essentially dominated by herbivorous species (*Brycinus macrolepidotus, B. nurse, Coptodon zillii*, but also *Labeo senegalensis, Chromidotilapia guntheri, Sarotherodon galilaeus*) and insectivores (Mormyridae, *Chrysichthys auratus*).

Similar observations were also made in the residual pools of the upper course of the Baoulé River (upper basin of the Senegal, in Mali) (Paugy, 1994). At the end of the period of low water, the community composition and structure of the largest residual pools, rare in number (two to three over the 500 km of the Baoulé), are essentially identical to what is observed in the major bed. They thus most certainly serve as refugia that allow species to recolonize the environment when the water rises. For smaller surface pools, there is a correlation between species richness and composition and the available water surface (figure 18.3). For these species, we can see the complete disappearance of *Labeo* spp., plentiful in normal conditions, still relatively numerous when the amount of water is sufficient and rocks are scattered over the biotope, and totally absent when water is scarce and the substrate is just a mixture of sand and mud. Another significant phenomenon is the decrease and disappearance of almost all the different Mormyridae species. Most of the members of this group are known to be sensitive to decreases in dissolved oxygen concentrations (Bénech & Lek, 1981). This is quite likely to be one of the possible causes for their disappearance.

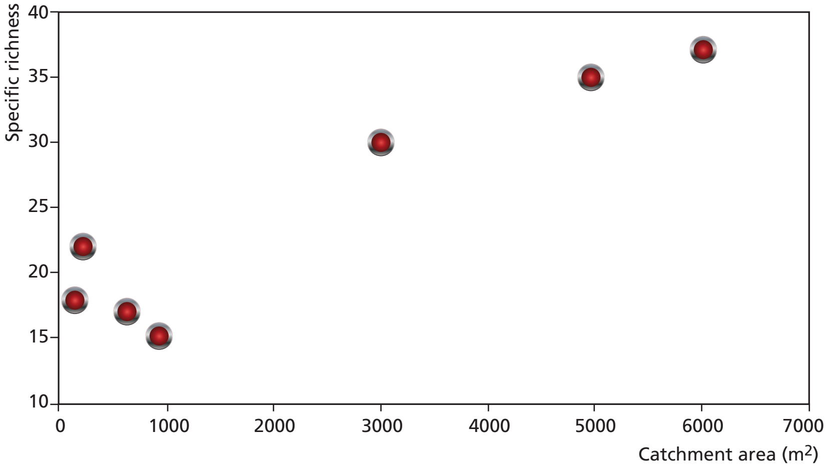


FIGURE 18.3.
Relationship between the ponds area and the specific richness (Baoulé River, upper Senegal basin, Mali) (from Paugy, 1994).

In the residual pools of the floodplain of the Sokoto River, a tributary of the Niger in Nigeria, species composition remains relatively similar from one year to another (Chapman & Chapman, 1993). However, the observations were only made for a short period and cannot be generalized.

The floodplains

In river systems with floodplains, there is a large variety of habitats ranging from small temporary pools to permanent swamps and lakes, and whose distribution and dynamics vary according to hydrological season (Welcomme, 1979; Welcomme & Mérona, 1988). The role of floodplains in the functioning of river systems has been studied in Africa, where these environments are well-developed in nearly all basins of the savannah zone: the Senegal, Niger, Volta, Ouémé, Chari and Logone, Nile rivers, etc. Floodplains are both food sources and breeding areas for fishes. They serve as a refuge for fry that find shelter from predators there.

Based on his observations in the Ouémé River during the dry season, Welcomme (1979, 1985) proposed a general outline for the distribution of fishes in floodplains. The distinction between "white fish" and "black fish" was an attempt to distinguish between two sets that differed in terms of ecology and behaviour. A third set, the "grey fish", was also suggested (table 18.I) (Regier *et al.*, 1989).

TABLE 18.I

Black-grey-white: three ecological assemblages of riverine fish and some African taxa and characteristic features (from Regier *et al.*, 1989).

	White fish	**Grey fish**	**Black fish**
Families	Alestidae Cyprinidae Mormyridae (*Mormyrops*)	Cichlidae Citharinidae Cyprinidae (*Labeo*) Distichodontidae Mochokidae Mormyridae (*Gnathonemus*) Schilbeidae	Anabantidae Channidae Clariidae Gymnarchidae Mormyridae (*Pollimyrus*) Notopteridae
Respiratory organs	gills	gills with some physiological adaptations to low oxygenation	gills and air-breathing organs with physiological adaptations to low oxygenation
Respiratory tolerance	highly oxygenated waters	medium to low oxygenation	low oxygenation - anoxic
Muscle fibre type	red	red / white	white
Migratory behaviour	long distance longitudinal	short distance longitudinal, often long lateral migrations	local movements
Body form	round, fusiform	laterally compressed, spiny, often heavily scaled	aterally compressed or soft; lelongated and flabby; scales reduced or absent
Colour	silvery or light	dark, frequently ornamented or coloured	very dark, often black
Reproductive guild	non-guarders; open substrate spawners; lithophils; pelagophils	guarders; nests spawners; open substrate spawners; phytophils	guarders; internal or external bearers; complex nests builders
Dry season habitat	main channel; lake	backwaters or main channel fringes	floodplain waterbodies
Wet season habitat	main channel or floodplains	floodplains	floodplains or marshy fringes

- The first group, or "*white fish*", depends heavily on the main channel for reproduction, even though many species enter the floodplains to breed and feed. Long-distance migrations may occur towards areas found upstream to reproduce just before the start of the flood.
- The second group, or "*black fish*", lives in floodplains or their marshy fringes. Their movements are limited to lateral migrations, and species have adapted to resist difficult environmental conditions, particularly water oxygenation. These species generally have interval spawning spread over time, with a breeding season that begins prior to the flood and continues throughout it.

- The third group or "*grey fish*" lives in marshy zones and the floodplain's lake borders, as well as the main channel during the dry season. They carry out lateral migrations from the main channel to the floodplain during the flood to breed and find food. The species of this group have a more flexible behaviour pattern than the previous ones, and adapt rapidly to changes in hydrological conditions.

The flood areas of the Sudd in Sudan occupy some 30,000 km^2 and include a permanent complex of rivers, lakes, *Papyrus* and *Typha* swamps, as well as floodplains in periods when the water level rises. Four main types of habitats, corresponding to characteristic fish communities, have been identified by Bailey (1988). The spatial and temporal distribution of species depends on their ecological thresholds and their requirements in terms of food, shelter, breeding areas, etc:

- river courses where common species are Alestidae (*Hydrocynus forskalii*, *Alestes dentex*, *Brycinus nurse*, *B. macrolepidotus*), Bagridae (*Bagrus bajad*), Claroteidae (*Auchenoglanis biscutatus*), Mochokidae (*Synodontis schall*, *S. frontosus*), Schilbeidae (*Schilbe intermedius*), Nile perch (*Lates niloticus*), Cichlidae (*Oreochromis niloticus*);

- lakes and drainage channels that offer the greatest diversity to fishes (Hickley & Bailey, 1986). The most abundant species, in descending order, are: *Alestes dentex*, *Hydrocynus forskalii*, *Synodontis frontosus*, *S. schall*, *Schilbe mystus*, *Auchenoglanis biscutatus*, *Clarotes laticeps*, *Oreochromis niloticus*, *Labeo niloticus*, *Distichodus* spp., *Citharinus* spp., *Mormyrus cashive*, *Heterotis niloticus*, *Lates niloticus*;

- *Cyperus papyrus* and *Typha domingensis* swamps are rather inhospitable habitats owing to poor water oxygenation. Many fishes with aerial or accessory respiration are the most common inhabitants, that is, only 23 species of the 62 identified in the Sudd: *Protopterus aethiopicus*, *Polypterus senegalus*, *Heterotis niloticus*, *Gymnarchus niloticus*, *Brevimyrus niger*, *Clarias gariepinus*, *Ctenopoma petherici*, *C. muriei*, *Hemichromis fasciatus* and *Parachanna obscura*;

- in floodplains that are *Oryza longistaminata* prairies, 33 fish species have been collected: Cyprinodontiformes, *Ctenopoma muriei*, *Clarias gariepinus*, *Oreochromis niloticus*, *Nannaethiops unitaeniatus*, *Barbus stigmatopygus*, *Polypterus senegalus*, *Parachanna obscura*, small Mormyridae (*Brevimyrus niger*).

Fishes perform "lateral" migrations between the minor bed and the floodplain, then back in the opposite direction. Bénech *et al.* (1994) have studied the precise conduct of migrations between the Niger River and a floodplain in relation to seasonal hydrology. They distinguish three main types of migratory patterns:

- a group of species that follows water movements, with a preponderance of entries as the pool fills, and a preponderance of exits as the water level falls. This group includes juveniles of *Lates niloticus*, juveniles and adults of *Schilbe intermedius*, *Brycinus leuciscus*, as well as small-sized species: *Barbus* spp., *Petrocephalus bovei*, *Siluranodon auritus*, etc. For *B. leuciscus*, lateral migrations appear to be very complex, influenced by both hydrology and the lunar cycle;

- a group of species characterized by late entry and early exit, thus making a short stay in the floodplain. This group includes small-sized species (*Pellonula, Physailia, Micralestes, Chelaethiops*) as well as juveniles of *Alestes baremoze* and *Hydrocynus forskalii*;
- a group of species that is mainly present as the water level falls, and mostly leaving the floodplain, composed mainly of large-sized forms: *Hyperopisus bebe*, *Auchenoglanis occidentalis*, *Mormyrus rume*, *Clarias anguillaris*, *Citharinus citharus*, *Distichodus brevipinnis*, *Malapterurus electricus*, etc.

Fish assemblages in the riffles

Fishes that live in the riffles are adapted to turbulent conditions (table 18.II). Three groups can be distinguished (Welcomme & Mérona, 1988):

- those clinging to the surface of the bottom or to vegetation. They are generally elongated and flat so that the current pushes them against the bottom. Some species have also developed special adaptations such as ventral fins or suckers for mouths. The Amphiliidae (*Amphilius* spp., *Phracura* spp., *Doumea* spp.), some Mochokidae such as *Chiloglanis* and *Synodontis* spp., Cyprinidae belonging to the genera *Labeo* and *Garra*, are in this category;

TABLE 18.II

Species composition of fish assemblage sampled with electric fishing gear, in middle course riffles of different coastal river systems from Côte d'Ivoire.

	Léraba	Bandama	N'Zi	Sassandra
Mormyridae				
Petrocephalus bovei		●	●	
Alestidae				
Brycinus imberi	●	●	●	●
Brycinus nurse	●	●	●	●
Micralestes occidentalis	●			
Distichodontidae				
Nannocharax occidentalis	●	●		●
Cyprinidae				
Barbus bynni waldroni		●	●	●
Barbus macinensis	●			
Barbus macrops	●			●
Barbus sublineatus	●		●	●
Barbus wurtzi		●	●	●
Labeo parvus	●	●	●	●
Raiamas senegalensis	●	●	●	●
Amphiliidae				
Amphilius atesuensis	●	●	●	●
Phractura intermedia	●			
Mochokidae				
Chiloglanis occidentalis				●
Synodontis bastiani	●	●	●	
Synodontis comoensis	●			
Cichlidae				
Hemichromis spp.	●	●	●	
Tilapia spp.	●	●	●	
Mastacembelidae				
Mastacembelus nigromarginatus	●	●	●	●

- those that find shelter in the openings and holes between rocks. These species are generally elongated and small, and this is the case for the different species of Mastacembelidae, some Clariidae (*Gymnallabes, Clariallabes*), the Polypteridae *calabaricus*, some Mormyridae belonging to the genera *Mormyrops*, *Brienomyrus* or *Brevimyrus* and Cichlidae such as *Leptotilapia irvinei* or *Gobiocichla* sp.;
- those that can swim well enough to resist the current up to certain resistance thresholds. They include for instance *Barbus altianalis*, various species of Bagridae (*Bagrus*), Claroteidae (*Chrysichthys*), Alestidae (*Alestes, Brycinus, Hydrocynus*) and Cichlidae.

Biomass estimates

It is difficult to estimate biomass in watercourses, which explains why data are so scarce and often disparate. Sampling using ichthyotoxics were the most often carried out.

In West Africa, values range from 50 kg ha^{-1} (Daget *et al.*, 1973) at low water periods in the Bandama River (Côte d'Ivoire) upstream of the current Kossou dam, before its closure, to 5,260 kg ha^{-1} in the fluvial annexes of the Chari (Loubens, 1969). This latter value is probably exceptional given that the average for several measurements taken in the Chari is 1,430 kg ha^{-1}. Similar values have been observed in the Logone (1,210 kg ha^{-1}), but biomasses of around 100-500 kg ha^{-1} are more common.

The average of biomass measurements in the Maraoué is 100 kg ha^{-1} (Daget & Iltis, 1965), and that of the N'Zi is 102 kg ha^{-1} (Lévêque *et al.*, 1983). These two rivers are tributaries of the Bandama, in which average values of 125 kg ha^{-1} and 177 kg ha^{-1} have been obtained during the flood upstream from the current Kossou dam. In periods of low water levels, and downstream from the dam, average values of 305 kg ha^{-1} have been observed in river annexes (Daget *et al.*, 1973). These values are rather low compared with those obtained in the Kafue Flats which range from 339 in low water periods to 435 kg ha^{-1} during the flood (Lagler *et al.*, 1971).

During dam constructions (such as for the Kainji, on the Niger), or mass poisonings of large water surfaces, it has been possible to carry out relatively exhaustive sampling that allowed estimates of the contribution of different species to biomass. Some results (tables 18.III and 18.IV) show that the most of this biomass is generally represented by a small number of species. This is particularly true for the Kafue where only four Cichlidae species represent 75% of the biomass. In the Chari, the most abundant species were *Oreochromis niloticus*, *Sarotherodon galilaeus, Lates niloticus*, *Heterotis niloticus*, *Synodontis nigrita* and *Polypterus endlicheri*.

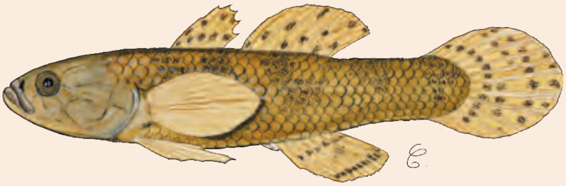
TABLE 18.III
The relative abundance of fish species caught in the 18 ha coffer-dammed lake in the Niger River at Kainji, 1966. Some specimens of *Polypterus, Heterotis, Gymnarchus, Malapterurus, Lates, Oreochromis, Tilapia* and *Tetraodon*, were also collected (from Motwani & Kanwai, 1970).

	Number of species	Number of individuals	% of individuals	Total weight (kg)	% weight
Mormyridae	**19**	**1198**	**20.7**	**219**	**19.5**
Hyperopisus bebe	1	166		49	
Mormyrus	3	180		47	
Mormyrops	3	122		55	
Campylomormyrus	1	366		38	
Marcusenius	4	292		27	
Hippopotamyrus	3	56		3	
others	4				
Alestidae	**8**	**2103**	**36.3**	**136**	**12.1**
Hydrocynus	2	28		11	
Alestes	2	1447		100	
Brycinus	4	628		25	
Citharinidae	**3**	**288**	**5**	**94**	**8.8**
Distichodontidae	**2**	**66**	**1.1**	**118**	**11**
Cyprinidae	**5+**	**192**	**3.3**	**48**	**4.3**
Labeo	2	183		47	
Barbus	2+	8			
Raiamas	1	1			
Bagridae	**2**	**187**	**3.2**	**157**	**8.2**
Bagrus	2	187		157	
Claroteidae	**5**	**235**	**4**	**47**	**10**
Chrysichthys + Clarotes	5	235		47	
Schilbeidae	**3**	**463**	**8**	**40**	**3.6**
Schilbe	3	448		40	
Mochokidae	**18**	**1064**	**18**	**209**	**18.7**
Total catch	**65**	**5796**		**1068**	

TABLE 18.IV
Relative abundance by weight of 19 species of commercial fish at high water (June-July) and at low water (August-September) in the Kafue Flats in 1970 (from Lagler *et al.*, 1971).

Species	**High water biomass, % total**	**Low water biomass, % total**
Oreochromis andersonii	26.6	31.7
Oreochromis macrochir	18.4	19.1
Coptodon zillii	17.4	5.0
Tilapia sparrmanii	13.0	2.1
Serranochromis angusticeps	3.0	2.3
Serranochromis macrocephalus	0.3	0.2
Serranochromis robustus	0.2	0.3
Serranochromis thumbergi	0.6	0.1
Sargochromis carlottae	3.2	0.8
Sargochromis codringtoni	0.2	
Sargochromis giardi	0.1	1.5
Hepsetus odoe	4.0	6.0
Marcusenius macrolepidotus	0.7	2.2
Schilbe intermedius	1.8	15.6
Clarias gariepinus	5.6	8.0
Clarias ngamensis	3.5	4.4
Synodontis macrostigma	0.4	0.4
Labeo molybdinus	0.6	0.3
Total ichthyomass of commercial species	84%	84%
Total ichthyomass of non-commercial species	16%	16%
Mean ichthyomass	435 kg ha^{-1}	339 kg ha^{-1}

Fish communities in East African rift lakes



Jos Snoeks

Christian Lévêque

Yves Fermon

Fabrice Duponchelle

The Great Lakes of East Africa are unique systems in various ways. The region has been subject to much tectonic activity. Hence, some of the deepest lakes of the world can be found in the area, most of them stretched in a north-south direction in the western branch of the Rift Valley (figure 19.1). The elongated and deep lakes Tanganyika and Malawi, together with the saucer-shaped, relatively shallow Lake Victoria form the three largest freshwater bodies in the region. All three figure amongst the top ten largest lakes in the world in terms of surface and volume. Other large lakes in the region include Kivu, Edward (with George), Albert, Turkana, Mweru and Rukwa.

However, what really makes these lakes unique is their biodiversity and especially their fishes. Nowhere else in the world can one find a larger number of fish species than in these lakes. Not only is the sheer number of species exceptional, but most of these fishes are also endemic to a certain lake. Remarkably, the largest compound of the fish fauna, over 95% for the three large lakes, belongs to only one family, the Cichlidae. These cichlids represent the largest radiation of vertebrates in the world. Hence these lakes are considered natural laboratories for the study of evolution and speciation.

While the fishes in these lakes represent an unparalleled biodiversity treasure, one should not forget that they are of prime importance as the largest source of animal protein for the riparian human population (Snoeks, 2001). It is clear that the exploitation and the conservation of these fishes give rise to conflicts. Increasing human activities in the region undeniably have a direct (fisheries) or indirect impact on the lake's fish communities. This is likely to increase and the sustainable management of the ecosystems of the large African lakes will become a huge challenge. In this respect, one should also not forget that most of these lakes have relatively long to very long flushing times, which makes them highly vulnerable to pollution.

Fish communities in East African rift lakes

JOS SNOEKS, CHRISTIAN LÉVÊQUE, YVES FERMON & FABRICE DUPONCHELLE

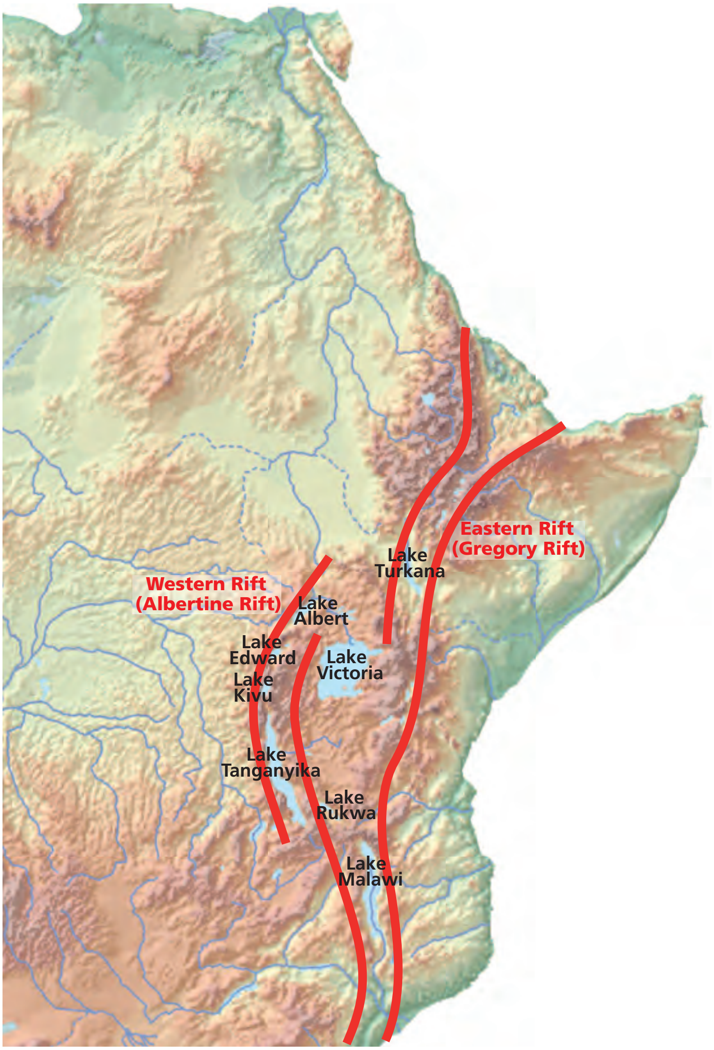


FIGURE 19.1.
Major lakes of the East African Rift system.

What determines the overall structure of the fish communities in these lakes is principally depth and substrate type. Depth distribution of fishes is limited by the oxycline. Therefore in the deeper lakes (Tanganyika, Malawi, Kivu), fish only occupy a small part of the lake's volume, *i.e.*, the upper oxygenated layer, the depth of which differs from lake to lake. In lakes Tanganyika and Malawi, the fish composition clearly changes with depth and both lakes harbour a typical deep-water benthic fish fauna. Pelagic species can effect daily vertical migrations in search of food.

Substrate type determines largely the horizontal component of the differences in fish community structure. Indeed, in most lakes, fish communities differ largely between muddy, sandy, rocky and intermediary habitats.

One of the most, if not the most important extrinsic factor in the evolutionary history of the endemic cichlids, is lake level change. During their history the lakes faced many periods of aridity resulting in a dramatic decrease in lake level volume, followed by an increase during wetter periods in which large stretches of new shorelines became available to invade. Small-sized lake level changes resulting in a split or admixis of populations could act as species pumps (Rossiter, 1995).

Many cichlid species are intrinsically linked to a particular habitat and are called stenotopes; others occur in various habitats and are eurytopes. Fish preferring rocky habitats are called lithophylic; those typical for sandy habitats psammophylic.

Other important aspects determining the fish community structure in the great lakes are migrations, either for reproduction or for food.

Communities in Lake Tanganyika.

Lake Tanganyika is the third largest lake in the world in volume, and the second in length and depth (Cohen *et al.*, 1993b). While its age is often set at between 9-12 million years (Cohen *et al.*, 1993b), other sources place the origin of the lake in its present form at 5.5 million years ago (Weiss *et al.*, 2015), still making it the oldest of the East African rift valley lakes.

Lake Tanganyika harbours the most phylogenetically diverse and ancient flock of endemic cichlids and has been regarded as an evolutionary reservoir for the endemic species flocks in the other lakes in the region (Nishida, 1991). It currently harbours some 219 cichlid species (Konings, 2015) and several tens are still to be described. It is not the species-richest lake in the region, but certainly the most diverse in terms of phylogeny, ethology, morphology, etc.

Lake Tanganyika is also special in having endemic assemblages of non-cichlid taxa, including radiations of *Synodontis*, *Mastacembelus*, Claroteinae and *Luciolates*. There are several endemic species in other groups as well. This non-cichlid endemism is linked to the ancient origin of the lake. The number of non-cichlid species for the Tanganyika basin exceeds 150, and new species are still being discovered (Banyankimbona *et al.*, 2012).

Much of our current knowledge on Lake Tanganyika fish communities is based upon the results of the 18-month Belgian Expedition in 1946-1947, which were written down by Max Poll in two classical monumental books on the non-cichlids and the cichlids (Poll, 1953 and 1956). Much of what we know since then about the cichlid fish communities is based on the observations of two pioneering aquarists and naturalists who summarised their knowledge in various books (e.g. Brichard, 1978 and 1989; Konings, 1988 and 2015). For many years, Japanese scientists have studied the ecology and ethology of the Tanganyika cichlids (summarised in Kawanabe *et al.*, 1997). Observations on the various ecosystems and fisheries were discussed in Coulter's classic book (1991).

In comparison to the other East African lakes, the fauna of Lake Tanganyika is unique in several aspects:

- the existence of various endemic radiations in non-cichlids (see above);
- the existence of a pelagic community comprised of two Clupeid endemics and their predators;
- the existence of a radiation of substrate-spawing cichlids (other than tilapias), the Lamprologini;
- the absence of *Chaoborus* larvae (lake flies, also absent in lakes Kivu and Turkana), which in the other lakes form an important part of the food chain.

Fish in Lake Tanganyika belong to four large communities: those inhabiting the rivers, the littoral and sublittoral, the benthic and bathypelagic, and the pelagic zone.

It is interesting to see that the occupation of the main habitats is somehow linked to the cichlids' phylogeny (Meyer *et al.*, 2015). Basal tribes such as the Bathybatini, Trematocarini, together with Cyprichromini, Cyphotilapiini and Limnochromini generally frequent the open-water column or deep water habitats, while the species-rich tribes of the so-called H-lineage (Eretmodini, Ectodini and Haplochromini), together with the major part of the Lamprologini occupy the coastal areas.

The pelagic community

The pelagic community is mainly composed of six endemic non-cichlid species. Two clupeid species, *Stolothrissa tanganicae* and *Limnothrissa miodon*, live in large schools feeding on phyto- and zooplankton (figure 19.2). Though belonging to different genera, they are sister taxa (Wilson *et al.*, 2008). They constitute a key element of the pelagic food chain as important food sources for piscivorous fish, notable the four *Lates* predators of the endemic subgenus *Luciolates*. These predator-prey relationships are a crucial element in the sustainability of the industrialized fisheries in the basin.

These clupeids, in their juvenile stages, have a more littoral lifestyle. As adults, *S. tanganicae* is the more specialized to a pelagic life of the two (Coulter, 1991). The larger-sized *Limnothrissa miodon* has a more generalized diet and preys upon *S. tanganicae*. Also young individuals of three of the *Lates* predators, *Lates mariae*, *L. angustifrons* and *L. microlepis*, live merely in littoral, weedy habitats. The former two have a mixed benthic-pelagic life, preying upon the sardines during daytime, while the latter remains in the pelagic zone as an adult. *Lates stappersii*, in contrast, spends its entire life in the pelagic habitat.

The predator-prey relationship between *Lates stappersii* and *S. tanganicae* traditionally have been regarded as crucial in explaining fluctuating patterns of the distribution of both taxa within the lake. However, planktonic abundance and physico-chemical parameters may be important drivers as well (Plisnier *et al.*, 2009).

While various other taxa occasionally venture into the pelagic zone, one other species, a small Cyprinid (*Chelaethiops minutus*), with a maximum standard length of slightly over 10 cm also occurs in this zone. While the young live in

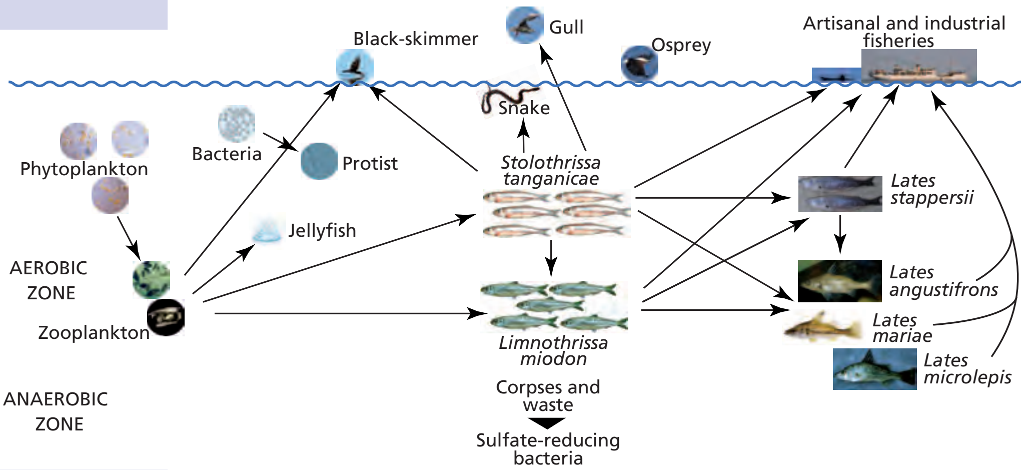


FIGURE 19.2.
Simplified trophic network of the pelagic community of Lake Tanganyika, illustrating the main types of food preferences.

the littoral, adults migrate towards the open water, but do not form schools, as the sardines do (Coulter, 1991). Interestingly, in all three large lakes, an endemic pelagic Cyprinid species occurs. While in lakes Victoria and Malawi these belong each to an endemic, monospecific genus, in Lake Tanganyika, the species belongs to a more widespread genus.

The littoral and sub-littoral communities

Generally, the littoral and sub-littoral communities are those living in the coastal stretch to a depth of about 40 m (Coulter, 1991). These communities are very species-rich with complex interactions and are dominated by cichlids. The major part of the littoral zone consists of rocky areas, often on a steep slope that reflects the sharp terrestrial gradient. These areas are interrupted by sandy or pebble-stone beaches, or muddy areas often associated with the mouth of affluent rivers. These disconnections can form ecological barriers for various stenotopic, lithophylic cichlid species. Many of these lithophylic species have narrow ranges of depth and substrate preferences (figure 19.3).

In the littoral and sublittoral environment plentiful species of other fish families occur. While some of them are clearly linked to the lake environment, for others it is difficult to assess whether they are merely riverine, occasionally frequenting the lake.

The largest catfish family are the Claroteidae with 16 species ranging from relatively small species within the endemic genera *Lophiobagrus* and *Phyllonemus* to the large non-endemic *Auchenoglanis occidentalis* of over 85 cm TL. The latter species is involved in a uncommon case of alloparental care; it can act as a host parent for the eggs and young of *Dinotopterus cunningtoni*, an endemic Clariid catfish. The brood of the latter species benefits from the parental care of the host species, but larger young are also observed to feed on the host brood (Ochi *et al.*, 2001).

Most of the claroteid catish in the lake are rock dwellers (Hardman, 2008). Though they are quite diverse in shape, they form a monophyletic flock, except for *Chrysichthys brachynema* (Peart *et al.*, 2014). This species is also a Lake

Tanganyika endemic, differing however clearly in morphology from the other larger endemic *Chrysichthys* clade (Risch, 1986). While various species have a lake-wide distribution, some are restricted to the northern part of the lake while others to the southern part (Hardman, 2008). Circum-lacustrine species appear to be living in shallow waters, whilst restricted species are found in deeper waters, perhaps reflecting a more specialized life history. As such, it is difficult to assess whether their distribution is restricted due to habitat availability, or whether the pattern observed is the result of a sampling artefact.

Mochokidae is the second largest catfish family, with 13 species of *Synodontis*, all of which except one, *i.e.*, *S. victoriae*, are endemic. However, the latter does not occur in the lake itself. While one would expect this lineage to have a Congo basin ancestry, the affinities of this flock are with Eastern African lineages within a larger Eastern African/Congo/Southern African clade (Pinton *et al.*, 2013; Day *et al.*, 2013) and genetically distant from the main Congo clade. Worth mentioning is the cuckoo behaviour of *S. multipunctatus*. During reproduction, a couple of these catfish disturb the mating cycle of certain mouthbrooding cichlids and lay their eggs on the mating spot of the cichlids. When these come back to continue mating, the cichlid female will take up the catfish eggs in the mouth as she does with her own eggs and guard them in her mouth. The catfish young develop more quickly than the cichlids and will feed upon the cichlid fry inside the female's mouth. At the end of the brooding cycle, the female cichlid will release the catfish young from her mouth and even then will still take care of the cuckoo young for several days.

Most Mastacembelidae or spiny eels live in rocky habitats, where the larger species such as *Mastacembelus moorii* are important predators. Smaller species can be caught on sandy habitats as well. Most species are nocturnal, while some are active during the day (Ochi *et al.*, 1999). Some species may be obligate egg feeders following a lunar cycle (Ochi *et al.*, 1999). Two species, *M. micropectus* and *M. apectoralis*, are special in respectively their reduction and loss of the pectoral fins, probably as an adaptation to the highly complex rocky habitat they live in (Brown *et al.*, 2011).

A parallel with the genus *Synodontis* appears in *Mastacembelus*. Fifteen species of this genus occur in the basin, all endemic, except *M. frenatus*, which does not occur in the lake itself. This species again is shared with the Lake Victoria basin, but in contrast to *S. victoriae*, has a much wider distribution (Van Steenberge *et al.*, 2014). Also in this case, the Tanganyika clade (not including *M. frenatus*) is part of a larger Eastern African/ Congo/ Southern African clade (Brown *et al.*, 2010). However, in this study the number of Congo basin species was very limited and interestingly the sister group of the Tanganyika clade was an undescribed species from an affluent of Lake Mweru (upper Congo).

The seemingly most abundant non-cichlid in the littoral is the endemic Tanganyika poeciliid *Lamprichthys tanganicanus*, which occurs over every rocky shore area in large numbers, but occasionally also ventures in more pelagic waters (Brichard, 1989). This species has been introduced in Lake Kivu, where it showed up in commercial catches from 2006 onwards (Muderhwa & Matabaro, 2010).

Within the Cichlidae, the lamprologines are most abundant in terms of species (± 80 described species) and individuals in the littoral and sub-littoral habitats. These are substrate brooders that are more dominant in rocky habitats than on sand; they lack a clear sexual dimorphism in colour pattern, as is known for most of the mouthbrooding cichlid lineages. Lamprologines form a very diverse clade in terms of shape, ecology and behaviour. While most form pairs, others form harems. In at least eight species, lunar synchronization of spawning was observed, the adaptive significance of which still has to be assessed (Nakai *et al.*, 1990). In several species cooperative breeding has developed (Taborsky, 1984; Heg & Bachar, 2007). A unique component of the lamprologine benthic community are the shell-breeding cichlids. Large shell beds occur on gentle slopes between 10 and 35 m, often at the lower limits of the rocky habitat. At least 9 species are obligate shell brooders (Yanagisawa *et al.*, 1997), most of which are small. However in some species such as *Neolamprologus callipterus*, there is a strong sexual size dimorphism. Females are much smaller than regular males, which cannot enter the shells; however, much smaller, parasitic males can sneak fertilization at the entrance of or inside the shell (Sato *et al.*, 2004).

The periphyton is an important food source in the rocky habitat. Though species of many other tribes feed on the algae or the organisms associated (together known as "aufwuchs"), it is within the tribe of the Tropheini that we find most specialists feeding on the rocks. A commensalistic behaviour exists even between *Petrochromis polyodon* and *Tropheus sp.* 'black' (mentioned as *Tropheus moorii*), with the latter clearly preferring patches of algae that first had been combed by *P. polyodon* (Takamura, 1997).

Fishes from the littoral communities are not only preyed upon by other fishes, but also by other vertebrates; these include crocodiles, several bird species such as cormorants, otters and also the aquatic cobra, *Naja (Boulengerina) annulata*, a species with a venom deadly to humans. It is often encountered while diving or snorkelling in the lake; fortunately, it is not aggressive under water.

Densities of species and individuals are very high in the rocky habitat. Censuses of quadrats of 20 x 20 m in various parts of the lake, revealed 2,600 to 6,600 individuals belonging to more than 40 species (Hori, 1997). Long-term monitoring and removal experiments demonstrated that the littoral communities are very stable. Such densities obviously are accompanied by a large number of intraspecific and interspecific interactions, associated with commensalism and exploitative mutualism that are assumed to increase species richness (Hori, 1997).

One tribe of cichlids is typical for the surge zone where they eat algae and small invertebrates: the Eretmodini or goby cichlids.

The communities of the sandy and marshy habitats are less diverse and but also less well known. They are however more under threat because of the increasing pressure of beach seining, even with mosquito nets.

This is the domain of various Ectodini taxa, such as *Callochromis*, *Xenotilapia, Cardiopharynx, Lestradea, Ectodus* and *Grammatotria* and a few Lamprologini

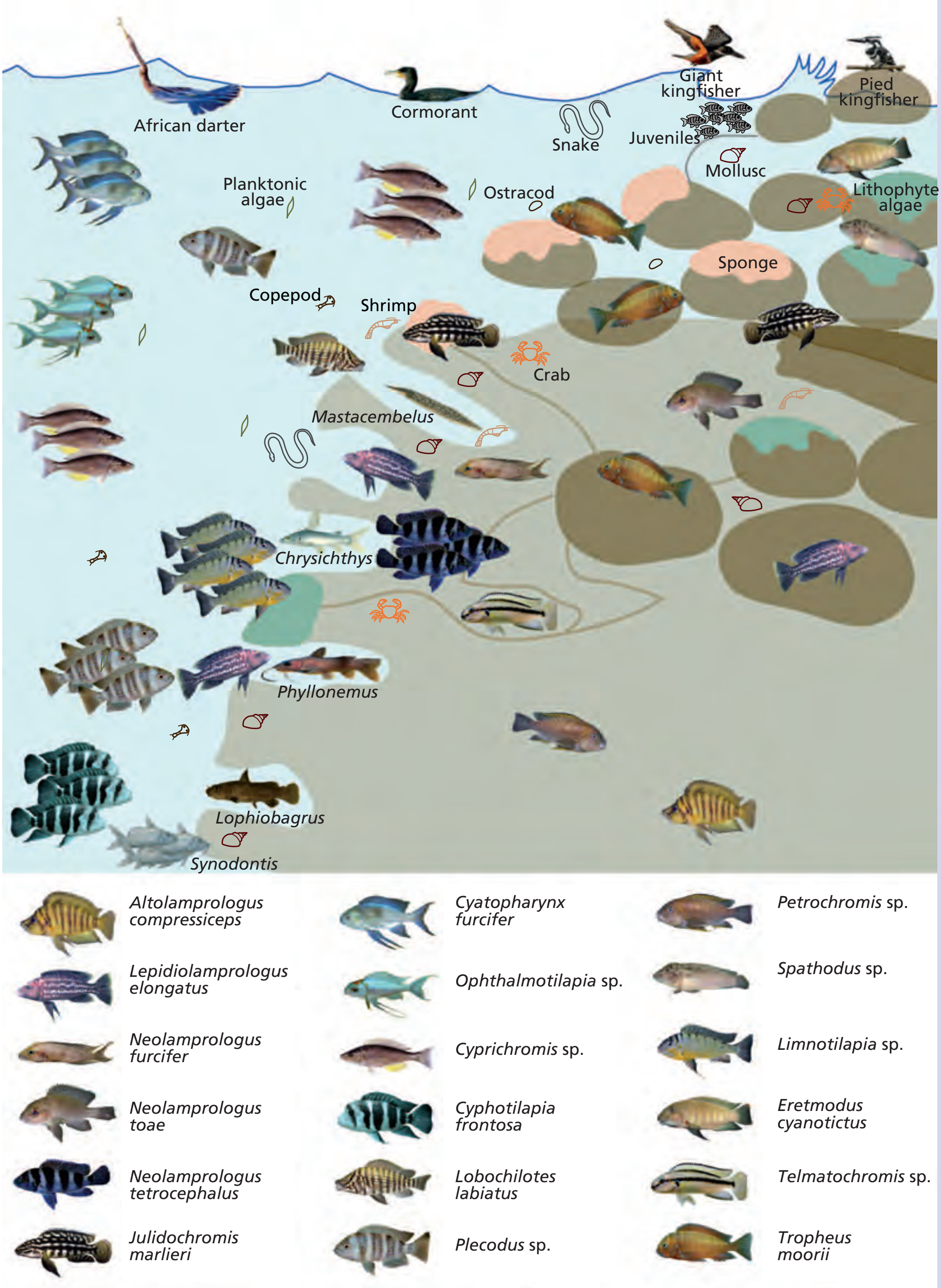


FIGURE 19.3.

Schematic presentation of the occupation of the rocky habitat in Lake Tanganyika by various fish species.

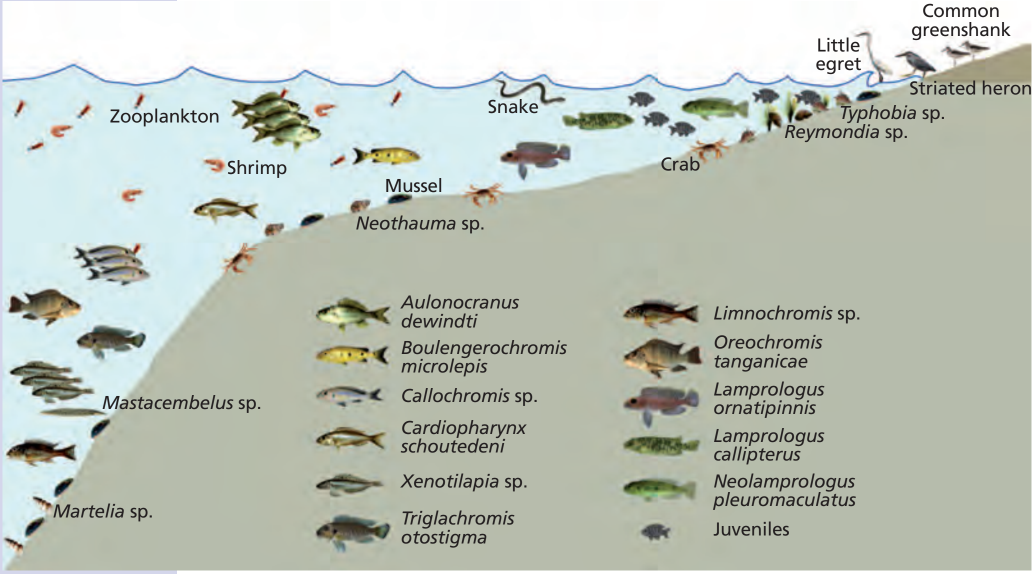


FIGURE 19.4.
Schematic presentation of the occupation of the soft bottom littoral habitat in Lake Tanganyika by various fish species.

(Konings, 2015), but also of *Boulengerochromis microlepis* (figure 19.4). This fish is supposed to be the largest cichlid on earth and has a high economic importance. The intermediate zone or the areas closer to the rocky habitat are frequented by various other cichlids and non-cichlids. In these areas one can find substrate brooding couples of *B. microlepis* vigorously defending their thousands of eggs or young in a shallow nest in the sand against the continuous attacks of all kinds of predators, as well as the leks of many Ectodini. Marshy areas are mostly associated with river mouths. They typically harbour a mixture of a few true lacustrine species and riverine species.

Deep-water communities

The deep-water communities are also dominated by cichlids. Coulter (1991) considered the benthic and bathypelagic communities to live from ± 40 m downwards to the oxycline. The oxygen concentration is the major factor limiting the depth distribution of these fishes. The oxycline is deepest at the southern end (about 200 m vs. 80 m in the north) and varies between seasons (Plisnier *et al.*, 1999). This zone is the most stable habitat, almost uninfluenced by wave actions and shifts in water level. However large seasonal oscillations do occur in the lake that may impact these communities. While they are not as species-rich as the littoral and sublittoral, still some 80 species have been recorded (Coulter, 1991). One of the more important guilds of the shallow waters, the algae eaters, are not present in this area, which is devoid of light. Typical tribes are the predatory Bathybathini and the Trematocarini that have large sensory canal pores on their head that probably aid in prey detection. Also the Limnochromini and the scale-eating Perissodini are well represented. Non-cichlids are represented by *Lates mariae* and *L. angustifrons*, several *Chrysichthys* and *Synodontis* species, and the endemic clariid *Dinotopterus cunnigtonii*.

The shelf areas are dependent on the rain of organic material from the pelagic zone. While cichlids are large in number, non-cichlids may represent the highest biomass. Most probably, fish are much less stenotypic here than in the shallower zones of the lake. The communities of the rocky slopes represent an extension of the rocky littoral habitat with many small-sized cichlids (Coulter, 1991). The *Trematocara* species living here appear to ascend the slopes into the littoral at night for feeding. The bathypelagic community living above the deeper bottoms is difficult to demarcate and consists of some ten relatively small zooplanktivorous cichlid species (Coulter, 1991).

The marshy areas and tributaries of the lake are dominated by the non-cichlids. Here occur 103 of the 145 species of non-cichlids present in the basin (De Vos & Snoeks, 1994). Most of them are known from the Malagarasi River, the largest affluent of the lake. The majority of the species belong to the Cyprinidae (by far the largest group), the Mormyridae, the Characidae and the Mochokidae. Most of these species are only exceptionally found in other habitats of the lake.

The communities of Lake Malawi

Lake Malawi is the fish species-richest lake on earth harbouring some 800, or even 1,000 cichlid species, only fewer than 400 of which are described. In addition, the basin, taken as the lake itself, its affluents and the associated Lake Malombe and the Upper and Middle Shire upstream of the Murchison cataracts, contains some 62 native non-cichlids belonging to 11 families (Snoeks, 2004b).

When Lake Malawi appeared in its present form is not clear. The minimum age of the rift basin currently including the lake, is about 8.6 Ma, but deep water conditions were only reached by 4.5 Ma (Delvaux, 1995). Like the other large lakes in the region, Lake Malawi went through periods of severe aridity. During the last mega-droughts between 160 000 and 60 000 BP, the water level dropped several times to about 550 m below the current level resulting in a small palaeo-lake with a 97% reduction of the current volume (Lyons *et al.*, 2011). Such mega-events but also smaller lake level changes must have had a profound impact on its fish fauna. The lake is anoxic below 170-200 m.

Roughly, the Lake Malawi cichlids can be divided in two groups of mouthbrooding haplochromines, the *mbuna* and the *non-mbuna*. The former is a morphological and ecological entity, encompassing a group of beautifully coloured, small to medium-sized, mainly rock-dwelling fishes. The *non-mbuna* include all other haplochromines. In addition there are some tilapiine cichlids, some of which are endemic, and a group of 62 non-cichlids (Snoeks, 2004b).

Non-mbuna cichlids can phylogenetically but also ecologically roughly be divided in a *Rhamphochromis* and a *Diplotaxodon*/*Pallidochromis* group, most species of which live in pelagic or deeper benthic habitats, and the remaining *non-mbuna* split up in a shallow-water and a deep-water component. For a long time the deep-benthic *non-mbuna* ended up in a clade not with the shallow water *non-mbuna* but with the rock-dwelling *mbuna* (Moran *et al.,* 1994), making the *mbuna* a non-monophyletic assemblage. However, recent molecular analyses (Genner & Turner, 2012) confirmed the common sense feeling (Snoeks 2000) that, based on morphology and ecology, there should be a closer relationship between the two *non-mbuna* communities.

Over 99% of the cichlids are endemic to the lake (Snoeks, 2000). Exceptions found in the lake are *Astatotilapia calliptera* [possibly the species represents a complex of species (Seehausen *et al.*, 2003)] and the two tilapias, *Coptodon rendalli* (Boulenger, 1896) and *Oreochromis shiranus* Boulenger, 1896. Of the latter, there is an endemic subspecies *Oreochromis shiranus shiranus* restricted to the Lake Malawi basin. Also the former *Serranochromis robustus robustus* (Günther, 1864) is restricted to the basin, but it should be considered as a valid species (Snoeks & Hanssens, 2004a). The non-endemic *Pseudocrenilabrus philander* (Weber, 1897) and *Tilapia sparmanni* (Smith, 1840) have not been found in the lake itself but are present in the associated lagoons and rivers (Snoeks & Hanssens, 2004a).

Several cichlid taxa were revised and earlier work on the Lake Malawi fauna reviewed by Trewavas at various instances during her career (e.g. Trewavas, 1931; 1935 and 1941) resulting in a new classification scheme of the *non-mbuna* cichlids (Eccles & Trewavas, 1989) that also included a synopsis on the distribution and ecology of the species.

Ecological research on the tilapias (local name *chambo*) started with the studies of Lowe-McConnell (e.g. Lowe, 1952 and 1953). Work on the *mbuna* was headed by Fryer (1959) and a special group of zooplanktivorous *non-mbuna*, the *utaka* by Iles (1960). Both joined forces in writing a classical volume on the biology and evolution of the cichlids of the great African lakes (Fryer & Iles, 1972). In the late seventies, a detailed programme started on the *mbuna* of the Malawi part of the lake (Ribbink *et al.*, 1983) that set the scene for a decades-long scientific exploration of this group.

Lake Malawi supports what probably is the world's richest multispecies freshwater fishery. In a twenty-minute shallow-water trawl, up to 72 species can be found (Snoeks & Hanssens, 2004b) and more than 200 species have been recorded from single fishing localities during recent surveys of the artisanal and industrial fisheries in southern Lake Malawi (Weyl *et al.*, 2010).

The pelagic community

The pelagic community for a long time was considered to be underexploited by fish with only shoals of the Cyprinid *Engraulicypris sardella* (locally known as *usipa*) occurring in large numbers but unable, due to their small size, to feed on the rather large lakefly (*Chaoborus*) larvae. Several projects, from the early 1990s onwards, have contributed largely to the current knowledge of the pelagic fish communities, which are much more important than previously thought. The off-shore zone is characterized by the genera *Rhamphochromis* (locally known as *ncheni*), and *Diplotaxodon* (*ndunduma*), but not all of the species of these genera live only in the pelagic (Turner *et al.*, 2004). These genera contain mainly zooplanktivorous and piscivorous fish and taxa comprise more than 80% of the biomass of the pelagic fish communities (Turner *et al.*, 2002). Many of the species aggregate in large numbers on the benthic shelves in breeding areas or leks. *Diplotaxodon* seem to be more active during the night while *Rhamphochromis* are caught more in daylight-set gillnets (Thompson *et al.*, 1995). The similarity between the elongated predatory *Rhamphochromis* from Lake Malawi and *Bathybates* from Lake Tanganyika is one of the classic examples of morphological convergence in cichlids of the African Great Lakes (Kocher *et al.*, 1993).

One species of the *utaka* group (see below) appears to be common in the pelagic zone, *Copadichromis quadrimaculatus*. In addition to this cichlid community, two non-cichlid taxa are common: the cyprinid *Engraulicypris sardella* and the mochokid catfish *Synodontis nyassae*. The complex diversity of true pelagic cichlids is a unique feature of Lake Malawi (Turner *et al.*, 2001).

Pelagic fish live in the oxygenated zone between 0 and 200 m. They all seem to have a lake-wide distribution (Turner *et al.*, 2002). The food taken by the pelagic cichlids differs according to their life stage. Small individuals feed on crustacean zooplankton, *Chaoborus* larvae and pupae, and juveniles of *E. sardella*. Larger individuals prey on fish, mainly *E. sardella* and small pelagic cichlids (Allison *et al.*, 1996; Turner *et al.*, 2002). Contrary to earlier reports, the lakefly biomass is efficiently utilised by the lake fish community (Darwall *et al.*, 2010).

The littoral communities

In general topography, the lake resembles Lake Tanganyika. However, for the littoral communities, one of the greater differences is that only about one-third of the shoreline is rocky habitat, while roughly two-thirds is sand (Weyl *et al.*, 2010), while in Lake Tanganyika, the major part of the littoral zone is rocky.

The rocky habitat is occupied by both *mbuna* and *non-mbuna*, while *non-mbuna* dominate the sandy habitats. Genner & Turner (2005) report about 400 species occuring on the rocky shores, and fewer than 200 on the sandy shores.

About 325 species of phylopatric and stenotopic *mbuna* live in the rocky habitat (Konings, 2007). Many *mbuna* species have not been scientifically described, but their general habitus and colour pattern, and their distribution, habitat preference and behaviour are often documented in the scientific, and even more so in the aquarium literature (e.g. Ribbink *et al.*, 1983; Konings, 2007). *Mbuna* display a high level of intra-lacustrine endemism, unmatched in any other vertebrate group. Many species are limited to one or a few islands or reefs or to small parts of the mainland (Ribbink *et al.*, 1983; Konings, 2007). Consequently, the rocky habitat community can be quite different from one area to another. In addition to community structure along this geographic spatial axis, *mbuna* communities also differ along a habitat-related axis. Konings (2007) distinguishes the communities of the upper surge zone, the sediment-free and the sediment-rich rocky habitat.

A gillnet survey on the rocky habitat in various parts of the lake revealed a strong decline in *mbuna* species numbers between 20 m and 30 m depth (Hanssens & Snoeks, 2004). Down to depths of 20 m, on average 10-11 species were found in the nets, while at 30 m, only six were found, decreasing to an average of four at 50 m. A few typical rock-dwelling *mbuna* were still present in a net set at 55 m. The species-richest catches were made at islands and reefs (Mbenji, Likwandje, Likoma), and the nearby mainland of the latter in Mozambique, but also at the north-eastern shores of the deeper parts of the lake. The rocky habitat of large islands are special in two respects; they harbour a higher species diversity of *mbuna* than comparable areas on the mainland and also a higher level of intra-lacustrine endemism (Hanssens & Snoeks, 2004).

There may be over 30 *mbuna* species living at a particular rocky site in combination with various *non-mbuna* species (Genner & Turner, 2005). While there is a large variety of micro-habitats in the rocky zone, as a result of the size of the rocks, the exposure to surge waves, the depth and slope, the amount of algae, etc., that create opportunities for fine-scaled differences in trophic niche of the numerous *mbuna* species at a given site, a substantial overlap in diet and space use has been found between coexisting morphologically similar *mbuna* species but also between coexisting species that differ widely in morphology. Ecological niche differentiation was found to occur on a fine scale among the *mbuna* (Genner *et al.*, 1999). According to niche theory, this differentiation is likely to promote coexistence if resources are limited. However, species were also found to co-occur without any evidence of niche differentiation (Genner *et al.*, 1999). After a full year of observations of two coexisting species couples in the lake, Martin & Genner (2009) concluded that, in contrast to predictions of ecological specialization during resource scarcity, substantial trophic overlap persisted in all seasons and no direct evidence of competition-driven divergent ecological selection was found.

Not much is known about the endemism of *non-mbuna* in the rocky habitat. Since there has not been a lake-wide survey for this group, the information is just not sufficient to draw conclusions. What is known is that some species have a lake-wide distribution, while others do not. Some species are only known from one or a few localities, reflecting the poor sampling effort (Snoeks & Hanssens, 2004b).

Lake Malawi harbours a special assemblage of small to medium-sized planktivorous cichlids that predominantly occur near rocky outcrops and reefs, feeding on plankton in the currents created by these "virundu". *Utaka* are characterized by numerous gill-rakers and long, protractile premaxillary pedicels which are part of a highly protrusible mouth that can form a sort of short sucking tube when feeding (Eccles & Trewavas, 1989). The group includes members of the genera *Copadichromis* and *Mchenga*. These fish form the basis of important fisheries with so-called "chirimila" nets (open-water seines). While indeed they frequent the water column, they are linked to the rocky habitat and are therefore more a component of the littoral community than of the pelagic, except for one species (see above). One species, *Copadichromis chrysonotus*, is a mid-water spawner (Eccles & Lewis, 1981).

The soft bottom littoral occupies the major part of the shoreline of Lake Malawi but represents clearly less diversity in micro-habitats than the rocky shore. A division can be made between the sandy habitat and the sediment-rich areas with aquatic plants associated with sheltered bays and river estuaries. Both these zones are mainly occupied by *non-mbuna*. While stenotopy is clearly less developed in these communities, genetic and morphological differences have been observed that either could be linked to a geographical pattern or not (e.g. Duponchelle *et al.*, 2000; various chapters in Snoeks, 2004a; Anseeuw *et al.*, 2008). One of the most important roles of the sandy zone is to provide space for reproduction, often in large leks. Many species also breed in the intermediate rock-sand habitat. Most studies did not distinguish between the littoral and the deep-water sand communities. Hence for further information, we refer to the part on the benthic communities.

The deeper benthic communities

Lake Malawi is special in harbouring a deep-water community, which appears to be more separated from the littoral and sub-littoral communities than in Lake Tanganyika. Duponchelle *et al*. (2003) reported a change in species composition between 50 and 75 m. The deep-water community is characterized by the presence of deep-water *Placidochromi*s, many species of *Diplotaxodon* and deep-water *Lethrinops*, and endemic *Bathyclarias*. In fact, with 47 species reported, the deep-water *Placidochromis*, represents one of the most species-rich assemblages in the lake (Hanssens, 2004). While there are no obvious barriers known in these deep benthic areas, the species seem to have limited distributions. However, since the assemblage is very poorly studied, it remains to be seen how much intra-lacustrine endemism this group displays.

While the littoral and sublittoral communities are clearly different from the deeper benthic communities in species composition, this does not result in sharp differences in species richness or fish biomass. A two year lake-wide biodiversity sampling programme with bottom trawling and gillnetting at various depths during five sandy and demersal cruises resulted in the following observations (Snoeks & Hanssens, 2004b). There is a slight decrease in catch weight with increasing depth for both the experimental trawl and the gillnet catches. Even so, the largest catch (exceptionally large) was taken at a mean depth of 128.5 m. This is probably due to the trawl having targeted one or more large leks with breeding cichlids. There is also a steady decrease in species richness with increasing depth for the trawl catches, though species numbers remain relatively high in the deeper regions (going from an average of ca. 40 in the littoral zone to ca. 25 at 150 m for a trawl of about 20 minutes). With regard to soft-bottom substrates, the highest species numbers were observed over fine sand habitats while the lowest numbers were found over sticky mud. Furthermore, for these habitats, species richness is not evenly distributed over the lake. Taking into account the influence of catch weight, relatively low species numbers were found in the trawls at Wissman Bay (north), Lukoma (north east) and the southern areas, while a relatively high species diversity was recorded at Nkhotakota, Chiwanga, and Senga Bay, all situated in the central or south-central part of the lake. Chilola and the central part of the southeast arm may also represent areas of a higher-than-average diversity, but this could not be confirmed for all depths (Snoeks & Hanssens, 2004b).

Darwall *et al.*, (2010) found evidence for a strong benthic–pelagic coupling; their model clearly demonstrated that the productive demersal fishery appeared to be over 80% reliant on production from the pelagic. Part of this link is also reflected in the presence of the same part of the fish community of both habitats, such as various *Diplotaxodon* species (see above).

Experimental trawls over one year at various depths clearly showed a change in communities with depth. This change was supposed to be linked to a change in granulometry of the bottom substrate (Duponchelle *et al.*, 2003). Cichlids dominated the captures at all depths with a biomass between 75 and 92%; the remaining part was mainly taken up by various catfish families (Bagridae, Mochokidae and Clariidae). This study also demonstrated that even if more than 150 species were found during the whole sampling programme, some ten species including three catfish made up 70 to 80% of the catches at a given depth. This suggests that the majority of the species, at least in the southern area, are relatively rare.

The communities of Lake Victoria

Lake Victoria is the largest tropical lake and second-largest lake in the world. In many aspects it is different from lakes Tanganyika and Malawi. It is saucer-shaped with a surface area of about 68,800 km^2, and relatively shallow (maximum depth 84 m and average depth ca. 30 m) (Kolding *et al.*, 2008), which means it harbours no real deep-water community. In addition, the major part of the littoral zones consists of sandy areas, with rocks being relatively rare. Its origin is relatively recent, ca. 400 000 BP (Fuggle, 2004), and the lake went through a desiccation phase ca. 15 000 years ago. Whether or not it dried out completely is a matter of debate (e.g. Johnson *et al.*, 1996; Fryer, 1997 and 2004; Snoeks, 2000; Verheyen *et al.*, 2003; Stager & Johnson, 2008; Elmer *et al.*, 2009). The lake supports one of the most productive inland fisheries of the world (Ogutu-Ohwayo & Balirwa, 2006).

A discussion on the fish communities should start with highlighting that, much more than any other large lake in the region, the ecology of Lake Victoria has changed dramatically in the last three decades. These changes have been so profound that a comparison can be made in the terrestrial environment with a shift from a biodiversity-rich equatorial rain forest to an almost desert. While these changes can be attributed to a large part to the introduction of Nile perch in 1954 (Goudswaard *et al.*, 2008) into a complex system that was mainly supported by the interactions of some 600 or more haplochromine cichlids, the situation is much more complex, with many other factors having influenced and still influencing the lake's fish communities. Among these are deforestation, pollution and eutrophication, introduction of water hyacinth, and overfishing, most of which are directly linked to the quickly growing riparian human population. As a result, occasional hypoxia in the deepest waters turned into a permanent anoxia below 50 m, with levels of low oxygen concentrations extending into the sublittoral waters (Njiru *et al.*, 2011).

The lake's native fish fauna is dominated by some 500-600 closely related haplochromine cichlids. Because of anthropogenic changes, some 200 are supposed to have become extinct, which has been referred to as the greatest vertebrate mass extinction in the modern era (Baskin 1992). While reports mention the return of some species in recent years, it is clear that many have disappeared forever. In addition, the lake harbours some 46 other fish species (Witte *et al.*, 2007a).

Greenwood studied Lake Victoria haplochromines extensively during several decades, based on fieldwork in the fifties and sixties (e.g. Greenwood, 1981). During the late seventies the Dutch Haplochromis Ecology Survey Team (HEST) started surveying the Mwanza Gulf, collecting data in collaboration with the Tanzania Fisheries Research Institute (TAFIRI) over several decades, thus providing much needed collections and baseline information on the ecological changes in the lake. These studies were triggered by the development of a more intensive trawl fishery on the poorly known haplochromines.

Many different trophic groups exist among the haplochromines of the lake: detritivores, phytoplanktivores, zooplanktivores, insectivores, molluscivores, crabeaters, prawneaters, parasite-eaters, scale-eaters, higher plant eaters and algae-eaters and piscivores amongst which paedophages. Many of them display characteristic morphological features (Witte & van Oijen, 1990).

Lake Victoria cichlids do not present the level of intra-lacustrine endemism found in lakes Tanganyika and Malawi, except maybe for the specialized rock dwellers. However, since haplochromine taxonomy is very difficult and lake-wide surveys resulting in detailed distribution data of the taxa have never been done, this assumption is difficult to verify. Wider distributional range, however, does not mean the haplochromines have a random distribution; horizontal and vertical ecological segregation patterns have been observed in certain groups such as the piscivorous and zooplanktivorous species (van Oijen, 1981; Goldschmidt *et al.*, 1990).

After the Nile perch boom, the haplochromine catches in the sublittoral and deeper zone decreased to virtually zero, but haplochromines in the littoral zones remained less affected, because of the lower densities of Nile perch in shallower areas (Witte *et al.*, 1992a). Concomitant with the decrease of the Nile perch came a resurgence of haplochromines. However, the recovery is limited to certain trophic guilds, but is noticed all over the lake.

Trophic group composition differs between habitats. Rocky habitats are relatively scarce in Lake Victoria, compared to lakes Tanganyika and Malawi. However, they also harbour a characteristic stenotopic cichlid community, named Mbipi (Seehausen *et al.*, 1998). More than 100 of these lithophylics have been discovered in the nineties. Before that time, this diverse community was virtually unknown to scientists. In these rocky habitats, many trophic guilds are represented but most characteristic are the algae scrapers.

An analyses of the catches within the Mwanza gulf before the introduction of the Nile perch revealed that on soft bottom substrate, species diversity was higher in the littoral sandy zone compared to littoral and sublittoral muddy zones (table 19.I) and the number of species within each trophic group differed considerably according to the zone (Witte *et al.*, 1992b). Insectivores dominated shallow soft bottom habitats. Oral shelling molluscivores and insectivores were mainly associated with the sandy habitat, while detritivores/phytoplanktivores and zooplanktivores were dominant on sub-littoral mud bottoms (table 19.II). Piscivores, representing about 40% of the species in the lake (van Oijen *et al.*, 1981), were clearly the species richest group in the lake but were only caught in small numbers (<1%).

TABLE 19.I.
Species number by trophic group, caught during experimental bottom trawls in different stations in the Mwanza Gulf (following Witte *et al.*, 1992b).

Depth	**2-6 m**	**2-6 m**	**7-8 m**	**10-11 m**	**13-14 m**
Trophic group	Sand	Littoral mud	Sublittoral zone		
Detritivores/phytoplanktivores	7	6	9	9	10
Grazers	4	0	0	0	0
Mollusc eaters	12	6	10	3	3
Zooplanktivores	8	10	9	9	10
Insectivores	8	6	7	3	4
Prawn eaters	0	0	1	2	1
Piscivores *sensu stricto*	14	11	7	9	9
Paedophages	4	2	2	4	4
Scale eaters	1	1	1	1	1
Parasites eaters	0	0	0	0	1
Unknown	7	1	1	0	1
Total	65	43	47	40	44

TABLE 19.II.
Proportion (% number of individuals) of haplochromines by trophic group, caught by bottom trawling between 1979 and 1982, in a sublittoral station over a muddy bottom (depth 7-8 m) in the Mwanza Gulf (following Witte *et al.*, 1992b).

Trophic groups	**1979/1980 (% number of individuals)**	**1981/1982 (% number of individuals)**
Detritivores/phytoplanctivores	77	75
Zooplanctivores	18	23
Insectivores	2	<1
Mollusc eaters	<1	<1
Piscivores	1	<1
Others	1	1

The pelagic community is dominated by the cyprinid *Rastrineobola argentea*. It sustains the second most important fishery (Wanink, 1999). In contrast to some pelagic zooplanktivorous haplochromines, *R. argentea* continued to thrive after the upsurge of the Nile perch.

The other lakes in the region

Lake Kivu

Lake Kivu is a high altitude, natural deep dam lake of relatively recent origin. The proto Lake Kivu, for a long time, was connected with Lake Edward until the connection got blocked by the Virunga volcanoes. For part of its subsequent history, the basin was endorheic, until it found its outlet via the Ruzizi, some 9500-9200 years ago (Snoeks *et al.*, 2012). At present 29 species are recorded from the basin, including five introduced species.

The majority of the fishes belongs to the large group of haplochromines; all fifteen species are endemic to the lake (Snoeks, 1994). Lake Kivu is regarded as the cradle of the haplochromines in the region, known as the Lake Victoria region super flock haplochromines (Verheyen *et al.*, 2003; Elmer *et al.*, 2009). While the lake is currently part of the Congo basin, zoogeographically it is part of the East Coast ichthyofaunal province (Snoeks *et al.*, 1997).

In addition to the endemic haplochromines, there is one autochthonous tilapia, *O. niloticus*, five cyprinids and two *Clarias* species. In the fast flowing parts of the affluents, *Amphilius cf. uranoscopus* occurs.

Of the five introduced species, the most successful in economic terms is *Limnothrissa miodon*. This freshwater sardine, endemic to Lake Tanganyika, was introduced in 1959, accidentally mixed with *Stolothrissa tanganicae* that was targeted to feed on the supposedly unexploited pelagic resources. Currently, a pelagic fishery is thriving, targeting these sardines. Recently, another Lake Tanganyika endemic species popped up in this fishery, *Lamprichthys tanganicanus*. Either it was introduced with the sardines and was only discovered fifty years later, or it was introduced more recently, maybe by an aquarist (Muderhwa & Matabaro 2010; Snoeks *et al.*, 2012).

Most of the coastline is rocky shore, dominated by haplochromine cichlids. Some species are also found in vegetated areas over sand (*Haplochromis astatodon*) or in the more pelagic regions (*H. kamiranzovu*). No intra-lacustrine endemism has been found in Lake Kivu. Typical for Lake Kivu haplochromines is the large amount of polychromatism relative to the other lakes in the region. Polychromatism is the presence of two colour morphs within one species, in this case the presence of piebald or bicolour black-blotched specimens alongside the normal coloured morph. Four out of the fifteen species are polymorph. Almost all piebald specimens are females; in some species about half of the females are of the piebald type. It has been postulated that the success of polychromatism is linked with being less visible for predators. Indeed, in the very clear waters of Lake Kivu, this disrupted colour pattern may provide some evolutionary advantage (Snoeks, 1995).

Lake Edward/George

Lake Edward forms with the smaller Lake George one large system that is connected through the Kazinga channel. An estimated 60 haplochromines occur in the system, and some 21 non-cichlids (Snoeks, 2000). The basin is part of the Nile system, but lacks some typical Nilotic elements such as *Lates,* *Hydrocynus* and Polyteridae. Fisheries rely mostly on six species: *Oreochromis niloticus*, *O. leucostictus*, *Bagrus docmak*, *Protopterus aethiopicus*, *Clarias gariepinus* and *Labeobarbus altianalis*, but the numerous endemic haplochromines are increasingly becoming a target as well. Human impact has disrupted the ecosystem of the lake. This includes overfishing but also a reduction of the nutrient input though the severe reduction of the hippo population (Languy & de Merode, 2006) that were responsible for the transfer of plenty of nutrients from the terrestrial to the aquatic environment.

Lake Edward has a northern outflow, the Semliki towards Lake Albert. The falls and rapids on this effluent apparently block the migration of fish from Lake Albert into Lake Edward (Greenwood, 1976).

Lake Albert

Lakes Albert and Turkana are special as they are the only large rift valley lakes within the Nile system not having a large number of endemic haplochromines (Snoeks, 2001).

Forty-eight species are recorded from Lake Albert, amongst which some 37 non-cichlid species and only 11 cichlids, seven of which are haplochromines. Greenwood (1979) noted the haplochromine fauna to be Nilotic-Congolese, rather than Victorian, and included most species in his genus *Thoracochromis*. However, a quick review of some collections revealed that there are many new species that have not yet been described. Notably there seems to be a small group of rock-dwelling species that bear much resemblance to the Lake Victoria Mpibi (Snoeks, pers. obs.).

Lake Turkana

Lake Turkana is part of the eastern branch of the East African rift system. During its history in the early Holocene the lake regularly overflowed into the Nile but currently, it is part of an endorheic system (Johnson & Malala, 2009). Its fish fauna reflects the former connection with the Nile system and includes 36 non-cichlids and 8 cichlids (Snoeks, 2000).

Lake Rukwa

Lake Rukwa is situated in the western branch, to the east of the southern part of Lake Tanganyika. It is relatively shallow with a maximum depth between 10-15 m (Seegers, 1996). The total drainage area of this endorheic system includes 64 species, about half of which are found in the lake itself. The ichthyofaunal composition appears to be a mix from various neighbouring systems, but includes some endemic cichlids and non-cichlids, including six haplochromines (Seegers, 1996). Fisheries are mainly targeting tilapias and *Clarias*.

Lake Mweru

Some may debate whether or not Lake Mweru should be regarded as a rift valley lake, but in view of its geological setting, it is. It is situated south-west of the southern part of Lake Tanganyika. The lake has a maximum depth of about 27 m (Bos *et al.*, 2006) and is part of the Luapula-Mweru sub-region within the Upper Congo system; it contains some 135 fish species (Van Steenberge *et al.*, 2014). As in many other lakes in the region, overfishing is a serious problem.

Conclusion

The region of the East African lakes represents the world's richest region in terms of freshwater fishes. Each of the three large lakes, Tanganyika, Malawi and Victoria, harbour more species than any other lake in the world. In these lakes exceptional numbers of cichlid species, estimated respectively at 250, 800-1000, and 500-600, occur. In addition, more than 95% of these species are endemic to one particular lake. Given the extraordinary species richness and the high level of endemicity, these lakes are the largest centres of vertebrate diversity and unique natural laboratories to study adaptive radiation and explosive speciation.

The region of the East African lakes is experiencing a significant and ever-increasing demographic pressure, which translates to a more intense human impact on the aquatic environment and a higher demand for fish as the main source of animal protein in the region. Most lakes are shared between two or three countries, rendering decision-making on a lake-wide scale rather complex. In addition, multispecies fisheries are difficult to manage since the interactions between species are poorly understood. In many areas, cichlids are targeted, but several hundred still remain to be described from the region (Snoeks, 2001). Therefore, basic information on many taxa and their life history, including those of non-cichlids, is lacking.

In Lake Tanganyika, fisheries are merely concentrated on the pelagic sardines and its main predator *Lates stappersi*. However, the pressure on the littoral communities is dramatically increasing (e.g. Sturmbauer, 2008; Mushagalusa *et al.*, 2014).

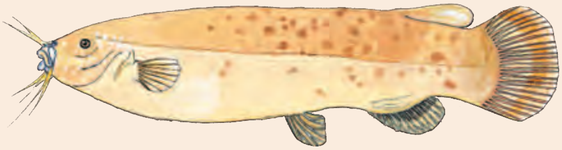
In Lake Malawi, fisheries are concentrated on the cichlids, though various non-cichlids are targeted as well. Overfishing has been ongoing for several decades in the southern part of the lake and several large cichlid species have virtually disappeared from the catches (Weyl *et al.*, 2010). Lake Malawi's high valued *chambo* (endemic tilapias) fisheries are overexploited or have collapsed in certain areas. In addition, the migratory cyprinid species, such as the endemic *Labeo mesops*, *Opsaridium microlepis* (local name *mpasa*) and *O. microcephalus* (*sanjika*) have been decimated through habitat degradation and intensive fishing efforts along their migrating route (Weyl *et al.*, 2010).

Lake Victoria is the setting for the largest vertebrate extinction in human history. A conservative estimate by Witte *et al.* (1992b) places the number of haplochromine species that disappeared at 200, due to a combination of anthropogenic factors. While the upsurge of *Lates niloticus* can be considered both an ecological disaster and an economic blessing, the economic benefits may well decrease dramatically in the future now that catches of Nile perch are dwindling.

Not only the big three, but also the other, smaller lakes in the region experience such impacts on various scales. Clearly the major challenge is a difficult one: reconciling the need to conserve these unique natural laboratories and their exceptional ichthyofaunas and the need for access to a much-needed natural food resource for the riparian human populations. Clearly both ambitions benefit from sustainable management of the ecosystems involved.

Fish communities in shallow lakes

Christian Lévêque



While there is an intuitive understanding of what "shallow lake" means, it is more difficult to provide a precise definition of the term. For our purposes, we could include in this category lakes with a depth not exceeding 10 m and with no permanent stratification of the water column (Lévêque & Quensière, 1988). Shallow lakes are thus lakes in which the coastal area and bankside vegetation play an important role in the function of the system, in contrast to deep lakes where the pelagic zone is particularly well-developed.

Shallow lakes generally occupy depressions in areas with moderate reliefs. Despite their diversity, they all share certain characteristics:

- **There is significant development of grassy zones that can occupy large surfaces.**
- **Macrophytes develop on the shoals and produce a large amount of organic matter;**
- **Fluctuations in the water balance (summation of water inputs and outputs) manifest as large fluctuations in water level and surface, owing to the basin's lack of relief.**
- **The water balance depends greatly on the local climate as well as the climate of the basin feeding the tributaries, and on the shape of the lake basin;**
- **The absence of permanent thermal stratification favours the rapid recycling of nutritive elements as well as the development of benthic fauna that helps increase the productivity of these physical systems.**

Elements for a physicochemical typology of shallow lakes

Different types of shallow lakes can be distinguished based on their hydrological function and physiochemical characteristics.

First, while many lakes are *open,* with one or more superficial outflows that allow the emptying of excessive water inputs, other types of lakes, called *endorheic* lakes, are closed basins with no outflows. These endorheic lakes are areas for the spread and evaporation of water, responding to fluctuations in water inputs by more marked variations in surface. Lake Chad, fed by the Chari, and Lake Ngami, fed by the Okavango, are examples of endorheic lakes in Africa.

We can also distinguish several major types of shallow lakes based on the characteristics of the water balance:

- **pluvial,** dominated by the precipitation-evaporation cycle. Lake Victoria, which receives 83% of its inputs from rainfall and loses the equivalent through evaporation, is a good example. This type is characteristic of many water bodies in semi-arid zones, including in temporary systems such as swamps. These lakes, which depend essentially on rainfall for input, are very sensitive to seasonal and inter-annual variations in rainfall;
- **riverine,** in which inputs and outputs arrive mainly by surface effluents and tributaries. Many shallow lakes are fed thus by floods in the fluvial system, as shown by the lakes of the Central Niger Delta or Lake Chad (83% of inputs from the Chari). Fluctuations in the level of these lakes are generally less pronounced than for lakes whose water input comes from the atmosphere, and fauna that are mostly of fluvial origin can find refuge in watercourses when there is a severe drop in water level.
- **evaporative** lakes for which groundwater inputs are important. These are often endorheic systems that function like evaporation basins. This is the case of Lake Assal (Djibouti), Lake Bogoria (Kenya), and the lakes of the Kanem region (Chad), whose waters contain high salt levels. Fish fauna is poor in this type of system, with a few rare species that have adapted to conditions of extreme salinity.

Endorheic shallow lakes

In an endorheic lake with no surface effluents, all water coming from rivers or precipitation either evaporates or seeps into the groundwater. For several riverine-type endorheic lakes in Africa, including Lakes Chad, Naivasha, Chilwa, and Ngami, water remains fresh. Meanwhile, for other types of evaporative lakes such as Lakes Nakuru, Magadi, and Turkana to a certain extent, waters are salty.

Evaporative type lakes

Only a few species are able to survive in the extreme conditions prevailing in lakes with salinities even higher than that of sea water. The Cichlidae *Alcolapia grahami* is endemic to Lake Magadi where it lives in pools fed by warm and salty water sources (Coe, 1966). Fishes are essentially concentrated in the upper 50 cm where oxygen content is higher.

Alcolapia alcalica lives in Lake Natron whose waters have a salinity between 30 and 40‰ while related species *Oreochromis amphimelas* lives in Lake Manyara where it has been found in waters reaching 58‰ salinity (Trewavas, 1983).

Alcolapia grahami was introduced into Lake Nakuru, where it flourished (Vareschi, 1979). Fishes are not evenly distributed over the entire area of the lake, and a distribution gradient from the banks to open water has been shown, with the smallest fishes concentrated near the former and the largest ones found in the latter. The average number of individuals by m² decreases, from 20 at 50 m from the shore, 18 at 150 m, 9 at 400 m, and 8 at 1,000 m. Meanwhile, biomass goes from 2.5 gm^{-2} (dry weight) at 50 m, to 5.25 at 250-400 m, and 4.2 at 600-1,000 m. In 1972, the average biomass of *Alcolapia grahami* was estimated at 80 kg ha^{-1}, and reached 425 kg ha^{-1} in 1973. In 1976 the average biomass stabilised at 300-400 kg ha^{-1} (Vareschi, 1979).

Riverine type lakes

In these freshwater lakes, the richness of fish fauna mirrors the species richness of the drainage basin and the environmental conditions available to fishes. These may vary over the season or from one year to another.

A familiar case is that of Lake Chad, found in a vast sedimentary basin in the centre of Africa. The lake covered an area of 25,000 km^2 in the 1960s, but in the 1970s, after several years of drought, it only covered 5,000 km^2 in the southern part of the basin directly supplied by the Chari (Carmouze *et al.,* 1983). The ecology of fish populations was studied between 1966 and 1978, including a period of relative stability from 1966 to 1972 and referred to as "normal Chad", and a drought period after 1972 called "small Chad" (Carmouze *et al.*, 1983).

During the "normal Chad" period, species distribution in the lake was strongly influenced by two factors: distance from the riverine system, and the types of aquatic facies (archipelago or open water) (Bénech *et al.*, 1983 ; Bénech & Quensière, 1989). In the southern basin, fauna was more diverse, with three characteristic species captured exclusively in the vicinity of the Chari delta on the lake's east coast: *Ichthyborus besse, Siluranodon auritus* and *Polypterus senegalus*. *Tetraodon lineatus* was also common in this zone, as well as juveniles of *Schilbe uranoscopus* and *Hyperopisus bebe* which were not found in other parts of the lake. In the open water area, *Labeo coubie, Citharinops distichodoides* and *Synodontis clarias* were abundant, as well as large *Synodontis membranaceus*, but no species were present exclusively in this type of environment. On the other hand, several species found in the archipelagic environments were absent from the open waters: *Oreochromis niloticus, O. aureus, Sarotherodon galilaeus, Coptodon zillii*, *Alestes baremoze, A. dentex, Brycinus macrolepidotus*, *Marcusenius cyprinoides, Petrocephalus bane*, *Heterotis niloticus*.

In the northern basin, fauna becomes poorer as one moves farther from the Chari delta. In the northern part, there is an absence of Mormyridae which could be due to the increase in salinity. But *Schilbe uranoscopus* also disappears, and *Hydrocinus brevis* and *Synodontis batensoda* become scarce.

The Sahel drought that began in 1972 triggered a fall in the lake's level and a significant reduction in its area. Environmental conditions underwent profound changes in the drying-out phase (1972-1974 period), with a shift from a lacustrine system to a marshy or swampy system during the so-called "small Chad" period. This change was followed in 1975 by the complete drying out of the northern basin of the lake, which thus shrunk to only the southern basin fed by the floods of the Chari.

This change in hydrology and reduction in lake surface had various consequences and led to serious disturbances in fish communities:

- an increase in the concentration of fishes in a smaller volume, leading to greater interspecies competition and increased vulnerability to fishing gear;
- the lacustrine landscape was overhauled with the lower depth: near-disappearance of vegetation-free open water and development of marshy biotopes encumbered by macrophytes colonizing the shoals;
- owing to the decreased depth, thunderstorms and strong winds stir up waters and sediments more easily, increasing turbidity and decreasing the oxygen content. These water deoxygenation phenomena were responsible for massive fish mortality (Bénech *et al.*, 1976);
- exundation of shoals led to isolation of parts of the lake, obstructing fish movement and the entry of floodwaters.

During the drying-out period, only those species that were adapted to the new ecological conditions prevailing in an increasingly swampy environment were able to survive. The evolution of captures through gillnet fishing in the lake's SE archipelago (table 20.I and figure 20.1) clearly illustrates these changes in terms of species presence.

The lowest level was reached in 1973, and the South-East archipelago was isolated from the rest of the lake in April 1973 as a result of the exposure of the shoals. Several species disappeared from July to September, at the time of the lowest waters, and before the arrival of the flood: *Hydrocynus forskalii, Citharinus citharus, Synodontis membranaceus, Lates niloticus, Alestes dentex* and *Labeo senegalensis*. Storms in June-July, in triggering anoxic conditions by stirring up waters, probably played a role in the disappearance of these species. But the decrease in depth also compromised the free movement of fishes and exchanges between the archipelago and the rest of the lake.

The 1974 flood allowed water to reach near-normal levels in the southern basin. However, before reaching the SE archipelago, this floodwater submerged a

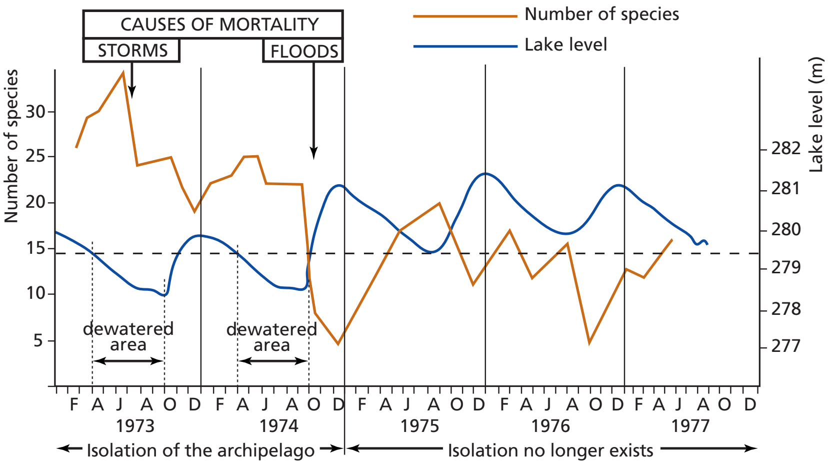


FIGURE 20.1.
Changes in water level and number of fish species caught with experimental gillnets in the South-East archipelago of Lake Chad during the drought period (from Bénech & Quensière, 1989).

TABLE 20.I.

Change in fish species composition in the Lake Chad South-East archipelago during a period of drought (from Bénech & Quensière, 1989).

M: large scale migratory fishes; R: aerial respiration; J-J: January-June; A-D: August-December; J-S: January-September; O-D: October-December.

	Species	**1971**		**1972**		**1973**		**1974**		**1975**	**1976**	**1977**
		J-J	**A-D**	**J-J**	**A-D**	**J-J**	**A-D**	**J-S**	**O-D**			
M	*Mormyrus rume*	●	●	●	●	●	●					
	Mormyrops anguilloides	●	●	●	●	●						
	Hippopotamyru ssp.	●	●	●	●	●	●					
	Bagrus bajad	●	●	●	●	●	●					
	Chrysichthys auratus	●	●	●	●	●						
	Labeo coubie	●	●	●		●						
	Brycinus macrolepidotus	●	●	●		●						
M	*Hydrocynus brevis*	●	●	●	●	●						
	Hydrocynus forskalii	●	●	●	●	●	●	●				
M	*Citharinus citharus*	●	●	●	●	●						
M	*Synodontis membranaceus*	●	●	●	●	●	●					
	Lates niloticus	●	●	●	●	●		●				
M	*Hyperopisus bebe*	●	●	●	●	●	●	●				
M	*Marcusenius cyprinoides*	●	●	●	●	●	●	●				
M	*Petrocephalus bane*	●	●	●	●	●	●	●				
M	*Pollimyrus isidori*	●	●	●	●	●	●	●				
M	*Labeo senegalensis*	●	●	●	●	●	●	●				
M	*Schilbe mystus*	●	●	●	●	●	●	●				
	Synodontis clarias	●	●	●	●	●	●	●				
MR	*Polypterus bichir*	●	●	●	●	●	●	●				
R	*Polypterus endlicheri*	●	●	●	●	●	●		●	●		
	Auchenoglanis spp.	●	●	●	●		●	●		●		
M	*Schilbe uranoscopus*	●	●	●	●	●	●	●		●	●	
M	*Synodontis batensoda*	●	●	●	●	●	●	●	●	●	●	
	Synodontis frontosus	●	●	●	●	●	●	●		●	●	
M	*Synodontis schall*	●	●	●	●	●	●	●		●	●	●
M	*Alestes dentex*	●	●	●	●	●	●	●		●	●	●
M	*Alestes baremoze*	●	●	●	●	●	●	●		●	●	●
	Brycinus nurse	●	●	●	●	●	●	●	●	●	●	●
M	*Distichodus rostratus*	●	●	●	●	●	●	●	●	●	●	●
R	*Gymnarchus niloticus*	●	●	●	●	●	●	●	●	●	●	●
R	*Clarias* spp.	●		●	●		●	●	●	●	●	●
	Coptodon zillii	●	●	●	●	●	●	●		●	●	●
	Sarotherodon galilaeus	●	●	●	●	●	●	●		●	●	●
	Oreochromis niloticus	●	●	●	●	●	●	●	●	●	●	●
	Oreochromis aureus		●	●		●	●	●		●	●	●
R	*Polypterus senegalus*			●	●	●	●	●	●	●	●	●
	Schilbe intermedius			●		●	●	●		●	●	●
R	*Heterotis niloticus*	●					●	●		●	●	●
R	*Brevimyrus niger*	●					●	●	●	●	●	●
	Siluranodon auritus						●	●		●	●	●

large quantity of decomposing plants, which led to an oxygen deficit lasting at least 3 months. Most of the common species that had survived up to that time thus disappeared due to the hypoxic conditions: *Labeo senegalensis, Schilbe mystus, Lates niloticus, Polypterus bichir, Synodontis clarias, Marcusenius cyprinoides, Hyperopisus bebe, Petrocephalus bane, Pollimyrus isidori.* The Mochokidae which accounted for 45% of captures a month earlier disappeared in a few days, and the number of species fell sharply in experimental gillnet captures, from 23 in September to 8 in October. In December 1974, only fishes with accessory respiratory organs could be found (table 20.I) such as *Polypterus senegalus, Brevimyrus niger* and *Gymnarchus niloticus*, along with a few individuals from other species with good resistance to hypoxia: *Distichodus rostratus, Oreochromis niloticus, Synodontis batensoda* (Bénech & Lek, 1981).

The persistence of a connection with the southern basin in 1975 allowed recolonization by a few species: *Sarotherodon galilaeus, Oreochromis* spp., *Schilbe mystus, Siluranodon auritus, Distichodus rostratus*, as well as pelagic species such as *Alestes baremoze* and *Alestes dentex* that rapidly recolonized the archipelago. The fish community during the 1975-1977 period remained stable, despite the disappearance of 3 species that had survived up to that point: *Schilbe uranoscopus, Synodontis batensoda, Synodontis frontosus.* There were fewer than 20 species after 1975, compared with 34 in 1973. The species richness of the SE archipelago shows a seasonal cycle, with a sharp decline at the onset of the flood, followed by an increase until the end of the next water outflow period.

Despite the speed of changes in the environment, the fish community has adapted to the succession of different lake facies, as manifested by the appearance and disappearance of species depending on environmental conditions. The prevalence of hypoxic conditions at certain periods favoured species with respiratory adaptations, and the annual flood, by restoring connections with the southern basin, allowed recolonization by the fluvio-lacustrine stock which more or less acted as a refuge zone.

In the open waters of the southern basin, the connection with the Chari was not interrupted, and after 1974 the system reacquired a lacustrine facies with areas of open water surrounded by thick belts of vegetation.

The northern basin evolved differently. In mid-1973 it was isolated from the Chari's floods owing to the exposure of a shoal area known as "Grand barrière". Only the water brought by the Yobe River, which emptied into the northern portion of the lake, compensated in part for losses by evaporation, but by November 1975 the northern basin of the lake had dried up. The concentration of fishes during this period attracted many fishers, and *Heterotis niloticus, Hydrocynus brevis, Citharinus citharus, Mormyrus rume, Pollimyrus isidori* and *Tetraodon lineatus* progressively disappeared in the second half of 1974. Massive mortalities as a result of storms were also observed (Bénech *et al.*, 1976). The abundance of species such as *Polypterus senegalus* increased in the captures, as did *Sarotherodon galilaeus, Oreochromis aureus* and *O. niloticus*. After 1975, the northern basin was partially flooded each year and a swamp community containing numerous Clariidae colonized this marshy zone.

These fluctuations in the environment and fish communities explain why there are no endemic species in Lake Chad, and all the species present there have also been observed in the Chari. It has even been suggested that Lake Chad is simply an extension of the fluvial system whose species can recolonize the lake after periods of dryness.

Lake Chilwa, southeast of Lake Malawi, is another example of an endorheic lake showing significant fluctuations in area. It is formed primarily by a vast zone of open water surrounded by large marshy areas dominated by *Typha domingensis*. Unlike Lake Chad, Lake Chilwa is only fed by small tributaries, but it has also run into periods of drying out. In 1968 for example, the lake had its lowest recorded level since 1920 and almost completely dried out (Kalk *et al.*, 1979). These variations in level were accompanied by changes in salinity, with high values (16,720 µS) in 1968.

Approximately 30 species are known in the Lake Chilwa basin, but many have only been observed in tributary watercourses. In high water periods, only 3 species constitute the bulk of captures: *Clarias gariepinus, Barbus paludinosus, Oreochromis shiranus*. During the dry season and in periods of low water levels, these species migrate to neighbouring pools where they find waters that are less saline and less turbid. They recolonize the lake when water levels rise. Meanwhile, marshes and tributaries are inhabited by much richer fish fauna that colonize the open waters during floods: *Petrocephalus catostoma, Marcusenius macrolepidotus, Brycinus imberi, Labeo cylindricus, Barbus trimaculatus, Coptodon rendalli, Pseudocrenilabrus philander*, etc. (Kirk, 1967 ; Furse *et al.*, 1979).

Lake Baringo in the Rift valley in Kenya is also endorheic, supplied by two small rivers. Fish fauna is poor, composed essentially of one Cichlidae (*Oreochromis niloticus*), a Clariidae (*Clarias gariepinus*), and two Cyprinidae (*Labeo intermedius* and *L. cylindricus*) (Worthington & Ricardo, 1936).

The fish fauna of Lake Naivasha is almost exclusively composed of introduced species: *Micropterus salmoides* was introduced in 1925, *Oreochromis leucostictus* and *Coptodon zillii* in 1956. *O. leucostictus* preferably inhabits *Papyrus* grass patches, as does *M. salmoides*. Meanwhile *C. zillii* prefers *Nymphea* patches and feeds on macrophytes. The lake's endemic species, *Aplocheilichthys antinorii*, still recorded in 1962, probably disappeared as the result of predation by *Micropterus* (Elder *et al.,* 1971).

Lake Turkana is currently an endorheic lake supplied by the Omo River, whose slightly saline waters have a conductivity of up to 3500 µS (Kolding, 1992). Strictly speaking, it is not a shallow lake, but its average depth is low for most of its area and the lake is not stratified. In the past it was connected to the Nile basin which explains why most of its fish fauna tends to the nilotic.

Of 48 fish species known in the basin, 36 are regularly found in the lake and 12 have a distribution limited to the Omo River delta (Hopson, 1982 ; Lévêque *et al.*, 1991). Some species, such as *Lates niloticus, Synodontis schall, Barbus bynni bynni, Neobola stellae* have a rather wide distribution, but most of the others are limited to specific habitats. Three types of communities have been identified in the lake itself:

- the *coastal community*, limited to a belt covering the edge of the lake and a depth of 4 m. This community contains especially *Oreochromis niloticus* and *Clarias gariepinus,* as well as *Coptodon zillii* and *Raiamas senegalensis* in the rocky bottoms or *Sarotherodon galilaeus*, *Brycinus nurse*, *Micralestes acutidens* and *Chelaethiops bibie* in the mobile bottoms;
- the *demersal community*, comprising benthic species living near the banks between depths of 4 to 10-15 m. The characteristic species are *Labeo horie*, *Citharinus citharus*, *Distichodus niloticus* and *Bagrus docmak*. In deeper zones, the species are *Bagrus bajad*, *Enteromius turkanae*, and *Haplochromis macconneli* which live close to the bottom;
- the *pelagic community*, which includes species such as *Hydrocynus forskalii* and *Alestes baremoze* that are more numerous in the upper layers, and *Brycinus minutus*, *B. ferox*, *Lates longispinis,* and *Schilbe uranoscopus* in open waters.

A large proportion of species carry out seasonal migrations in the Omo River to breed. Among the species breeding in the lake, some have demersal eggs (*Bagrus* spp.), or pelagic eggs (*Lates* spp. and *Brycinus* spp.), while other species provide parental care (*Oreochromis, Sarotherodon, Haplochromis, Tilapia, Heterotis*).

Experimental fishing carried out in 1986-1987 were compared with results obtained during campaigns done in 1972-1975 (Bayley, 1977; Hopson, 1982). There were no significant changes for demersal communities, while for pelagic communities, the populations of *Hydrocynus forskalii, Alestes baremoze* and *Schilbe uranoscopus* declined by about 70% compared with the 1972-75 results (Kolding, 1992). It appears that the pelagic community, whose production is based on the use of zooplankton, was most sensitive to the drop in the lake's levels over a decade or so.

Open shallow lakes

In open lakes, there is a permanent or seasonal connection with a river. These lakes are periodically recolonized by fluvial species, so species richness is generally rather high.

Lake George (Uganda), which has an average depth of 2.4 m, has been the target of numerous limnological investigations. Most of its waters come from the Rwenzori and it has an effluent, the Kazinga River, which empties into Lake Edward (Viner & Smith, 1973). This in turn is connected to Lake Albert via the Semliki River. Lake George's watershed was isolated from Lake Victoria's owing to tectonic movements.

Lake George in its current form is relatively young, at around 4,000 years. Its formation took place after a period of volcanic activity that occurred some 8 to 10,000 years ago and which proved fatal to many species living in Lake Edward (Beadle, 1981). The presence of waterfalls and rapids that were difficult to navigate apparently prevented reinvasion from Lake Albert, and current fauna originated from the fauna of the lake's small tributary rivers as well as the fish fauna of Lake Edward itself.

Two fish groups were identified based on their distribution in the lake (Gwahaba, 1975). The first group includes species captured near the banks and in the open: *Protopterus aethiopicus, Haplochromis nigripinnis, H. pappenheimi, H. angustifrons, Lacustricola vitschumbaensis.* For some species such as *Bagrus docmak, Clarias gariepinus, Haplochromis squamipinnis, Oreochromis niloticus* and *O. leucostictus*, a gradient of diminishing abundance from the banks to the open was observed. In fact, the abundance of juvenile forms near the banks may account for this gradient.

The second group includes 15 species captured only near the banks: *Astatoreochromis alluaudi, Enteromius kerstenii, E. neglectus, Ctenopoma muriei, Marcusenius nigricans* and several *Haplochromis* species. This type of distribution may be due to food requirements. *Haplochromis aeneocolor* feeds mainly on macrophyte debris and *Haplochromis limax*, which feeds on periphyton, remains close to emerging vegetation such as *Vossia cuspidata*. *Haplochromis mylodon* consumes the gastropod *Melanoides tuberculata*, *H. taurinus* feeds on eggs and embryos, and *H. petronius* feeds in the coastal rocky substrate.

TABLE 20.II.
Fish species composition in some shallow lakes from Tropical Africa.

Lakes	species number	Mormyridae	Alestidae	Cyprinidae	Clariidae	Mochokidae	Cyprinodontiformes	Cichlidae	Schilbeidae	Polypteridae	*Lates*	Citharinidae	Bagridaeidae/Claroteidae	others	Source
Salt lakes															
Magadi	**1**							1							Coe, 1969
Nakuru	**1**							1							Coe, 1969
Natron	**1**							1							Coe, 1969
Endorheic lakes															
Chad	**137**	16	12	27	5	14	7	11	6	3	1	15	7		Blache *et al.*, 1964
Ngami	**48**	5	3	10	2	4	3	15	1			2	1	2	Skelton *et al.*, 1985
Chilwa	**31**	3	2	12	2	1		5					1	5	Furse *et al.*, 1979
Turkana	**49**	3	9	2	2	3	7	7	1	2	2	2	4	5	Hopson, 1982
Baringo	**4**			2	1			1							Worthington & Ricardo,1936
Open lakes															
Awasa	**3**			1	1			1							Gasse, 1987
Ziway	**8**			7				1							Gasse, 1987
Abaya	**28**	3	1	13	2	4		2	1		1		1		Gasse, 1987
Tana	**20**			16	3			1							Gasse, 1987
Mweru	**114**	16	10	32	11	9		16	3			3	3		De Kimpe, 1964
Albert	**41**	3	6	8	2	2		6	2		2	3	3	4	Hulot, 1956
Ihema	**34**	7	3	8	2	1	1	10	1					1	Plisnier *et al.*,1988
George	**30**	2		3	1			21					1	4	Gwahaba, 1975
Tumba	**86**	23	16	4	11	3	5	9	3	3	1	14	9	?	Matthes, 1964
Liambezi	**43**	3	3	10	3	4	2	15	1					2	van der Waal, 1980

Three species, *Oreochromis niloticus, Haplochromis nigripinnis* and *Haplochromis angustifrons*, make up nearly 80% of the fish biomass (Gwahaba, 1975). The first two (60% of biomass) are herbivorous and consume cyanobacteria. There is a marked gradient in the distribution of biomass which goes as high as 900 kg ha^{-1} near the banks and only 60 kg ha^{-1} in the centre of the lake, with the average for the entire lake at 290 kg ha^{-1}.

Several lakes of the Ethiopian Rift Valley (Galla lakes) are shallow lakes with a relatively poor fish community (Riedel, 1962). In Lake Ziway only a few species of Cyprinidae and one Cichlidae (*Oreochromis niloticus*) can be found. Lake Abijatta and Lake Awasa, located south, are just as species-poor, whereas in Lakes Abaya and Shamo, even further south, species diversity is greater. There are 28 species belonging to different families in Lake Awasa (table 20.II).

Ethiopian lake fauna is impoverished Nilotic fauna. During the wet periods of the quaternary, Lakes Ziway and Abyata, as well as the deeper Lakes Langano and Shala, formed a single lake, Ziway-Shala, which emptied northwards in the Awash River and towards Lake Abbe in Afar.

Lake Tumba is located in the central region of the Congo basin. It has a permanent connection with the Congo River through the Irebu channel in the north. Its fishes were investigated by Matthes (1964). The fauna is diverse (120 species), because of the permanent connections with the river, but also due to the diversity of biotopes found in the lake's banks. In open water, schools – sometimes large ones – of planktivorous fishes (*Barbus, Clupeopetersius, Microthrissa*) as well as predators such as *Odaxothrissa losera, Mormyrops anguilloides, Hydrocynus*, etc. can be found. A group of fin-eating predators (*Belanophago, Phago, Eugnathichthys*) is especially well-represented in Lake Tumba.

The hydrology of Lake Liambezi (Namibia) is complex. It receives water from different sources including the Zambezi which sometimes empties southward (Seaman *et al.*, 1978). The lake's tributary to the Chobe River is intermittent and depends on the lake's level. Depth is less than 5 m and practically constant throughout the extent of the open waters (100 km^2) which are surrounded by a vast marshy zone (200 km^2). About 43 species, including 15 Cichlidae, were captured in the lake itself, and all are also present in the Upper Zambezi where 73 fish species were identified (van der Waal & Skelton, 1984). In the Chobe River and its floodplains, 56 species are known and are also present in the Zambezi. Most of the fishes observed in the lake and marshes are palustrine species, and some of these are highly tolerant to anoxia and can survive in environments that are completely convered by *Salvinia molesta,* an introduced floating plant.

Conclusions

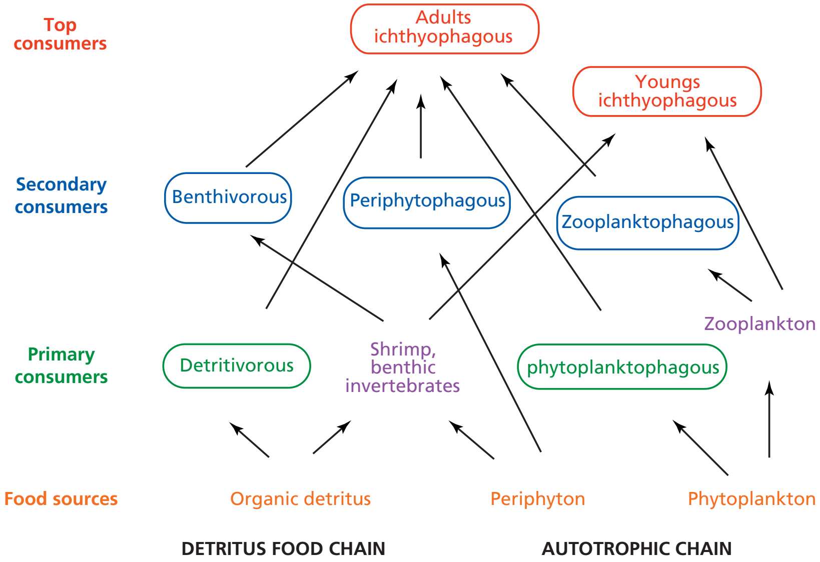
Saltwater lakes fed by groundwater have very poor communities, formed essentially by one Cichlidae species adapted to these extreme East African environments. Many of these salt lakes do not host a single fish species, as can be seen in the many salt lakes of the Kanem region north of Lake Chad.

The fish population of shallow freshwater lakes is highly dependent on that found in the rivers with which the lakes are associated. The biogeographic situation, the area of the drainage basin (see chapter *Biogeography and past history of the ichthyological faunas*) and the basin's climate and geological history (see chapter *Geographical distribution and affinities of African freshwater fishes*) determine the possibilities for lake population. In general, there is a low rate of endemism. Despite its high number of species, Lake Chad does not have a single endemic species. Lake George is an exception, with 16 endemic *Haplochromis* species, that is about half of all species found in it.

Because of their depth, shallow lakes are subject to significant variations in area depending on fluctuations in water supply, which are in turn dependent on climate variations. During periods of water deficit, these fluctuations select species adapted to palustrine conditions that are able to tolerate poor water oxygenation and more or less prolonged periods of anoxia (see chapter *Diversity of responses to extreme environmental conditions*). Meanwhile, during periods with a good supply of water, the area expands, depth increases, and a pelagic system may be established. The latter may nonetheless be strongly influenced by the coastal area and the benthic system, whether in terms of food supply or biogeochemical interactions. Because of the shallowness, significant disturbances can nonetheless occur, such as those triggered by tornadoes which bring sediment particles in suspension in the water, and even lead to massive fish mortalities (see chapter *Diversity of fish habitats*).

Shallow lakes such as Lakes Chad, Chilwa, or Ngami are highly dependent on water supply, which makes them particularly vulnerable to the impact of human activity. In particular, water collection from their tributaries disturbs the water balance, and at present, the water surface of these lakes tends to be going down.

FIGURE 20.2.
Simplified representation of the main components of a food web in a shallow lake with a high specific richness.



The fact that these shallow lakes can more or less be considered vast coastal zones is a factor that favours high productivity in these environments, where fishing is generally active (see chapter *Fisheries*). In species-rich lakes such as Lake Chad or Lake Mweru, trophic networks are organized around two chains: the detritus food chain and the autotrophic chain (figure 20.2). This results in a very complex network of interactions between fish species, given that juveniles of some species compete with adults of other species for the same trophic resources. In reality, though, many species have opportunistic regimes and are probably capable of adapting to available trophic resources.

We must remember that shallow lakes are not closed systems but have important exchanges with the terrestrial environment surrounding them. There are thus many live or dead organisms that fall into the lakes, as well as detritus of terrestrial origin. Stomachs of *Schilbe mystus* captured in open waters, tens of kilometres from the banks of Lake Chad, have been found to be full of orthopteran insects (Lauzanne, 1976). Meanwhile, vertebrates such as birds (see chapter *Role of fish in ecosystem functioning*) and some mammals can take out significant numbers of fishes from the aquatic environment.

Exchanges also take place during migrations of certain fish species in the tributaries. These are often breeding migrations (see chapter *Life-history strategies*) or trophic migrations, but the latter are still poorly documented.

Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes

DIDIER
PAUGY

CHRISTIAN
LÉVÊQUE

Small aquatic ecosystems generally have several similar physical and biological characteristics. Except for their size, they are, most of the time, extreme ecosystems. For example, soda lakes have very high salinity and/or alkalinity; crater lakes are deep with a low level of oxygen in the deep layers of the water; in gueltas and chotts, the water is perennial in only a few and the temperature is high; in caves, organisms live in permanent darkness. In relation with these severe conditions, fish have developed physiological and behavioural adaptations that allow them to survive and perpetuate. Thus, specific and usually endemic species inhabit these environments. In some cases, small species flocks exist, as can be observed in the Great Lakes of East Africa. Finally, most of these environments are vulnerable to even minor disturbances. Continued vigilance, protective measures and conservation recommendations must be a high priority to protect them from actual or potential local threats.

Strictly speaking, the crater lakes and the graben/horst lakes are different, while they both owe their formation to tectonic events.

A crater lake is a lake that formed in a volcanic crater or a caldera. In Africa, most of the crater lakes are located in dormant or extinct volcanoes, and tend to be freshwater. The water clarity in such lakes can be exceptional due to the lack of inflowing streams and sediment. Crater lakes are well represented in tropical Africa, especially in the Guinean rainforest zone of Cameroon, where there may be 36 or more (McGregor Reid & Gibson, 2011). There are also crater lakes in Eastern Africa, mainly high-mountain crater lakes in Ethiopia (Degefu *et al.*, 2014), but the natural fish richness is generally very low or non-existent.

A graben is the result of a block of land being downthrown, producing a valley with a distinct scarp on each side. Grabens often occur side-by-side with horsts. Horst and graben structures are indicative of tensional forces and crustal stretching. This kind of lake is very present in the eastern arm (Gregory branch) of the African Rift Valley. This Gregory rift valley is most clearly defined in Kenya where classical grabens penetrate the regional domal upwarping. A string of lakes follow its course southward through Kenya and into Tanzania, including Turkana, Baringo, Bogoria, Nakuru, Elmenteita, Naivasha, Magadi, Natron, Eyasi and Manyara.

Lake level is a product of the balance of inputs (precipitation, inflowing streams, groundwater inflows) and outputs (evaporation, outflows, groundwater seepage). The relative importance of these factors will govern the responsiveness of particular basins to changes in climate, and these will be examined in the following section (*Salt and alkaline lakes*).

Salt and alkaline lakes

A salt lake is generally a landlocked body of water whose concentration of salts (typically sodium chloride) and other dissolved minerals is significantly higher than most lakes (often defined as at least three grams of salt per litre). In some cases, salt lakes have a higher concentration of salt than seawater, but such lakes would also be termed hypersaline lakes. That is, for example, the case of Lake Retba in Senegal ("lac Rose" meaning "Pink lake" as it is known by locals) where the salinity is between 80-350 g/l according to the seasons (Sow *et al.*, 2008).

An alkaline lake that has a high carbonate content is sometimes called a soda lake. This type of lake is alkaline with a pH value above 7.5. In addition, many soda lakes also contain high concentrations of sodium chloride and other dissolved salts, making them saline lakes as well. High pH and salinity often coincide.

Salt and soda lakes form when the water flowing into the lake, containing salt or minerals, cannot leave because the lake is endorheic (without outlet). The water then evaporates, leaving behind dissolved salts and thus increasing its salinity, making a salt lake an excellent place for salt production.

The hypersaline and highly alkalic soda lakes are considered some of the most extreme aquatic environments on Earth. In spite of their apparent inhospitableness, soda lakes are often highly productive ecosystems, compared to their (pH-neutral) freshwater counterparts. An important reason for this high productivity is the virtually unlimited availability of dissolved carbon dioxide.

Nevertheless, overly high salinity or alkalinity will also lead to a unique flora and fauna in the lake in question; sometimes, in fact, the result may be an absence or near absence of life near the salt lake. In fact it depends on the tolerance of organisms to the mineral concentrations that exist in the lake. For African fish like cichlids, we generally agree that the highest salinity must not exceed 50-60 g/l (see also chapter *Diversity of responses to extreme environmental conditions*). Thus, some specialized species, like *Alcolapia grahami*, have been introduced with success in Lake Nakuru (Kenya), where salinity can reach 20-25 g/l (Vareschi, 1982). However, authors (Garnier & Gaudant, 1984) have recorded the presence of a tilapia (*Sarotherodon melanotheron*) in Lake Retba (Senegal) where salinity reaches at least 80 g/l but can rise up to 350 g/l during the dry season.

In their paper the authors say "In its North-Eastern part, the lake is extended by an intermittent creek that is supplied in water through inputs from groundwater.

It is in one of these water holes that we have observed many cichlid fish of which one specimen was captured in April 1978". At present these holes no longer exist, but there are still small ponds of brackish water where a dwarf form of *Sarotherodon* still lives. In these ponds as well as the ancient holes, water is less concentrated than in the lake itself, which is really unsustainable for tilapines.

Soda lakes occur naturally throughout the world (see Table 21.I below for African ones), typically in arid and semi-arid areas and in connection to tectonic rifts like the East African Rift Valley. The pH of most freshwater lakes is on the alkaline side of neutrality and many exhibit similar water chemistries to soda lakes, only less extreme.

TABLE 21.I.

Chemical characteristics (pH and salinity) for major African salt lakes.

Name	Country	pH	Salinity (g/l)
Wadi Natrun lakes	Egypt	9.5	50
Malha Crater Lake	Sudan	9.5-10.3	
Lake Abbe	Ethiopia	9.8-11	115
Lake Arenguadi (Green Lake)	Ethiopia	9.5-9.9	2,5
Lake Basaka	Ethiopia	9.6	3
Lake Shala	Ethiopia	9.8	18
Lake Chitu	Ethiopia	10.3	58
Lake Abijatta	Ethiopia	9.9	34
Lake Magadi	Kenya	10	>100
Lake Bogoria	Kenya	10.5	350
Lake Turkana	Kenya/Ethiopia	8.5-9.2	2,5
Lake Nakuru	Kenya	10.5	5-90
Lake Logipi	Kenya	9.5-10.5	20-50
Lake Manyara	Tanzania	9.5-10	40
Lake Natron	Tanzania/Kenya	9-10.5	100
Lake Rukwa	Tanzania	8.5-9.2	
Lake Eyasi	Tanzania	9.3	5

Generally speaking, tilapias *s.l.* have a wide and varied diet and can occupy a large range of habitats, from freshwater to hypersaline conditions; therefore, its distribution is unlikely to be limited by many environmental, physical or chemical conditions. However, the one factor that appears to affect tilapia is its vulnerability to cold temperatures. Tilapia is traditionally viewed as a tropical to warm-temperate species.

Salt concentration may constitute a limiting factor for fish and for other many organisms. Thus, in Africa a marked decrease has been observed in the number of zooplankton and foraminifera species in increasingly confined water (Debenay *et al.*, 1989). Likewise, studies on the Casamance river have shown that fish taxa disappear with increasing salinity and that fish fauna becomes monospecific (*Sarotherodon melanotheron*) above 75‰ (Albaret, 1987). The capacity of *S. melanotheron* to withstand salty environments suggests that this species has the capacity to modify its life-history traits, mainly reproductive and growth ones. The most profound changes are only visible in hypersaline conditions where the species is able to limit its growth, to reduce its size-at-maturity, and to change its fecundity (Panfili *et al.*, 2004b). The main modification in the reproductive traits concerns the change in size at maturity, which decreases in *S. melanotheron* as salinity increases. Conversely, the influence of intermediate or high salinities (35-90‰) don't show any clear significant relationship with fecundity or oocyte size of this species (Panfili *et al.*, 2004b).

Some authors mentioned several species of tilapias isolated in the alkaline lakes of the Great Rift Valley of Africa, living in extreme conditions of temperature, salinity and pH (Reiter *et al.*, 1974). It is true for some of them like *Oreochromis mossambicus* or *Sarotherodon melanotheron*, which may survive for some time in harsh conditions. But, it seems that only one complex of fish species (*Alcolapia*) can actually be found in saline and alkaline lakes and is adapted to very harsh conditions. Much research has been performed on these fish, indicating that the fish have adapted to live in temperatures up to and possibly above 44°C, a pH varying between 5-11 (though the lake naturally ranges from pH 9-11), low oxygen levels in the water (as low as 1.1 mg O_2/L of water), and a salinity concentration of up to 4% (Reiter *et al.*, 1974). These tilapia developed many adaptations to survive in this lake where, due to the lake's extreme conditions, little other non-microbial life exists.

Until recently only one cichlid species (Soda tilapias) was known from the Lake Natron basin, *Alcolapia alcalica*, assumed to be very closely related to *A. grahami* from Lake Magadi, some 20 km to the north of Lake Natron. But today we know that the Lake Natron basin hosts a small species flock of four polymorphic tilapiine cichlids (Seegers & Tichy, 1999). Later, it was found that the Soda tilapias are fairly distant (mitochondrial DNA sequences) compared with related *Oreochromis* species in the area that are closer together. These results, as well as morphological data, confirm that the Soda tilapias must be considered as a new genus, *Alcolapia* (Seegers *et al.*, 1999).

In natural salt lakes like Lake Nakuru and Lake Elmenteita, where no fish at all was present (Kenya), *Alcolapia alcalica* and *A. grahami* were introduced in the early 1960s and naturalized. Conversely, in Lake Bogoria (Kenya), which is alkaline (pH>10) and saline (from 100 to 300 g/l, total dissolved salt), fish life seems impossible, although the lake is highly productive with abundant cyanobacteria and rotifer. But the ecological conditions are too harsh for fish.

Gueltas and chotts: the Sahara fish fauna

These collections of water are other types of harsh biotopes (see box "Some definitions concerning some particular small isolated patches of water"). Their common characteristic is to have very impoverished fauna constituted by

SOME DEFINITIONS CONCERNING SOME PARTICULAR SMALL ISOLATED PATCHES OF WATER

NOTE 1

Originally, wadi refers to a dry (ephemeral) riverbed of North Africa that contains water only during times of heavy rain or simply an intermittent stream. Nevertheless, in the Maghreb, the term *wadi* is, most of the time, applied to all rivers including regular ones.

A **guelta** is a pocket of water left in drainage channels or wadis[1] during the dry season in the Sahara (Ramdani *et al.*, 2010). The size and duration will depend on the location and conditions. It may last year-round through the dry season if fed by a source such as a spring. When rivers (wadis) dry up there may remain pockets of water along its course.

A **chott** is ephemeral and usually possesses brackish water (Ramdani *et al.*, 2010). In geology, a chott is a dry (salt) lake in the Saharan area of Africa (mainly in Tunisia, Algeria and Morocco) that stays dry in the summer, but receives some water in the winter. These lakes have changing shores and are dry for much of the year.

A **cave** is an underground natural hollow. Some caves, connected to a dynamic hydrographic system, may include an underground lake or a river.

some resistant fish species belonging to three main families, Cyprinidae, Cichlidae and Clariidae. These species have evolved abilities to survive in extreme conditions (see also chapter *Diversity of responses to extreme environmental conditions)*.

For a long time the Sahara Desert was considered to be an obstacle to dispersals of humans and animals. But nowadays it is evident that the Sahara was not an effective barrier and that both animals and humans had been present during the past humid phases (Drake *et al.*, 2011). Dispersal was facilitated during the Holocene humid period when linked lakes, rivers, and inland deltas were present. Furthermore, the presence of several fish species in more or less perennial collections of water attest to wet conditions in this area during the Holocene. Finally, it was interesting to note that this relict fish fauna is always housed in mountainous massifs from Mauritania to Chad.

Fish communities in gueltas

Here, we exclude the fish fauna in the Atlantic slope and only take into account the southern part of the Maghreb province including the Sahara desert. Most of the perennial water bodies where fishes have survived since the last humid period match with gueltas or wells located in the main Saharian mountains (figure 21.1):

- Ahaggar (Hoggar), Mouydir and Tassili n'Adjer in southern Algeria;
- Adrar in Mauritania;
- Tibest, Ennedi and Borkou in northern Chad.

Gueltas are mainly encountered in mountains because of the soil composition, which is generally rather water impermeable. So, gueltas are fed by rainwater that has accumulated in rocky pools (sandstones, basalts, granites) or in ponds with clay bottoms. If some Chadian gueltas, in Ennedi or Tibesti, may have relatively large dimensions (a few hundred square meters) those of Mauritania are conversely very small and their surface does not exceed one square meter with a depth of 15-20 cm. Nevertheless, such small collections of water may contain more than 50 *Barbus* (Daget, 1968).

FIGURE 21.1.
Saharian mountains (except Tenere) where fishes survive in gueltas or wells.

The presence of fish in the Sahara was reported in the early 20th century (Pellegrin, 1937). Later, the inventory of perennial water bodies was expanded in the 1950s (Monod 1951; 1954; 1955; Daget, 1959a). More recently, systematic revisions and re-examination of collections hosted in different museums have clarified and completed the inventory (Lévêque, 1990). Finally, very recently, a series of surveys were carried out in the Adrar Mountains in Mauritania (Trape, 2009) and in the Tibesti Mountains, the Borkou plateaus and the Ennedi Mountains in northern Chad (Trape, 2013).

Sixteen species of fish belonging to six families were reported in perennial bodies of water in the Sahara desert (table 21.II). Most of them are relict populations of Sudanese fish species, but one of them, *Barbus callensis*, restricted to the Hoggar mountains (Ahaggar and Tassili N'Ajjer) in the Sahara area is a northern colonizer widespread in most of the coastal wadis in the Maghreb province (figure 21.2). *Astatotilapia desfontainii* is one among doubtful fish species occurring in the considered area. This species is native from Algeria and Tunisia (the type locality is Gafsa in central Tunisia, north of Chott El Jerid). In Algeria, its most southern distribution reaches Ouargla and Hassi Massaoud (Schraml, 2010). Unfortunately, no fish collection confirms such an austral extension. Trape (2009 and 2013) also mentions the presence of this species in the Mouydir basin which is an extension of the Tassili n'Ajjer, but none of the cited references provide such information. In the collections housed in different museums, the most austral presence of the species is Biskra. Finally, this species was never reported in the Sahara fish fauna synthesis (Doadrio, 1994). Therefore, at the moment we consider that the presence of *A. desfontainii* in southern Algeria (Hoggar Mountains) seems very doubtful. Trape (2009 and 2013) reports two sub-species of *Sarotherodon galilaeus*, the first *S. g. galilaeus* (Linnaeus, 1758) present in the Adrar Mountains (Mauritania) and the second *S. g. borkuanus* (Pellegrin, 1919) present in the northern Chad desert. But according to Trewavas & Teugels (1991), all subspecies

FIGURE 21.2.
Distribution of the 16 species recorded in the Sahara region.

of *S. galilaeus* must be synonymised. Finally, we must consider some introduced species reported in data collections (Paugy *et al.*, 2014). Trape (2009) specifies that there are no fish in the Aïr massif of Niger, but some specimens of *Oreochromis aureus* have been introduced and apparently naturalized in the Dirkou oasis. In the Fezzan desert, Libya, several species of the poeciliid *Gambusia* (*G. affinis* and *G. holbrooki*) have been introduced. There is no date for the introduction of these species in Libya, but it could have been introduced by the Italians in 1929 (Jawad & Busneina, 2000). Currently the genus is widespread to almost local ponds and wells, frequently at the expense of other (native) species (Hughes & Hughes, 1992).

It appears that the relict fish fauna of the northern Chad area exhibits the highest diversity and this fauna is clearly related to the fauna that exists in Sudanese basins, *i.e.*, Nile and Chad in the region.[2] The Mauritanian fish fauna is also of Sudanese origin, but it is slightly different (*C. gariepinus* substituted by *C. anguillaris*) and only a third as diverse (4 species *versus* 12 in Chad area).

Despite the extreme aridity, it seems that the perennial water bodies in Chad region are more persistent and resistant, particularly in water volume, in this

NOTE 2
For the evolution from Mega-Chad to marshy Chad, see also chapter *Variability of the climate and hydrological systems*.

Families	**Species**	**Adrar Mauritania**	**Tassili Algeria**	**Ahaggar Algeria**	**Ennedi Chad**	**Tibesti Chad**	**Borkou Chad)**
Polypteridae	*Polypterus senegalus*						*
Cyprinidae	*Barbus apleurogramma*				*		
Cyprinidae	*Barbus callensis*		*	*			
Cyprinidae	*Barbus macrops*	*	*	*	*	*	
Cyprinidae	*Barbus occidentalis*					*	
Cyprinidae	*Barbus pobeguini*	*					
Cyprinidae	*Labeo niloticus*					*	
Cyprinidae	*Labeo parvus*				*	*	
Cyprinidae	*Raiamas senegalensis*					*	
Clariidae	*Clarias anguillaris*	*	*				
Clariidae	*Clarias gariepinus*		*		*	*	
Nothobranchiidae	*Epiplatys spilargyreius*						*
Poeciliidae	*Poropanchax normani*						*
Cichlidae	*Hemichromis bimaculatus*		*				*
Cichlidae	*Sarotherodon galilaeus*	*			*	*	*
Cichlidae	*Coptodon zillii*		*	*	*	*	
Total number of species		**4**	**6**	**3**	**6**	**8**	**5**

TABLE 21.II.
Distribution of the 16 relict fish species in Sahara.

region than in the Mauritanian area. Thus, pools, gueltas or wells prospected in the 1950-60s (Bruneau de Miré and Quézel in 1956; Gillet, Lauzanne and Monod in 1967) are still present and seem in good health. Conversely, with the drought that has lasted nearly forty years, the relict fish fauna in the Adrar region of Mauritania appear to be highly endangered. Thus, of the thirteen sites mentioned in the literature, four are no longer home to fishes, at least on a permanent basis, and one appears to be highly endangered (Trape, 2009). The repetition of severe climatic conditions in this region is perhaps the reason for the poverty of the fish fauna in this region.

In southern Algeria, the fish fauna is also rather poor, with six species. One, *Barbus callensis* is Palaeoarctic while the other five have a Sudanese origin, with an intermediate composition between Mauritanian and Chadian faunas (table 21.III).

Algeria	**Mauritania**	**Chad**
Barbus macrops	*	*
Clarias anguillaris	*	
Clarias gariepinus		*
Hemichromis bimaculatus		*
Coptodon zillii		*

TABLE 21.III.
Sudanese faunistic similarity between Algeria on the one hand versus Mauritania and Chad on the other hand.

All species of the relict fauna of the Chadian area are found in Chad and Nile basins, except *B. apleurogramma*. The record of this species in the Ennedi is more surprising as it is nowadays known from the Lake Victoria basin. Knowing that the species no longer occurs in the Chad and the lower Nile, it could well be the relict of a more ancient fish fauna extending northwards, and whose representatives later disappeared from Sudanese river basins. It may well be that *B. apleurogramma* from Ennedi was part of an ancient fauna which was more widely distributed than nowadays, and whose representatives probably disappeared during an arid climatic phase, with relict populations subsisting in particular zones. That could imply that the isolation of *B. apleurogramma* would be older than the last humid period.

Fish communities in chotts

The chotts, vast shallow temporary lakes of saline character, lie along the northern border of the Sahara, in the Sahara/Mediterranean transition zone, and are large salt flats. Some are flooded every winter; others seldom carry surface water. In Algeria, chotts are the major wetlands. Most of the chotts are of importance to wintering and migrating waterfowl, and support large numbers of ducks. Conversely, due to their high salinity and also because water is not generally perennial, most of the chotts are not inhabited by fish.

However, there are some exceptions such as the Chott Djerid and Chott el Fedjadj complex in Tunisia (Doadrio, 1994). The chotts proper are devoid of fish, amphibians, reptiles or mammals. By contrast much more diverse floras and faunas, including fishes, are found in the beds of the oueds that feed the chotts and in the springs around the margins. Several species of fish live in the oases, including *Aphanius fasciatus*, *Barbus callensis*, *Clarias gariepinus*, *Haplochromis desfontainesi* and *Hemichromis bimaculatus* (Doadrio, 1994). *Oreochromis niloticus*, *Poecilia reticulata* and *Gambusia affinis* have been introduced, this last one for mosquito control.

In Egypt, Lake Qarun (or Birket Qarun or Lake Moeris) (figure 21.3) was freshwater in prehistory, but it is a saltwater lake today and could be compared to a chott. Lake Qarun is endorheic and was, in the past, artificially fed by water from the Nile, but now, with modern agricultural practices, it receives only the

FIGURE 21.3.

Lake Qarun is an ancient lake in the northwest of the Faiyum Oasis, 80 km southwest of Cairo, Egypt. It persists in modern times as a smaller lake and the lake's surface is about 45 m below sea level and covers about 200-250 square kilometres. The lake has a mean depth of 4.2 m and a maximum depth of 8.5 m in the western basin. The rate of salinization has increased since the closure of the Aswan dam. Artificial fertilizers are used to replace the nutrients formerly provided by the sediment deposited during the annual flood, and these raise the concentration of salts in the waters entering the lake (© IRD/D. Paugy).

run-off from the irrigated peripheral lands, which enters the lake via two canals at the eastern end. The lake is becoming increasingly saline. At the turn of the 20th century salinity was measured as 13‰, but this had risen to over 34‰ in some parts of the lake by 1976. The most important species of fish are *Liza ramada*, *Mugil cephalus*, *Solea vulgaris* and *Coptodon zillii*. All of these were first introduced in 1928 and are now restocked annually (Hughes & Hughes, 1992). The evolution of the salinity of Lake Qarun has led to modifications in fish composition; its gradual increase led to the gradual disappearance of *O. niloticus* and *O. aureus* and their replacement by *C. zillii* (Fryer & Iles, 1972).

Although in some cases, as in Lake Qarun, there is a rather flourishing fishery, chotts or sebkhas are not suitable ecosystems for the development of fish. Most of the time in these environments, fish populations are very reduced and are restricted to freshwater areas close to springs or in tributaries.

Fish communities of caves

Caves are generally fed by tributaries of larger river basins. The fish fauna show adaptations in relation to a permanent darkness. Some species use caves only occasionally to avoid unfavourable conditions outside. Others live permanently in caves and these fishes are discussed here. According to Parzefall (1993), these true cave-dwellers can be called “troglobionts”. Their striking morphological differences in comparison with epigean relatives concern the reduction of the eye and generally uncoloured pigmentation. Most of them are blind, but the degree of eye reduction in different species seems to be connected with phylogenetic age of cave colonization (Parzefall, 1993).

All around the world, there are 87 species of troglomorphic fishes belonging to 18 families (Romero & Paulson, 2001; Sparks & Chakrabarty, 2012). In the teleostean fish of Africa, 9 species belonging to four families have colonized caves successfully (table 21.IV and figure 21.4).

TABLE 21.IV.

Blind fish recorded from caves of Africa. Non-troglomorphic fishes found in caves as well as blind fish not found in caves are not included.

family/species	location	descriptor	year
Cyprinidae			
Barbopsis devecchii	Somalia	Di Caporiacco	1926
Caecobarbus geertsi	DRC	Boulenger	1921
Phreatichthys andruzzii	Somalia	Vinciguerra	1924
Clariidae			
Clarias cavernicola	Namibia	Trewavas	1936
Uegitglanis zammaranoi	Somalia	Gianferrari	1923
Gobiidae			
Glossogobius ankaranensis	Madagascar	Banister	1994
Eleotridae			
Typhleotris madagascariensis	Madagascar	Petit	1933
Typhleotris mararybe	Madagascar	Sparks & Chakrabarty	2012
Typhleotris pauliani	Madagascar	Arnoult	1959

FIGURE 21.4.
Localities of the nine troglomorphic fish species in Africa.

Two others species (*Mastacembelus brichardi* and *Platyallabes tihoni*) are also considered blind fish, but they live in riffles under flagstones in the Stanley Pool, so they cannot be considered as cave-dwellers. Finally, two clariids (*Channallabes apus* and *Dolichallabes microphthalmus*) are sometimes collected in caves near Kanka (ex-Thysville) in DRC, but these species have a larger distribution and are recorded in many epigean watercourses, so they must not be considered as strictly cave-dwellers.

Although the scientific community has known of cavefishes for more than a century, they have not been studied in any detail with regard to their basic biology and/or species diversity, due to the difficulty of access to their habitats. Furthermore, these species are scarce and generally vulnerable or endangered, so it is very difficult to carry out samplings to study their basic biology.

However an exception exists and some important insights in ecology, variation and adaptation were obtained in the 1950s for *Caecobarbus geertsii* (Heuts, 1951) (figure 21.5).

FIGURE 21.5.
A preserved specimen of *Caecobarbus geertsii* from the cave 'Grotte de Lukaku', DRC (© Royal Museum for Central Africa).

Firstly, not all caves of the region are inhabited by *Caecobarbus*, even when they provide ample occasion for the development of aquatic life. Clearly caves have to offer a combination of ecological conditions if they are to be populated by *Caecobarbus*. This combination seems to be achieved only in particular caves of a selected area. According to the conclusions of Heuts (1951), we can summarize the situation as follow. First, a cave inhabited by animals is not just a dark subterranean hole but an ecologically complex and specialized habitat where many factors play a role. Among these factors, the darkness seems to have no more importance than others. All the others – high calcium, bicarbonate and carbon dioxyde concentrations, absence of photoperiodism, scarcity of food, isolation, and the constancy of all these – exert an influence on the inhabitants.

Some caves must be considered as a more or less long subterranean course of an epigean stream. Such caves never contain any blind fish populations. Conversely, all *Caecobarbus* caves are in locations that receive, during the rainy season, an inflow of water through intermittent stream beds. The first important ecological consequence of this periodicity is that the food resources are also subjected to a similar cycle. Examination of the stomach contents of the fishes show that they eat exogenous insects which are brought into the inside of the cave by the rain during the wet season. In other words, food is only supplied for more or less six months of the year. In connection with their periodical inundation, and the consequent instability of certain conditions, other typical cave animals, especially terrestrial insects, are absent in *Caecobarbus* habitats, so that the exogenous fauna is really the only resource for the fish. In conclusion, the species lives under specific ecological characteristics, but due to the heterogeneity and the discontinuity of the entire area, each population may live in different conditions so long as these lie within the limits of the species' requirements.

In addition to diet, two other biological features were studied. But the results are quite disappointing, because the hypotheses issued by the author (Heuts, 1951) seem questionable. According to observations of scale rings, Heuts considers that the maximal longevity varies from 10 to 14 years. This result is very surprising when we know that the maximal length of the species reaches 80 to 90 mm SL, even if the species must have slow growth because of the scarcity of the food availability and the severity of ecological conditions. With regard to reproduction, the author has never found young specimens and all the individuals caught measured more than 40 mm. Two hypotheses have been put forth to explain this feature. First, reproduction takes place with a maximal intensity about every ten years, regularly increasing and falling to zero with the same periodicity. Second, reproduction takes place every year, but the juvenile stages are bound to live in special habitats exhibiting the most ideal cave conditions, and as such, inaccessible to man for investigation. These two explanations are unsatisfactory and only a study of populations during successive years will be able to reveal the real state of the parameters concerning the reproductive cycle in *Caecobarbus geertsii*.

Crater lakes

Worldwide, crater lakes are relatively rare, usually small and specialized freshwater habitats formed in geological depressions. But they are well represented in tropical Africa, especially in the Lower Guinean rainforest zone of Cameroon (figure 21.6), where there may be 36 or more (McGregor Reid & Gibson, 2011). Crater lakes may contain a substantial number of endemic organisms, including fishes. All Cameroonian crater lakes are formed through volcanism and are calderas (deep inverted cones)[3] or maars (shallow cones with a low profile).[4] For example Lake Nyos (see box "Nyos, an extreme example", in the chapter *The diversity of aquatic environments*) is a simple maar lake, but a relatively deep one, whereas Lake Barombi Mbo is formed in a caldera.

NOTE 3

A caldera is a cauldron-like volcanic feature usually formed by the collapse of land following a volcanic eruption. They are sometimes confused with volcanic craters.

NOTE 4

A maar is a broad, low-relief volcanic crater that is caused by a phreatomagmatic (interaction between water and magma) eruption, which is an explosion caused by groundwater coming into contact with hot lava or magma. A maar characteristically fills with water to form a relatively shallow crater lake.

Fish fauna

Fish species from different families had entered lake basins, but that of the family Cichlidae proved to be the most versatile competitors and speciated extensively. The fishes of this family now exploit almost all available resources in these lakes. Among African fishes endemic to craters, small assemblages of species and genera belonging to the Cichlidae have been the most studied. In fact, the craters represent a younger, less complex ecosystem more easily studied than the East African Great Lakes. Such craters provide an opportunity to investigate the stages in ecological colonization from an initially lifeless environment, as well as the processes of population differentiation and speciation. While invariably occupied by invertebrates, not all western African crater lakes contain fishes and shrimp (Schliewen 2005).

Based initially on Lake Victoria results, the general eastern African hypothesis is that cichlid taxa evolved into lacustrine species flocks through a process of allopatric speciation, that is, one involving periodic geographical separation of populations. It was suggested that a regular rise and fall of waters created satellite lakes to isolate cichlid populations, which then differentiated ecologically, morphologically, behaviourally and genetically into distinct species. These isolates supposedly later returned to the main lake during high water levels, but by that time did not interbreed with their congeners.

An alternative model is that species can arise as monophyletic flocks within the lake itself without such total isolation, that is, through a process of sympatric

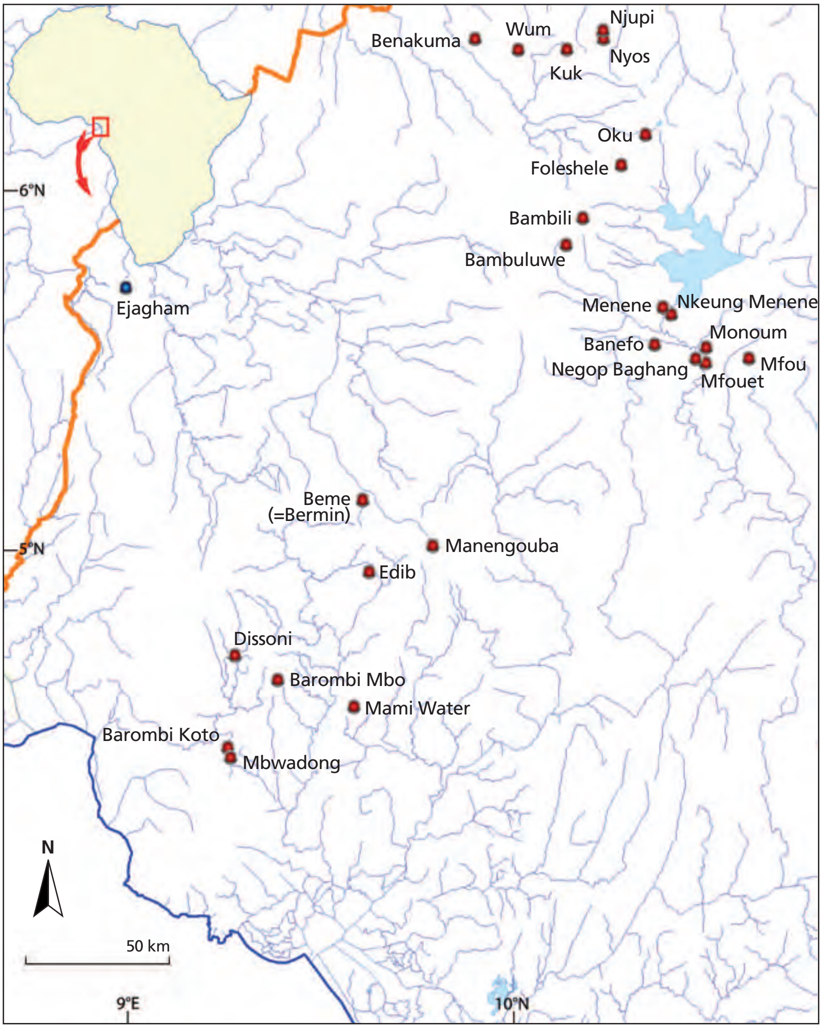
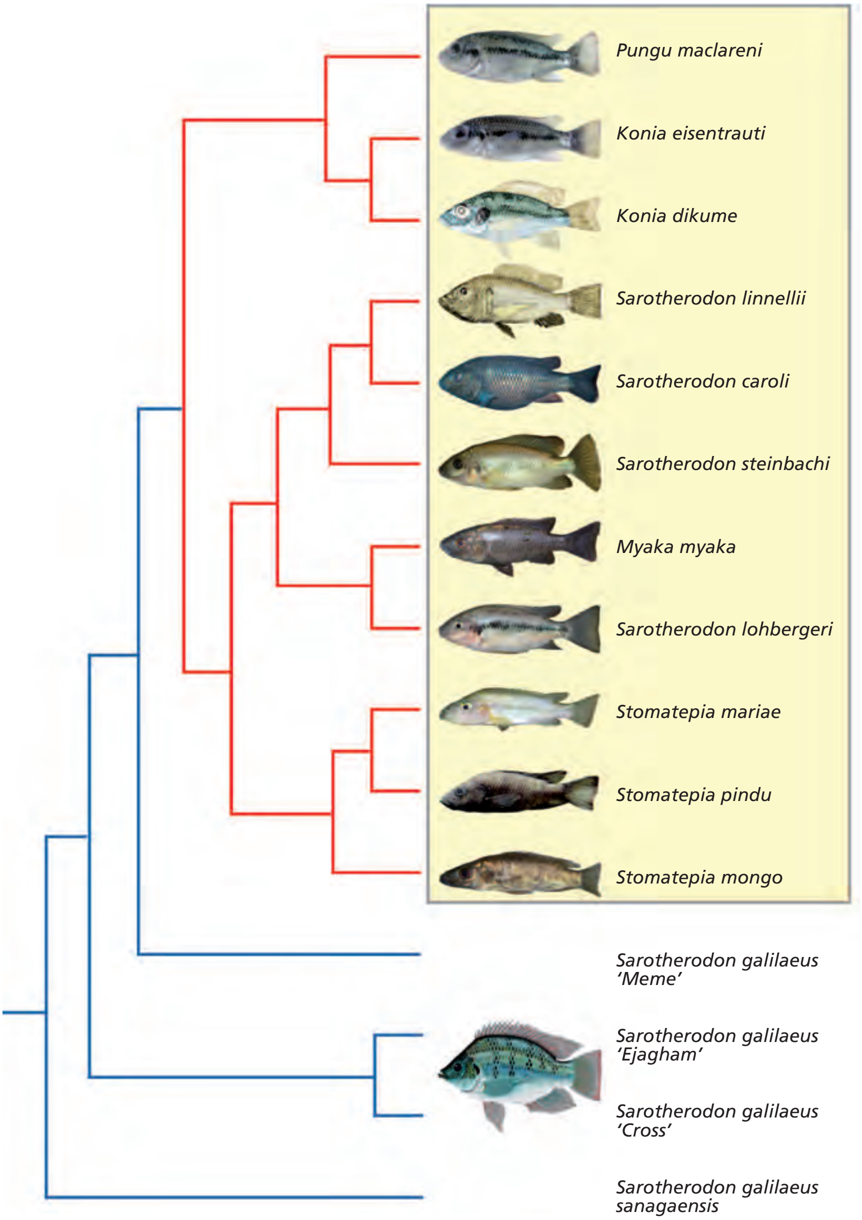


FIGURE 21.6.
Main crater lakes in the Lower Guinean rainforest zone of Cameroon (source: "Faunafri" and "GeoNames"). Lake Ejagham (blue point) is a special case because it is not a volcanic crater lake but it is geomorphologically and ecologically very similar to the other crater lakes.

speciation. Comparisons with a closely related riverine outgroup of cichlids from Lake Ejagham suggest that synapotypic colouration and 'differential ecological adaptations in combination with assortative mating could easily lead to speciation in sympatry' (Schliewen *et al.*, 2001). Comparable empirical research on post-colonization cichlids in a young crater lake in Nicaragua also supports the idea that sympatric endemic '*morphs*' of individual cichlid species may diversify rapidly (say, within a hundred years or generations) in ecology, morphology and genetics and this can be interpreted as 'incipient speciation' (Elmer *et al.*, 2010).

Barombi Mbo is the best known of the high-endemism lakes. The roughly circular lake basin has a diameter of 2.15 km and a maximum depth of 111 m. The area used by fishes is limited to the upper layers of the permanently stratified lake because below 40 m no oxygen is detectable (Schliewen, 2005). At present, fifteen fish species have been found in the lake, twelve of which are endemic, and except for the clariid catfish (*Clarias maclareni*), all endemics are tilapiine cichlid fishes. Four of the five tilapiine genera are endemic: *Konia* (two species), *Stomatepia* (three species), *Pungu* (one species), and *Myaka* (one species) (figure 21.7).

FIGURE 21.7.
Sympatric speciation of cichlids in Lake Barombi Mbo, Cameroon (redrawn from Schliewen *et al.*, 1994).



Some Barombi Mbo cichlids exhibit unique ecological and morphological specializations. For example, *Pungu maclareni* is a sponge-feeder that uses its very strong jaw musculature and specialized teeth to crush sponge spicules (Dominey 1987). Similarly, *Konia dikume* temporarily enters deep waters with extremely low oxygen concentrations to feed on *Chaoborus* larvae. This unique fish can spend short amounts of time in deoxygenated water because a high hemoglobin concentration allows storage of large amounts of oxygen in its blood (Green & Corbet 1973).

Lake Bermin (figure 21.6), with a diameter of only approximately 700 m and a maximum depth of approximately 16 m, is much smaller than Lake Barombi Mbo. It is home to nine endemic cichlid species, which all belong to the tilapiine subgenus *Coptodon*. No exact determination of the crater's age exists, although the degree of erosion of the crater rim suggests an age of much less than a million years (Schliewen, 2005). This finding seems to be corroborated by the lesser degree of morphological specialization in comparison with the Barombi Mbo cichlids. However, several species exhibit striking features. For example *Coptodon spongotroktis* feeds predominantly on the freshwater sponge of Lake Bermin. Another species, *C. snyderae*, is approximately 5.5 cm long, making it the smallest known tilapiine cichlid fish.

Lake Ejagham (figure 21.6) is a special case because it is not a volcanic crater lake but is ecologically and geomorphologically very similar to the other crater lakes. The lake's outlet is isolated from the nearby Munaya River by a waterfall that is insurmountable for cichlid fishes. Its oval-shaped lake basin (approximately 1,050 x 700 m) has a maximum depth of 18 m. In contrast to Barombi Mbo and Bermin lakes, this lake was colonized both by *Coptodon* and *Sarotherodon* tilapias (Schliewen *et al.*, 2001). The *Coptodon* gave rise to four different species (Dunz & Scliewen, 2010), whereas the *Sarotherodon* split into two.

On the basis of the analysis of mitochondrial DNA, these different studies have shown that cichlid species in each of these lakes are monophyletic flocks that have evolved within the body of the lake from a single colonizing species. Given the size and the shape of these lakes, it is unlikely that geographical micro-barriers have facilitated a micro-allopatric speciation. Because the lakes are isolated from nearby river systems, are conical in shape, and geomorphologically homogenous, the results implied that speciation had taken place entirely within the limits of these lakes and therefore in full sympatry. Finally, the authors of these studies suggest that the diversification of trophic behaviour, and resulting ecological behaviour, has been the main factor of this sympatric speciation in each of these lakes.

Several other lakes do not harbour endemic cichlids but support endemic fishes from other groups. For example, Lake Dissoni harbors one endemic poeciliid (*Procatopus lacustris*) and probably one endemic *Barbus* and *Clarias* (Schliewen 2005).

The impact (meteoritic) crater Lake Bosumtwi (Ghana) is dominated by cichlids, while the non-cichlids predominate in the riverine situations. More than 37 streams drain into the lake, but only five of these are permanent and the main

FIGURE 21.8.
Only wooden planks ('*padua*') can be used for fishing in Lake Bosumtwi (© IRD/C. Lévêque).

source of water entering Lake Bosumtwi is rainwater flowing inwards from the crater rim (Whyte, 1975). Unlike the crater lakes of Cameroon, no endemic species and species flock can be found in this lake. Due to its age (± 1.07 million years ago) and the isolation of this lake, it is strange that no endemic species had developed, as observed in Cameroon. Perhaps the geological history and the climate alternation in the region are the main reasons. Locals consider this a sacred lake where souls of the dead come to bid farewell to the god Twi. Due to local beliefs, fishing here is only allowed from wooden planks (*padua*) (figure 21.8) – it is taboo to touch the water with iron.

Conservation

Despite the high levels of endemicity and the unique behaviours of the fish that live in these lakes, conservation efforts to protect the lakes' ecosystems are poor. Such unique lake environments and endemic species are clearly of national and international importance. The small size of the lakes renders them extremely vulnerable to even minor disturbances. In particular, the most diverse and famous lake, Barombi Mbo, is under immediate threat. Partial deforestation of the interior crater rim has already taken place because of increased demand for agricultural land by the local Barombi people and by people from nearby Kumba town. This is likely to cause increased erosion and consequently increased sediment input into the oligotrophic lake system. Water extraction has also temporarily caused lake level alterations, which have changed breeding habitat needs for some of the endemic cichlid species, especially *Sarotherdon linnellii* (Schliewen, 2005). The use of modern gillnets has supposedly decreased populations of target fish species, although all fish species are still present in the lake (Schliewen, 2005). Water pollution from insecticide use in small farms within the crater rim and from increased waste-water inflow from the small Barombi village is also likely to affect the lake's ecosystem. Last but not least, the introduction of exotic fish species most likely would have disastrous results. Although no direct action has been planned, the mere chance that either molluscivorous fish species for bilharzia control or nonindigenous tilapias for increased fishery revenue would be introduced is a serious threat (Schliewen, 2005). These threats to Barombi Mbo also largely apply to the other lakes.

Among conservation recommendations that have been proposed, the following summary can be given (McGregor Reid & Gibson, 2011):

- Red List threat assessments;
- formal designation of lakes as legally and practically protected aquatic nature reserves of national and international importance;
- *ex situ* programmes for the conservation breeding of species at risk, with the prospect of eventual reintroduction in appropriate circumstances.

Despite the persistent threats outlined above, a survey of Lake Barombi Mbo in 2002 found all fish species to still be present (Schliewen 2005). However, many of the species present are threatened (even Critically Endangered *sensu* IUCN), but there have been no recorded fish or invertebrate population declines to the point of extinction in any of the crater lakes. Nevertheless, continued vigilance, conservation monitoring, threat assessment, mitigation and protective measures certainly remain highly appropriate.

Fish communities in estuaries and lagoons

JEAN-JACQUES ALBARET

Estuaries and lagoons, along with mangroves and maritime marshes, occupy a considerable area along the coast of the African continent. Often subjected to strong marine influence, both in terms of their physical structure and their bio-ecological functioning, lagoon and estuarine environmental systems (abbreviated later as LEE) are nonetheless generally attached to the field of continental waters. In fact, the diversity of situations makes it difficult, if not impossible, to classify them as either marine or continental, and the term "interface environment" perfectly captures their nature and environmental functioning.

Introduction

Dufour *et al.* (1994) point out that the plethora of definitions proposed to express the concept of "lagoon" indicates that there are no universally-accepted criteria for differentiating them from bays, estuaries, coastal marshes, and other parts of the coastal landscape (Mee, 1978). According to the outline proposed by Davies (1973), there is a continuum within the broad category of estuarine environments (figure 22.1). One end of the spectrum contains lagoons of marine origin (wave action), sheltered behind a sedimentary belt formed by

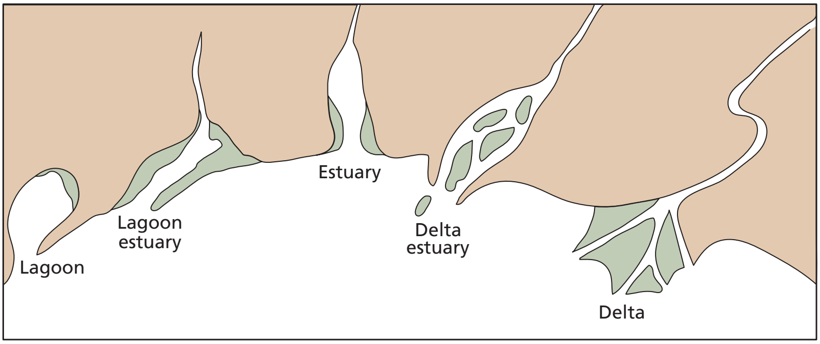


FIGURE 22.1.
Schematic representation of the continuum from lagoons to deltas (adapted from Davies (1973).

relatively large-sized particles (sand). On the other end of the spectrum can be found deltas, resulting from the action of rivers rather than marine activity, and characterized by the small size of sedimentary particles (silt). Between these two, there are different types of environments that display a mix and a gradation of the two extremes of coastal environments. A large number of type classifications of lagoon and estuarine environmental systems have been proposed, each favouring a specific approach: geological, morphological, hydrodynamic, physico-chemical (water quality, particularly salinity levels), bio-ecological. A typology of LEEs can thus not claim to be either exhaustive or multipurpose. To give an example of a morphological and hydrodynamic approach, we can mention the classification proposed by Lankford (1977) which prioritises the dynamics of formation, with sub-classes taking partly into account a given system's opening to the marine environment (figure 22.2), and that of Nichols and Allen (1981) which distinguishes two main dynamic factors that determine both the evolution and the function of lagoons (figure 22.3):

- the effect of tidal currents and continental discharge;
- the effect of waves and coastal current.

Based on the dominant influence of each of the two factors, lagoons can be classified into four principal types (Nichols & Allen, 1981) (figure 22.3).

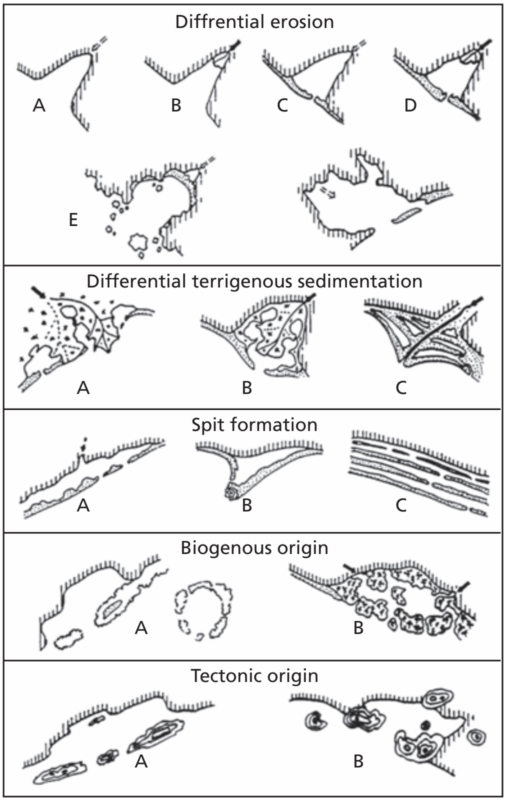
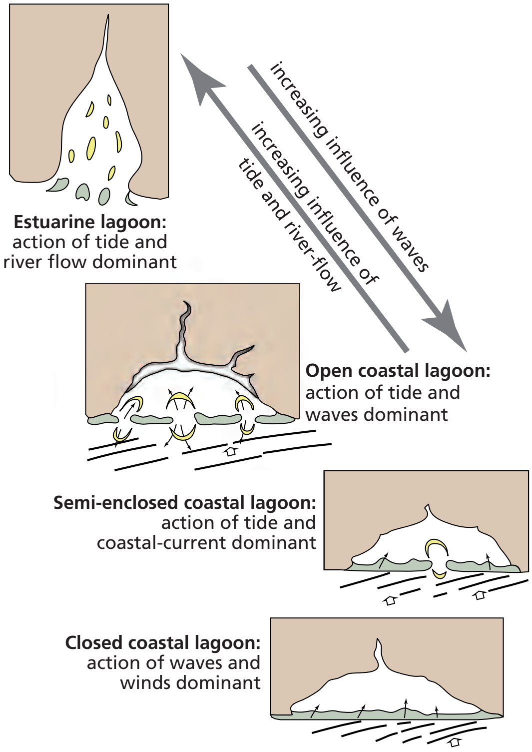


FIGURE 22.2.
Different lagoon types based on formation process (from Lankford, 1977).

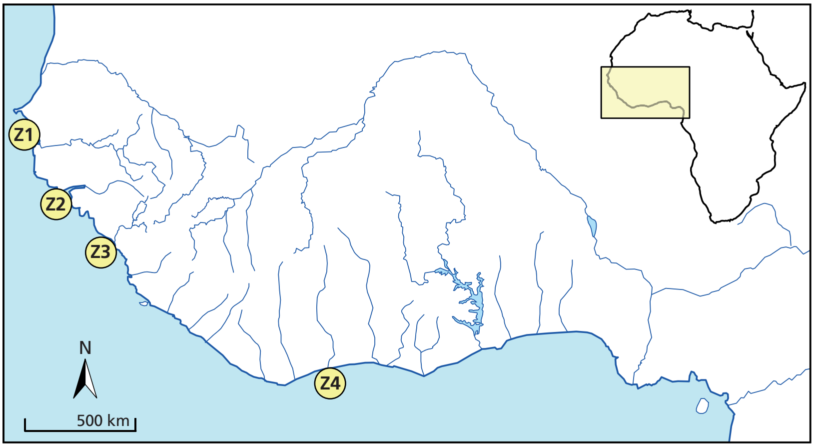
FIGURE 22.3.
Four lagoon types based on the importance of dynamic and energetic factors (from Nichols & Allen, 1981).



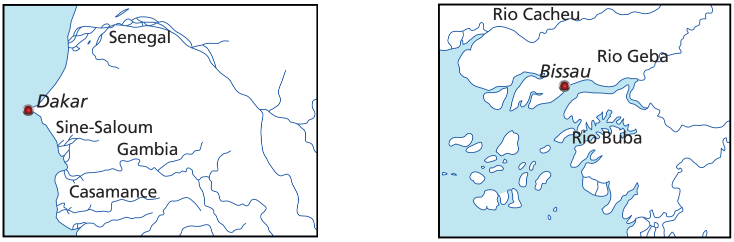
For various reasons that essentially have to do with their apparent complexity (if only for the mixture of fauna of different origins) but also the difficulty of defining and demarcating these fluctuating systems in space and time, the study of these systems as ecosystems in their own right is relatively recent, particularly in the intertropical area. Moreover, available information remains fragmented and often sparse. Nonetheless, in recent years LEEs have become the focus of growing scientific interest, tied in large part to the development of multiple human activities that are performed within or near them, such as fishing, aquaculture, tourism, urban and port planning. In addition, their generally small dimensions (compared with oceans and large fluvial basins), the intensity of physical and biological gradients, and the diversity and scope of hydro-climatic variations make them desirable sites for the application of ecological methods and theories.

Because of its halieutic and aquacultural applications, ichthyology has been one of the most frequently-tackled scientific fields.

Two large areas that are particularly rich in LEEs, West Africa and Southern Africa (sometimes referred to as sub-continents), have been the subject of extensive ichthyological investigations and will provide most of the information and bibliographical elements mentioned in this chapter (figures 22.4 and 22.5). It can be noted that in both cases, the scientific approach and reasoning were essentially the same. Initially research focused on the systematic inventory and

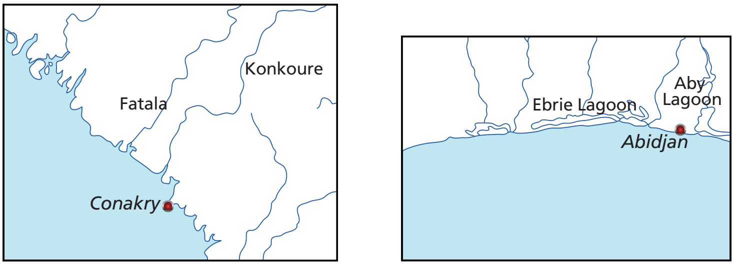


West Africa



Z1: Senegal

Z2: Guinea-Bissau



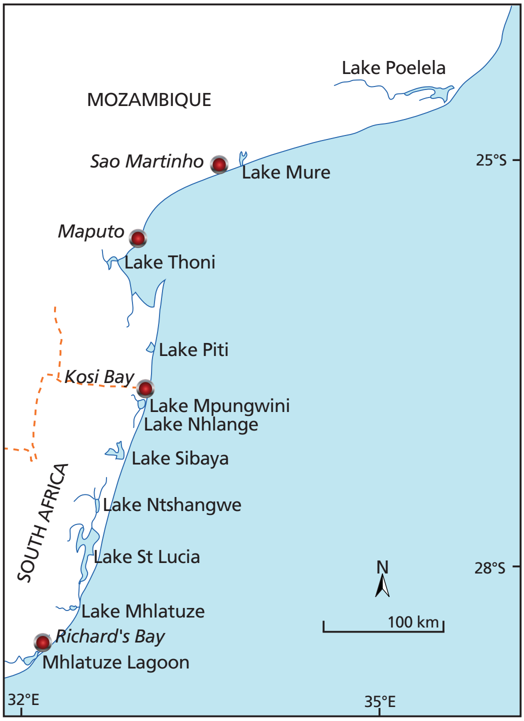
Z3: Guinea

Z4: Côte d'Ivoire

FIGURE 22.4.
Location of some of the main LEEs studied in West Africa (based on Diouf 1996).

taxonomy of species, which sometimes allowed a biogeographical approach. Studies on the biology and ecology of the major species developed at the same time. Subsequently, synecological research developed, as scientists attempted to describe and sometimes explain the ecological functioning of the communities of specific systems: the Ébrié lagoon, Casamance, Lake Togo, Sine Saloum, Fatala estuary for West Africa; St Lucia System, Lake Nhlange (Kosi System), Poelela Lagoon for Southern Africa. The acquisition of this body of knowledge, which will be referred to extensively in this chapter, now allows a twofold comparative approach – firstly geographic, with the comparative analysis of faunistic and functional characteristics of several systems, but also

FIGURE 22.5.
Coastal lagoons of south-east Africa (based on Blaber, 1985).



diachronic, making it possible to follow and understand the evolution of an estuary system subjected to considerable changes (particularly climate-related) to which it is sometimes possible to make a connection with changes in the composition and structure of communities. In this chapter, we will attempt to provide the elements that explain what an estuarine species is, what its origin may be, how ichthyological communities are formed and organized and to point out the essential factors (biotic or physical) that influence their structure. We will examine the vital strategies used by species to take the greatest advantage of these supposedly stressful and inhospitable environments. Some pressing current issues regarding LEEs will also be discussed, particularly the debate regarding their biodiversity (is it high or not?) and the vital question – as their survival sometimes depends on it – of the ecological and economic role of these systems. We will conclude by discussing the concepts of the fragility and sturdiness of these environments and the threats that face them.

General characteristics of fish communities

By definition, LEEs are found at the interface of continental and marine areas. Like the physical system, the fauna and flora of these environments are influenced by the adjacent systems based on an equilibrium that varies according to situation. The question then arises whether the faunistic compositions that occupy these ill-defined environments present a certain degree of structure and meet some general organizational principles, or if on the contrary they are simple, more or less random aggregates of opportunistic fish originating from either the adjacent continental plateau or from continental tributaries.

Lagoon or estuarine environments: strong biodiversity or species-poor systems?

Depending on the author, lagoon and estuarine environments are presented as species-poor environments (Remane & Schlieper, 1971; Kiener, 1978; Day & Yañez-Arancibia, 1985) or as ecosystems that are rich in species (Albaret, 1994; Albaret & Diouf, 1994; Baran, 1995). The main cause of this divergence is the absence of a consensus on the definition of estuarine ichthyofauna during species inventories (what is an estuarine species; what are the limits of the estuary; what should be counted?). In the first case, generally the only species taken into account are those that complete their entire life cycle in estuaries and lagoons, species that are exclusively confined to brackish environments. Species of marine or continental origin that are found temporarily in LEEs, or those that can complete their life cycles in or out of the estuary environment are excluded from inventories. Yet for some of these species, lagoons and estuaries serve an extremely important function ("nursery" role) that is sometimes indispensable for the completion of the life cycle (Wootton, 1992; Beckley, 1984; Ross & Epperly, 1985; Day *et al.*, 1989). Moreover, the interactions (predation, competition) of these migratory species with resident ichthyofauna are an important contributor to the structure of fish populations (Monteiro *et al.*, 1990; Blaber, 1985). If we are to study how these systems function, it thus seems necessary – going beyond inventory and classification – to include migratory and amphibiotic species in estuarine ichthyofauna and discuss the notion of species richness in LEEs while taking them as open systems.

An examination of the structure of fish communities in estuaries and lagoons around the world shows that, in general, only a few species contribute to most of the biomass of these otherwise species-rich systems (table 22.I and 22.II) (Kennish, 1990; Yañez-Arancibia *et al.*, 1985; Chao *et al.*, 1985; Horn & Allen, 1985; Whitfield, 1994a; Kromer *et al.*, 1994; Albaret, 1987; Baran, 1995; Diouf, 1996).

TABLE 22.I.
Species richness of ichthyofauna in different countries of West Africa (adapted from Baran, 1995).

	Senegal	**Gambia**	**Guinea**	**Côte d'Ivoire**	**Nigeria**
Senegal River	Gambia River	Fatala River	Comoé River	Niger River	
Number of freshwater species	111	96	41	96	193
Number of estuarine species	133	89	102	153	79
Number of marine species	292	337	158	103	-

TABLE 22.II.

Species richness of ichthyofaunal of some LEEs around the world (Diouf, 1996).

	Environment type	Country	Specific richness	Source
Africa				
Senegal	estuary	Senegal	111	Reizer, 1988; Diouf *et al.*, 1991; Kébé *et al.*, 1992
Sine Saloum	inverse estuary	Senegal	114	Séret, 1983
Gambia	estuary	Gambia	89	Daget, 1960; Dorr *et al.*, 1985
Casamance	inverse estuary	Senegal	86	Pandaré & Capdeville, 1986; Pandaré, 1987; Albaret, 1987; Pandaré & Niang, 1989; Badji, 1990
Rio Buba	ria	Guinea-Bissau	92	Kromer *et al.*, 1994
Fatala	estuary	Guinea	102	Baran, 1995
Ébrié lagoon	lagoon	Côte d'Ivoire	153	Albaret, 1994
Aby lagoon	lagoon	Côte d'Ivoire	82	Charles-Dominique, 1994
Lagos lagoon	lagoon	Nigeria	79	Fagade & Olanyan, 1974
Niger	delta	Nigeria	52	Boeseman, 1963
Ogowe	estuary	Gabon	66	Loubens, 1966
Santa Lucia	lagoon	South Africa	108	Blaber, 1988
Poelela	lagoon	South Africa	12	Blaber, 1988
Nhlange (Kosi)	lagoon	South Africa	37	Blaber, 1988
Sibaya	lagoon	South Africa	18	Blaber, 1988
Swarvlei	lagoon	South Africa	25	Blaber, 1988
Richard's Bay	lagoon	South Africa	74	Blaber, 1988
Morrumbene	estuary	Mozambique	114	Day, 1974
Pangalanes	8 small lagoons	Madagascar	10 to 43	Lasserre, 1979
America				
Teacapan-Agua Brava	lagoon	Mexico	75	Flores-Verdugo *et al.*, 1960
Terminos Lagoon	lagoon	Mexico	122	Yañez-Arancibia *et al.*, 1980
Santa Lucia	estuary	Mexico	83	Chavez, 1979
Nichupte	lagoon	Mexico	37	Chavez, 1979
Tuxpan	lagoon	Mexico	126	Chavez, 1979
Alvarado	lagoon	Mexico	71	Chavez, 1979
Laguna Madre	lagoon	Mexico	111	Chavez, 1979
Tamiahua	lagoon	Mexico	49	Chavez, 1979
Mandinga	lagoon	Mexico	24	Chavez, 1979
La Mancha	lagoon	Mexico	42	Chavez, 1979
Tabasco	lagoonal system	Mexico	62	Resendez-Medina, 1979
Tamiahua	lagoon	Mexico	56	Resendez-Medina, 1979
Zontecopopan	lagoon	Mexico	50	Resendez-Medina, 1979
Nicoya Gulf	coastal mangrove	Costa Rica	61	Philips, 1983
Punta del Este	coastal mangrove	Cuba	55	Valdes-Muñoz, 1983
Laguna Joyuda	lagoon	Puerto Rico	41	Stoner
Belle-Plaine	lagoon	Guadeloupe	25	Louis *et al.*, 1985
Mancha à Eau	lagoon	Guadeloupe	24	Louis *et al.*, 1985
Fort-de-France bay	coastal mangrove	Martinique	87	Louis *et al.*, 1985
Cayenne River	estuary	French Guiana	59	Tito de Morais & Tito de Morais, 1994
Barrier reef complex of Belize	reef	Belize	87	Sedbery & Carter, 1993
Jaguaribe	estuary	Brazil	86	Oliveira, 1976
Huizache-Caimanero	lagoon	Mexico	44	Warbuton, 1978
Tijuana estuary	estuary	USA (South California)	21	Nordby & Zedler, 1991
Los Penasquitos Lagoon	lagoon	USA (South California)	13	Nordby & Zedler, 1991
Wells estuary	estuary	USA (Maine)	24	Ayvazian et al., 1992
Waquoit Bay	Bay	USA (Massachusetts)	46	Ayvazian et al., 1992

	Environment type	Country	Specific richness	Source
Asia				
Pagbilao	coastal mangrove	Philippines	128	Pinto, 1988
Klang-Langat	delta	Malaysia	119	Chong *et al.*, 1990
Oceania				
Labu Estuary	estuary	Papua New Guinea	38	Quinn & Kojis, 1986
Moreton Bay	coastal mangrove	North Australia	112	Weng, 1988
Trinity inlet system	estuary	North Australia	91	Blaber, 1980
Dampier Bay	coastal mangrove	North Australia	113	Blaber, 1980
Leanyer Swamp	coastal mangrove	North Australia	38	Davis, 1988
Alligaror Creek	estuary	North Australia	128	Robertson & Duke, 1990
Embley estuary	estuary	North Australia	197	Blaber *et al.*, 1989
Botany Bay	coastal mangrove	North Australia	46	Bell *et al.*, 1984
Swan River	estuary	West Australia	71	Loneragan *et al.*, 1989
Deama	coastal mangrove	New Caledonia	75	Thollot, 1989
Europe				
Ria Aveiro	estuary	Portugal	55	Rebelo, 1992
Ria Formosa	estuary	Portugal	67	Monteiro, 1989
Étang de Thau	lagoon	France	53	Bach, 1985
Mauguio	lagoon	France	71	Bouchereau, 1994

The diversity in the definition of limits both upstream and downstream of LEEs (Caspers, 1954; Rodriguez, 1975; Fairbidge, 1980; Day, 1981; Baran, 1995), is also a source of controversy regarding the species richness of these systems.

In a given biogeographic province, the species richness of LEEs in West Africa is comparable to that of rivers and never less than a third of the number of species found at sea on the neighbouring continental plateau (Baran, 1995) (table 22.I). At the global level, we can note that the richness of Africa's estuaries and lagoons is greater overall compared with other LEEs (table 22.II).

Factors influencing or regulating diversity

The LEEs of West Africa thus play temporary or permanent host to a large number of species. This richness can be traced to certain characteristics of these ecosystems.

Size of the system

In the ecology of aquatic systems, it is common for scientists to describe the species richness of an ecosystem according to its extent (see chapter *Species richness of fish communities*). The main condition for the application of this model stipulates that ecosystems should form isolated ensembles such that on their borders, their fauna does not undergo any pressure from neighbouring fauna. Yet one of the fundamental characteristics of LEEs is, indeed, to allow the integration of elements from adjacent systems into the animal communities that they host. Another essential characteristic of these ecosystems is that they rely primarily on exchanges (of matter, energy, and biomass) with adjacent systems. While their dimensions have an influence on their species richness, the area/species richness model does not apply to LEEs.

Extent, number, diversity, and permanence of interfaces

The reasons for the extent of species richness in a lagoon or estuary must be treated as having more to do with the extent, diversity, and permanence of its interfaces with adjacent systems (Albaret, 1994). The moment and duration of their connection with the ocean also play an essential role on the diversity and abundance of fish in a given lagoon or estuarine system. LEEs that have a permanent connection to the ocean show greater species richness compared with systems that have temporary connections (Whitfield & Kok, 1992).

Diversity of available habitats

The morpho-edaphic (shape of water body, depth, nature of bottom) and bankside vegetal variety, heightened by the diversity of hydrological and hydro-climatic situations, leads to a great diversity of habitat types available to fish communities in the LEEs. (Blaber, 1974; Branch & Grindley, 1979; Marais 1982; Whitfield, 1983; Cyrus & Blaber, 1987a, b, c; Albaret 1987; Diouf 1996.).

Population potential (diversity of colonization sources)

This high "hosting capacity" also corresponds to very high colonization potential from coastal marine, estuarine, and continental species.

A large proportion of the fish species making up the neritic communities of the African coasts is liable to penetrate into neighbouring estuaries and lagoons for varying periods and at different life stages.

Estuarine species, which are euryhaline and have generally low endemicity, can (little by little, and at another time scale) also colonize new LEEs via the sea.

Continental species, generally less numerous than the others, come from rivers that are tributaries of the LEEs.

The species of the first two groups have a vast biogeographic distribution whereas the majority of continental species have a more restrained area of distribution. This contributes to the regional, even local (endemic species) specificity of estuarine communities.

Biogeography

Biogeography also plays an important role in determining the "availability" of species for recruitement in a given estuary (Blaber, 1981).

Whitfield (1994a, b) notes that in general, tropical and sub-tropical estuaries have more species richness than temperate systems owing mainly to the greater richness of fauna associated with habitats that are close to the equator, be they marine or riverine. In South Africa, Wallace and van der Elst (1975) have shown that there is a decrease in ichthyological diversity when one moves from the sub-tropical estuaries of the Natal (Indian ocean) to the "temperate-warm" ones of the Cape's coast then the "temperate-cold" ones of the Atlantic shoreline.

Other factors that may influence species richness

Other factors, often interdependent, can be mentioned: the strength and duration of floods, (Marais, 1982), physico-chemical characteristics of water and their spatio-temporal variations (Blaber, 1974; Whitfield *et al.*, 1981; Cyrus & Blaber, 1987a, b, c; Albaret, 1987; Diouf, 1996), trophic richness and resource availability (Marais, 1984; Whitfield, 1988); presence, abundance, and health state of mangroves (Diouf, 1996). The composition of LEE communities is also modified, sometimes considerably, by human interventions such as the construction of engineering works (ports, dikes, dams, etc.), creation of connections to the ocean, halieutic and aquacultural activities, pollution from urbanisation and industrialization as well as agricultural activities (Blaber *et al.,* 1984*;* Plumstead, 1990; Albaret & Diouf, 1994).

Finally, we should note the essential role of historical factors (at various time scales) in the creation of fish communities as we know them today. How, indeed, would it be possible to understand the current organization of the highly saline Casamance and Sine Saloum estuaries (Senegal) if we were not aware of past climate evolution and the recurrent rainfall deficits typical of this Sahelian region?

On another scale, it can be useful to remember that the existence of LEEs, tied to major climatic changes and ocean level fluctuations, have existed for a relatively short time compared with lakes, rivers, seas, and oceans. To a certain extent we can thus think of them as being ephemeral (on a case-to-case basis, as there will always – more or less – be lagoons and estuaries regardless of sea level) on a geological (and evolutionary process) time scale. This is probably one of the reasons for the low level of speciation in LEEs (as indicated by the low number of species per family) compared with other aquatic systems and, consequently, the relatively low number of true, uniquely estuarine species.

As an example, the Ébrié lagoon, with more than 150 species, is one of the LEEs with the greatest species richness, and combines many factors that encourage population diversity (Albaret, 1994). Located near the equator (5° North), it is the largest lagoon system in West Africa (566 km^2), possessing interfaces with a wide range of aquatic ecosystems: forest rivers, Sudanese-Sahelian river, other lagoons, mangrove, marshes, a continental shelf with over 300 fish species. The connection with the ocean occurs mainly through the Vridy canal, an artificial permanent opening (width: around 300 m, average depth: 15 m) allowing the transit of considerable water masses (annual entry 38.10^9 m^3, annual discharge 50.10^9 m^3) (Varlet, 1978). The extreme variety of landscapes and the diversity of hydro-climatic situations round out the list of factors encouraging the temporary or permanent hosting of many species from different origins, and showing a wide range of ecophysiological adaptations and biological cycles.

Classification of species in ecological categories

Undoubtedly more than for any other type of aquatic system, specialists have run into the problem of defining and classifying estuarine and lagoon communities, an essential step for describing and comparing communities, then for investigating certain aspects of their functioning. Typologies based in the main on the osmoregulatory capacities of species have been proposed (Kiener, 1978) but these have turned out to be largely unsatisfactory when put in practice. A classification that takes not only the degree of euryhalinity into account, but also the characteristics of each species' bio-ecological cycle (distribution and regularity, breeding sites and conditions, place in the trophic network, abundance and location of ecophases), makes it possible to gain a better grasp of the origin, nature, and certain functional aspects of ichthyological communities. Such classifications, undergirded by the concept of estuarine dependence and adapted to the study of vast regions, have been proposed for the subtropical and temperate estuaries of southern Africa (Whitfield, 1994a, b) and the LEEs of West Africa (Albaret, 1994; Albaret & Diouf, 1994). The Whitfield classification has five main categories, three of which are subdivided, for a total of nine categories or sub-categories. The one proposed by Albaret (figure 22.6) includes eight bio-ecological categories, which from a central point of strictly estuarine species, splits unevenly on two gradients of continental and marine affinities. Four of these groups (strictly estuarine, estuarine of marine origin, estuarine of continental origin, marine-estuarine species), composed of largely euryhaline and eurybiotic species, make up the basic elements of the ichthyocenosis of the LEEs of West Africa. About thirty of these species constitute the core of communities owing to their ubiquity, their abundance (or at least their regularly), and the essential role they play in the halieutic economy and ecology of these systems (table 22.III). The other groups comprise species that are variously referred to in literature as "complementary", "accessory", "rare", or "occasional" species. They are found on the extreme ends of the marine and continental axes, their number and diversity varying according to type, size, and hydrological and hydroclimatic characteristics of the system in question.

TABLE 22.III.
List of species common to West African LEEs (Diouf, 1976).

Arius latiscutatus	*Gerres nigri*
Citarichthys stampflii	*Porogobius schlegelii*
Caranx senegallus	*Pomadasys jubelini*
Chloroscombrus chrysurus	*Liza dumerili*
Trachinotus teraia	*Liza falcipinnis*
Hemichromis fasciatus	*Liza grandisquamis*
Sarotherodon melanotheron	*Mugil curema*
Tilapia guineensis	*Galeoides decadactylus*
Ethmalosa fimbriata	*Ilisha africana*
Sardinella maderensis	*Pseudotolithus elongatus*
Cynoglossus senegalensis	*Pseudotolithus senegalensis*
Dasyatis margarita	*Scomberomorus tritor*
Elops lacerta	*Sphyraena afra*
Eucinostomus melanopterus	*Monodactylus sebae*

Different types of estuarine communities

In the diverse and varied LEEs of West Africa, the different ecological categories described are more or less well-represented (figure 22.6) and we can schematically describe the theoretical evolution of fish populations based on hydroclimatic characteristics (Diouf, 1996) (figure 22.7).

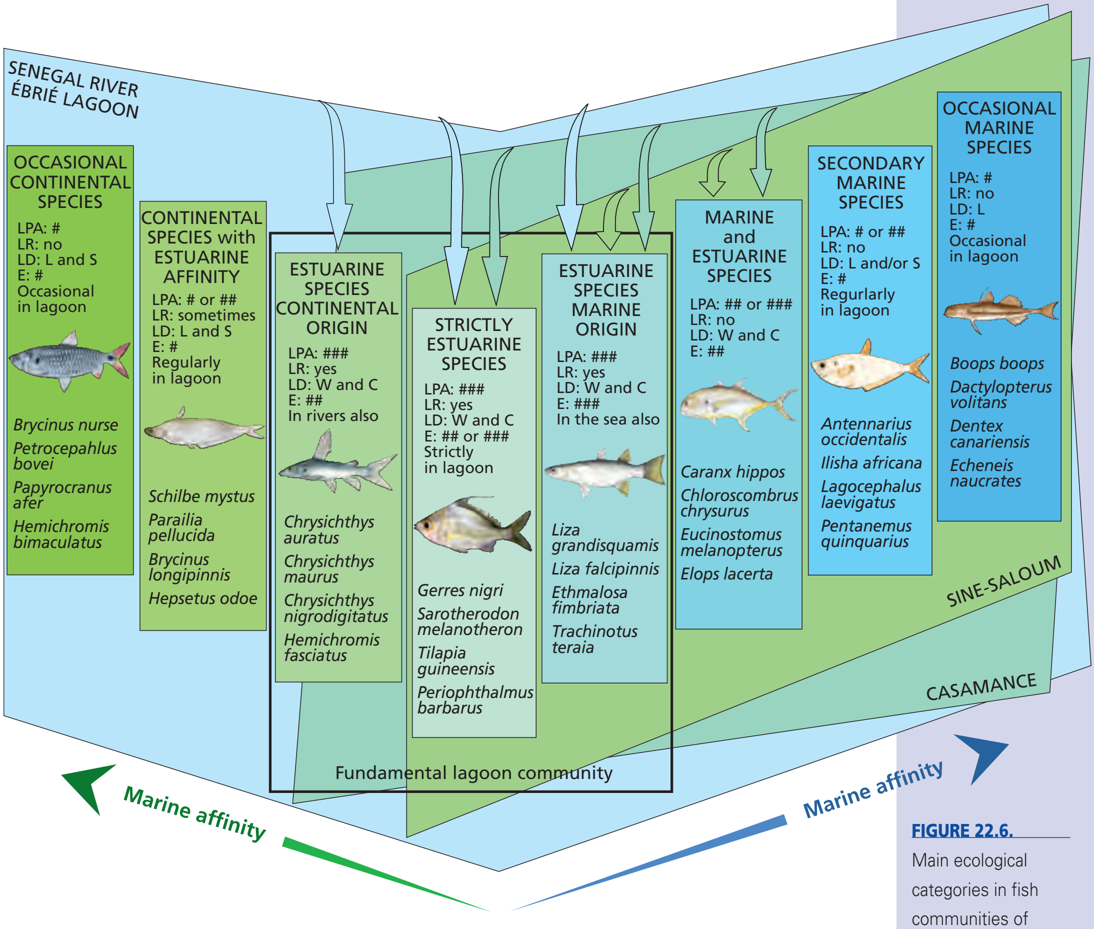


FIGURE 22.6.

Main ecological categories in fish communities of West African LEEs. LPA : lagoonal populations abundance (# rare, ## abundant, ### very abundant); LR: lagoonal reproduction; LD: lagoonal distribution; W: wide; L: limited; S: seasonal; C: continuous; E: euryhalinity (# low, ## high, ### quasi-total)

All the ecological categories are represented in certain LEEs, largely open to both marine and continental domains (type E). This is the case of the Ébrié lagoon, of the Senegal River estuary before the commissioning of the Diama dam, and of the estuaries of the Gambia and the Niger Rivers. Type M is characterized by the reduction of continental influence and the predominance of oceanic influence. This situation is seen in the Rio Buba in Guinea-Bissau, for example. In the inverse estuaries (type I) of Casamance and Sine Saloum (Senegal), the "centre of gravity" of the population shifted towards the marine side with a near-disappearance of the continental component (one or two species of group E.c. can remain). In the case of certain lagoons or certain lagoonal estuaries, the shift occurred in the other direction and the categories of the marine affinities axis are absent (M.o., M.a., M.E.) or hardly represented (E. m). Lake Togo during its closed-off period (Laë, 1992a) and the Potou and Aghien lagoons in Côte d'Ivoire (Albaret, 1994) are good examples of this type of situation (type C).

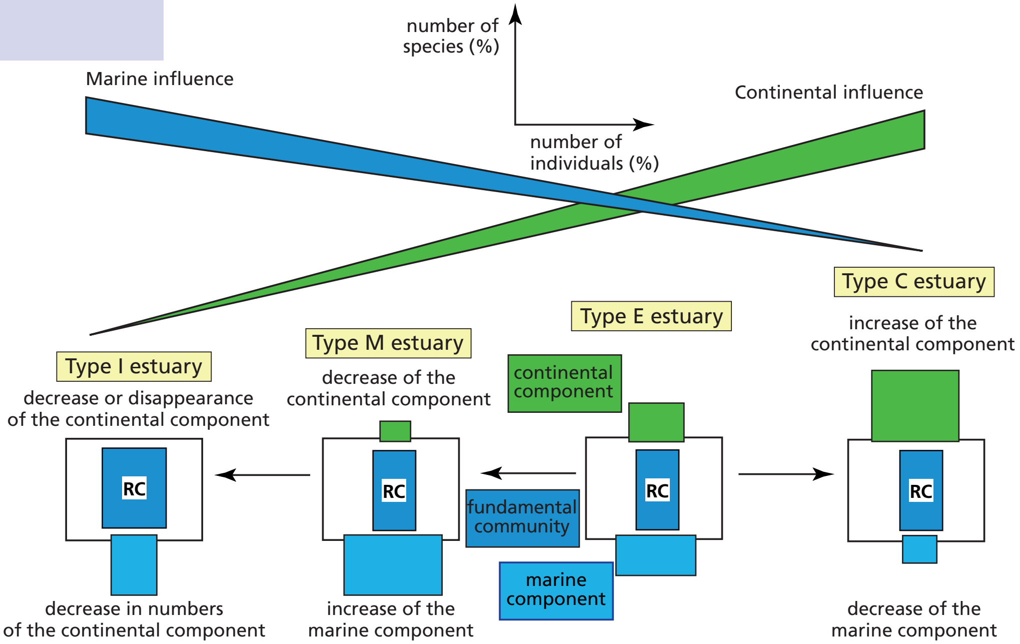


FIGURE 22.7.
Theoretical evolution of LEEs in Western Africa on the basis of their hydroclimatic characteristics (after Diouf, 1996); RC: resistance community.

Organization of communities

The recruitment of fish in LEEs has three distinct sources: marine species and continental species that penetrate the estuarine area at a more or less advanced stage of their development, and juvenile forms of species that reproduce there obligatorily, regularly, or occasionally. From these different population sources, fish communities organize themselves according to the bio-ecological cycles of species (first of all in terms of their eco-physiological aptitudes), the biotic capacity of the system (in particular trophic availabilities), and interspecific relationships (spatial competition, trophic competition, predation, etc.).

The great diversity and extreme variability of LEEs corresponds to very uneven degrees of organization and stability. Some communities are characterized by high species richness but highly unequal abundance distributions. These types of communities are characterized by the marked dominance of a very small number of species (or even a single species, generally a pelagic Clupeiform one, *Ethmalosa fimbriata* or *Sardinella maderensis* in West Africa) and correspond to juvenile communities undergoing constant renewal and with high biological activity (production, life cycles, energy transfer). Conversely, other communities with often lower species richness but a more even distribution of abundance reflect greater environmental stability and a higher degree of maturity and structure of the communities in place.

Factors for community structuring

The species composition and structure of fish populations in a given location is a result of the action of a series of ecological filters (Wootton, 1992). The most obvious and striking characteristic of LEEs is without a doubt the high spatio-temporal variability of the aquatic environment. Therefore among these filters, environmental factors are generally considered to play a crucial role in the organization of fish communities in these systems that are considered highly "physically controlled". When interspecific relationships have been studied, this was most often owing to their intrinsic interesting nature and not for the purpose of understanding the structure of communities. Hence, in some cases, an overestimation of the role of physico-chemical parameters (particularly salinity) and an erroneous or incomplete identification of factors that structure the ichthyocenosis have been achieved. It is thus important, in the quest for explanatory hypotheses accounting for the structure of fish communities in LEEs, to take into account the roles of the hydrobioclimate and of inter-species relationships simultaneously.

Structuring role of environmental factors

Salinity, temperature, turbidity, and dissolved oxygen concentration have a strong influence on the composition, distribution, and abundance of communities in estuarine waters (Kennish, 1990). Diouf (1996) points out that for some fifty studies carried out in estuarine waters, turbidity (in 75% of cases) is one of the most frequently mentioned structuring factors for populations, followed by salinity (58%) and temperature (40%). Other factors are trophic richness (30%), nature of sediments (24%), depth (12%), current (11%) and finally oxygen (10%). However, while a wide variety of structuring factors are generally taken into account, a closer examination of their correlations show that the main ones are turbudity, salinity, and temperature; other factors are often no more than co-variables (McLusky, 1993).

Importance of interspecific relationships

Sedentary and migrant (adult and juvenile) fish species living in LEEs may reach very high densities, which often results in strong intraspecific competition (Wootton, 1992). In extreme cases, the youngest stages are cannibalized.

As juveniles of many large species have the same dietary requirements as adults of small species, LEEs are the venue for strong interspecific competition. However, the spatial heterogeneity and temporal variability of the environment may limit such competition as a result of habitat segregation (Wootton, 1992; Blaber & Whitfield, 1977).

The intensity of predation is tied in large part to turbidity (Cyrus & Blaber, 1987b; Deegan & Thompson, 1985) since prey is hunted by sight for many species (Nikolsly, 1963; Hyatt, 1979; Wootton, 1992). As turbidity is often high in estuaries, predation there generally tends to be low. In some conditions, clear and deep waters, predation may increase (Blaber *et al.*, 1985).

In estuaries and lagoons, it has been shown that predators rarely specialize in a single species (dietary opportunism). As soon as prey populations decline, predators select a closely-related species (Sykes & Manooch, 1978).

Stability-instability

Fish communities in LEEs are often described as heterogeneous and unstable. This presumed instability (which sometimes earns them a reputation for fragility) must be revised after the findings of studies in West and Southern

Africa. Granted, the level of structural organization is never very high in LEEs (primarily in zones that are close to connections with the ocean) and seasonal variations are very marked, in terms of both composition and structure of communities). Yet, in the Ébrié lagoon, Albaret & Écoutin (1990) have shown that at the scale of the annual cycle as well as at an interval of nearly twenty years, a group of species, mainly estuarine (E.c., E.s., E.m.) but also marine-estuarine (M.E.), is constantly present, which thanks to their ecophysiological performance constitute a remarkably stable base community in an environment that displays extreme variability at different levels. Moreover, it is interesting to note that these species are essentially the same as the ones forming the base community for all the LEEs of West Africa mentioned earlier. Beyond the stability of the base community, we can also note an evolution described as the "marinization" of the population which is seen as a consequence of the general rainfall deficit in the region during the period under study (Albaret & Écoutin, 1990). This heightened importance of the marine component within the populations can be felt more in the structure of the community (rank and frequency of species with an oceanic affinity in abundance distributions) than in their species composition which, aside from the inclusion of a few "accidental" marine species, fundamentally remains the same. The highly-marked seasonal variations of the community are induced by the changes in the environment, with the abundance and distribution of fresh water inputs at the fore. The cycle appears to be stable from one year to another, although modulated by the modalities of these inputs: degree and precocity of the rainy season locally, and of the flood of the Comoé river determined by rains in the Sudanian region.

Whitfield (1994a, b) points out that despite the instability or rather, the strong physical variability of the Southern African estuaries at various temporal and spatial scales, the species composition of ichthyologic communities of these environments is relatively stable, and fishes there have more or less predictable distribution and abundance patterns (Day *et al.,* 1981). Moyle & Cech (1982) attribute this stability to four main conditions that apply to all Southern African estuaries (Whitfield, 1994a, b) and to West African LEEs:

- regular distribution of populations throughout the gradients of the environment;
- seasonal migrations of fishes in and outside the estuary;
- dominance of only a few species within communities;
- robust nature of food webs inside estuaries.

A fifth condition that seems essential can be added: the great physiological and ecological tolerance of species "using" estuaries (Whitfield, 1994b).

He also underscored the fact that LEEs differ from some other continental systems in that they have a low tendency to shift towards more mature animal and vegetal communities. In Lake Malawi, for example, the fish community is characterized by a growing proportion of specialized forms with progressively stronger interdependent relationships between species (Bruton, 1989). Meanwhile, the estuaries of South Africa, and African LEEs in general, are characterized by wide variations of abiotic conditions, the constant reorganization of biological communities and homeostatic mechanisms, and the frequent resetting of ecological successions to an earlier stage (Whitfield & Bruton, 1989).

Owing to the structural and functional complexity of LEEs, the stability and organization of fish communities, in the sense of the permanence of their species composition and structure, is subjected to two processes (Baran, 1995):

- mobility of species that affects the degree of organization of biocoenoses,
- ecophysiological plasticity of sedentary species that allow them to tolerate environmental variations and which encourage stability.

In the short term, that is at a seasonal level, the outcome of these two processes with antagonistic effects tends to encourage instability.

But, from year to year, the cyclical nature of climatological, hydrological, and hydrochemical factors that directly or indirectly determine the organization of communities through inter-species competition (Guiral, 1992) encourages a certain stability.

At the scale of one or two decades, this stability is also seen (Livingston, 1976; Whitfield, 1994a; Albaret & Écoutin, 1990) except in cases of rapid anthropogenic and/or natural changes in the environment (Albaret, 1987; Albaret & Écoutin, 1989; Albaret & Diouf, 1994).

Biology and adaptive strategies

In fishes as in other organisms living in LEEs, physiological (Vernberg & Vernberg, 1976) and behavioural (Smith *et al.*, 1966; McDowall, 1976; Day & Yañez-Arancibia, 1985; Day *et al.*, 1989) adaptations have been developed to deal with the stress generated by the degree and speed of fluctuations in physico-chemical factors (McHugh, 1985; Deegan & Thompson, 1985; Day & Yañez-Arancibia, 1985; Whitefield, 1994a).

The strategies in play can be outlined in three broad categories: breeding strategies, space occupation strategies, and resource use strategies (Lévêque, 1994).

Reproduction and breeding strategies

LEEs are often viewed solely as transit areas, "nurseries" for juvenile stages of fish whose adult life and reproduction occur in adjacent ecosystems, notably the marine environment. Only a few sedentary species, of small size and little ecological or economic significance, were believed to be capable of completing their full biological cycle in these systems whose strong variability and unpredictability are sometimes considered physiological obstacles to the reproductive process. In fact, studies conducted in West Africa (Albaret, 1987; Albaret, 1994; Diouf, 1996; Baran, 1995) show that lagoons and estuaries are the site of intense reproductive activity for a very wide range of species (table 22.IV). Reproductive activity is generally very widely spread out over time and space with, however, peaks of activity around the dry or rainy seasons depending on the marine or continental affinity of species. Environmental requirements, particularly for salinity, are generally low. The euryhalinity of most estuarine species at the time of reproduction is remarkable (Albaret & Diouf, 1994).

Reproduction in lagoon	Advanced maturation in lagoon	Early stage of maturation in lagoon
Brycinus longipinnis	*Antennarius occidentalis*	*Brachydeuterus auritus*
Aplocheilichthys spilauchen	*Apogon imberbis*	*Drepane africana*
Chrysichthys auratus	*Chromidotilapia guntheri*	*Eucinostomus melanopterus*
Chrysichthys maurus	*Chrysichthys nigrodigitatus*	*Galeoïdes decadactylus*
Dasyatis margarita	*Eleotris senegalensis*	*Marcusenius bruyerei*
Citarichthys stampflii	*Fodiator acutus*	*Plectorhynchus macrolepis*
Arius parkii	*Hemiramphus balao*	*Pomadasys incisus*
Arius latiscutatus	*Heterobranchus isopterus*	*Sardinella maderensis*
Cynoglossus senegalensis	*Hyporamphus picarti*	*Scomberomorus tritor*
Eleotris daganensis	*Liza dumerili*	*Sphyraena afra*
Eleotris vittata	*Mugil curema*	
Ethmalosa fimbriata	*Petrocephalus bovei*	
Gerres nigri	*Pseudotolithus senegalensis*	
Gobionellus occidentalis	*Schilbe mystus*	
Hemichromis fasciatus		
Liza falcipinnis		
Liza grandisquamis		
Monodactylus sebae		
Parailia pellucida		
Pellonula leonensis		
Pseudotolithus elongatus		
Pomadasys jubelini		
Porogobius schlegelii		
Sarotherodon melanotheron		
Schilbe mandibularis		
Strongylura senegalensis		
Tilapia guineensis		
Tilapia mariae		
Trachinotus teraia		
Trichiurus lepturus		
Tylochromis jentinki		
Yongeichthys thomasi		

TABLE 22.IV.
List of species engaging in sexual activity in the LEEs of West Africa (Albaret & Diouf, 1994).

In the LEEs, reproductive strategies are aimed on one hand at minimizing the negative effects of environmental instability and on the other hand on combatting the dispersion of eggs, larvae, and embryos outside the estuary. Oviparous species have developed two "tactical choices" (Wootton, 1989). The first is based on maximizing the number of eggs released, and increases the probability that at least a fraction of the population will be transported to a favourable site in order to ensure recruitment (*Liza* spp., *Ethmalosa fimbriata*). The second tactic attempts to maximize the survival rate of eggs, larvae, and fry by limiting the number of eggs released and engaging in sometimes intensive parental care and/or seeking zones that are ecologically favourable to development. This, for instance, is the case of *Arius* spp, *Sarotherodon melanotheron,* and *Tylochromis jentinki* which practice mouth brooding, *Chrysichthys* spp whose clutches are attached and hidden in crevices or hollow pieces of wood, or *Tilapia guineensis* which build nests and guard the clutch and the fry (McKaye, 1989; Albaret & Diouf, 1994).

Viviparous (*Clinus superciliosus* in Southern Africa and *Dasyatis margarita* and *D. margaritella* in West Africa, for example) and ovoviviparous species (such as *Syngnathus acus* in Southern Africa and *Enneacampus kaupi* in West Africa) also have low fecundity. Embryos often reach a large size before hatching or release. Because of their large size, juveniles are less susceptible to predation or being carried away by currents (Whitfield, 1994a).

To reduce the risk of egg dispersal, groups with high estuarine affinity such as Atherinidae, Hemiramphidae and Gobiidae produce adhesive benthic eggs (Breder & Rosen 1966; Neira *et al.*, 1988; Potter *et al.*, 1990; Whitfield, 1990). Some species (mainly viviparous and ovoviviparous), sharply decrease or eliminate the initial larval stages and give birth to larvae that can swim well. It thus appears that the "precocial" reproductive strategy of some estuarine species can be traced to the fact that these fishes are attempting to limit the mortality risks associated with the uncontrolled dispersion of eggs and early larval stages (Whitfield, 1990). Other species such as *Amniataba caudavittata*, *Nematalosa vlaminghi* and *Gilchristella aestuaeria* (species from southwestern Australia and Southern Africa), spawn far from the river mouth, very high upstream in the estuary, thus reducing the risk that eggs are transported out to sea (Talbot, 1982; Chubb & Potter, 1984; Potter *et al.*, 1990).

In most of the species reproducing in the estuary, the period of sexual activity is long if not continuous. This spread of the reproductive season can be interpreted as the guarantee of sufficient recruitment in all eventualities (Wallace, 1975; Baran, 1995).

The "eco-reproductive" plasticity of most strictly estuarine species (E.s.) and estuarine species of marine or continental origin (E.m. and E.c.) is the reason for the high variability in reproductive modalities and energy allocation for reproductive activity depending on changes in the environment (Pauly, 1975) and biological interactions (Barbault, 1981; Legendre, 1992). This is the case in particular of *Ethmalosa fimbriata* and *Sarotherodon melanotheron* which display reduced size at first maturity when the environmental conditions become extreme: pollution (Albaret & Charles-Dominique, 1982), hypersalinity (Albaret, 1987); life in a confined system (Legendre & Écoutin, 1991).

Space occupation strategies

Heterogeneity, which increases the diversity of ecological niches, plays a fundamental role in the organization of communities (Barbault, 1992). It allows the maintenance of predator-prey systems by increasing the probability of survival of a fraction of the prey population which can colonize habitats that are not accessible to predators (Barbault, 1990).

Thus, in LEEs, many shoals, silt and sand bars, mangrove channels, as well as the root network of mangroves (stilt roots of *Rhizophora* and respiratory roots of *Avicennias*) are shelters that are accessible only to juveniles.

Moreover, the spatial segregation of species, related to heterogeneity, helps decrease the phenomena of inter-species competition (Blaber & Whitfield, 1977; Gorman, 1987; Wootton, 1992).

Species that use LEEs during their biological cycle demonstrate two occupation strategies to exploit to their advantage these nutrient-rich environments where predation is often low: migration and eco-physiological plasticity.

Migration is the solution adopted by a very large number of opportunistic species of marine origin and (to a lesser degree) species with a continental affinity that temporarily exploit the trophic richness of LEEs when the physico-chemical (Guiral, 1992) and biological (Sykes & Manooch, 1978; Day & Yañez-Arancibia, 1982) conditions are favourable. The space occupation strategies of these migratory species aim in many cases to reduce the distances between marine breeding areas and estuarine and lagoonal nursery zones (Whitfield, 1990).

The second strategy is adopted by sedentary species (at the scale of one lagoon or one estuary) that adapt to the variability of the system owing to their strong adaptability and great eco-physiological tolerance. In the case of very significant environmental stress, representatives of this category are capable of surviving, thriving, and in some cases proliferating. The extreme abundance of *Sarotherodon melanotheron*, the only species present in the hyperhaline upstream section of the Casamance during periods of rainfall deficit is one of the most spectacular examples of this ability to adapt (Albaret, 1987).

Food webs and resource use strategies

Fish diets and food webs have been the target of numerous investigations in both West Africa (Longhurst, 1957; Fagade & Olanyian, 1973; Pauly, 1975; Albaret 1994; Baran 1995; Diouf 1996.) and Southern Africa (Whitfield & Blaber, 1978a, b; Whitfield, 1980a, b).

LEEs are very productive ecosystems (Correll, 1978; Horn & Allen, 1985; Day & Yañez-Arancibia, 1982; Day *et al.*, 1989). Among aquatic systems, only coral reefs are generally seen as being more productive (Whittaker & Likens, 1973; Whitfield, 1993). This productivity, which is reflected in the great availability of nutrients for fishes, stems from the number and diversity of nutrient sources (Day & Yañez-Arancibia, 1982): runoff (Day & Yañez-Arancibia, 1985), fluvial (Yañez-Arancibia *et al.*, 1985) and marine (Cecchi, 1992) waters, remineralization of organic matter from river and submerged vegetation (William & Eric, 1972; Odum & Head, 1975; Twilley *et al.*, 1986; Day *et al.*, 1989; Alongi, 1988). In addition to all these advantages encountered by young fishes in estuarine systems, tropical zones are also characterized by the high production of mangrove formations (Odum & Head, 1975; Dor & Levy, 1984; Rodelli *et al.*, 1984). While tree production is not directly consumed by fish, it allows the creation of a rich and complex microbial network (Guiral, 1994). This bacterial and fungal biomass, which mineralizes litter, as well as the algal, phytobenthic and epiphytic production occurring on mangrove roots (Rodriguez & Stoner, 1990) that stem partially from that biomass, make up particularly rich and varied nutrient resources owing to their zooplanktonic, micro-, meio-, and macro-benthic communities (Alongi, 1989). Trophic chains in LEEs are thus characterized by the diversity of primary producers (Day

& Yañez-Arancibia, 1985; Flores-Verdugo *et al.*, 1990), which ensures abundant production throughout the year (Day & Yañez-Arancibia, 1982; Whitfield, 1980b). Phytoplankton is not the sole primary producer, nor is it necessarily the most important. Mangrove leaves, marsh vegetation, grasses, and the phytobenthos also play an important role.

In tropical LEEs, these resources display significant variability in time and space (Barett *et al.*, 1978; Deegan & Thompson, 1985). Adaptations developed by species living in these ecosystems are mainly intended to adjust to the unpredictable nature of food availability. Many migratory species, whether marine or continental in origin, optimize the use of lagoonal and estuarine trophic richness by synchronizing their reproduction and migration with periods of nutrient abundance (Yañez-Arancibia *et al.*, 1980; Day & Yañez-Arancibia, 1982).

There is little available information on food competition in LEEs. In general, it is believed that the absence of trophic specialization is an efficient way of preventing competition for resources that are abundant but of variable nature and quantity. However, in Southern Africa where detritivores are numerous, it has been shown that competition can be reduced by different mechanisms leading to a certain dietary segregation (Whitfield & Blaber, 1978b). This nonetheless seems to be very rare in many Mugilidae species (Blaber, 1977), which Whitfield (1996) interprets as an indicator that detritivores have access to extremely abundant nutrient resources in estuaries.

The most successful trophic strategy in these systems is based on low specialization and strong dietary opportunism. Omnivores (Deegan & Thompson, 1985) and unspecialized predators that can include fishes, crustaceans, molluscs, and insects in their diet are consequently the most numerous species (up to 80%, Albaret, 1994). Crustaceans, particularly Peneidae and Mysidacae shrimp, represent a crucial dietary source for estuarine fishes, particularly young predators (Albaret, 1994).

Although they are represented by a relatively low number of species (15 to 30% depending on the case), opportunistic filter-feeders such as *Ethmalosa fimbriata* that can feed on phytoplankton, zooplankton, and even microbenthos depending on the supply in the ecosystem, often make up the bulk of fish biomass in the LEEs of West Africa (Albaret, 1994).

Whitfield (1996) points out the absence of phytoplanktivorous fishes in the estuaries of South Africa where he notes, along with authors such as Blaber (1977), the importance of the detrital path also highlighted by Albaret & Diouf (1994) for the LEEs of West Africa which, according to Diouf (1996), is an addition to primary production-based trophic chains that are usually seen in aquatic systems.

We should still note the rarity of linear food chains and of exclusive or highly-determined predator/prey relationships in these ecosystems where, on the contrary, species show low dietary specialization, high adaptability, and even great trophic opportunism.

Functional role of lagoon and estuarine ecosystems

Exportation of organic matter and energy

The influence of LEEs on the halieutic production of coastal marine areas is well established (Moore *et al.*, 1970; Sutcliffe, 1973; Yañez-Arancibia *et al.*, 1980; Baran, 1995). One of the main paradigms of the ecology of coastal lagoons and estuaries these past three or four decades is that these systems produce an excess of organic matter and nutrients, a good part of which is exported out to sea. This is the so-called "outwelling hypothesis" (Darnell, 1967; Day *et al.*, 1973; Odum *et al.*, 1974).

Some studies call this hypothesis into question and suggest on the contrary that organic carbon may be imported into certain LEEs (Hains & Dunstran, 1976; Woodwell *et al.*, 1977). In fact, the direction of the net flow of exchanges between an estuarine environment and a marine coastal zone may depend on local conditions (Day & Yañez-Arancibia, 1982; Day & Yañez-Arancibia, 1985).

Fishes in the LEEs play an important role in the flow of energy and nutrients. As secondary consumers, they can constitute energy and nutrient reserves, thus limiting the exportation of nutritional elements. Moreover, through their migrations, they can allow nutrient and energy exchanges with coastal marine systems (Yañez-Arancibia & Nugent, 1977; Kitchell *et al.*, 1979). The exportation of juveniles after growing in lagoon and estuarine environments corresponds to a loss of energy for these systems and an energy gain for the ecosystems receiving them (Thollot, 1992). This energy loss can be considerable. In effect, juveniles migrating out to sea may have multiplied their individual weight by 2,000 during their stay in estuaries and lagoons (Wagner, 1973; Hinchee, 1977). This good growth is also accompanied by high survival rates for these juveniles in lagoon and estuarine ecosystems owing to food abundance and relatively low predation (Day *et al.*, 1989).

Nursery

The importance of estuaries as nurseries for the juvenile forms of many fish species has been seen in diverse latitudes (Johannes, 1978; Beckley, 1984; Ross & Epperly, 1985; Day *et al.*, 1989). In many cases, breeders spawn in coastal areas (Yañez-Arancibia, 1985; Whitfield 1990), then larvae arrive in the estuary through passive transport among plankton or through active swimming. The interpretations put forth to explain the adaptive advantage of this migration generally refer to water turbidity (suspension of mineral and organic particulate matter of a planktonic or detrital nature) and high trophic availability observed in LEEs. Post-larval and juvenile fishes in the estuary thus find favourable trophic conditions that are diverse and suited to their filtration and capture capacities (May, 1974; Miller & Dunn, 1980; Mann, 198; Legett, 1986). The aggregating behaviour of fry with limited swimming and escape capacities, combined with the frequent turbidity of LEE waters that reduce a predator's distance of perception, increases the probability of escape for prey and thus the overall survival rate for the population. Such a mechanism has been verified experimentally by several authors (Viniyard & O'Brien, 1976; Cyrus & Blaber, 1987a, b, c; Gregory, 1993). Moreover, the abundance of shoals in LEEs restricts the access of large ichthyophagic predators, thereby contributing to less predation pressure on juveniles and small species (Blaber, 1980; Blaber & Blaber, 1980; Kneib 1987). Finally, compared with the marine system, the diversity and structural complexity of habitats in LEEs encourages the concentration and retention of juvenile forms (Fraser & Cerri, 1982; Cowder & Cooper, 1982; Nelson & Bonsdorff, 1990).

Such favourable conditions for the nutrition and survival of juvenile forms, combined with the relatively high temperatures often found in LEEs, encourage rapid growth (Potter *et al.*, 1990; Lenanton & Hodgkin, 1985).

However, to benefit from these advantages, these forms must have acquired certain ecophysiological adaptations that allow them to thrive in a variable and often unpredictable environment. Thus, the metabolic effort associated with temperature and ion regulation in these tolerant, opportunistic species in the juvenile stage may remain two to three times less than the energy they would consume by actively swimming out of estuaries (Miller *et al.,* 1985).

There is broad scientific consensus about the role of LEEs as systems favourable to hosting, survival, and growth of juveniles of many coastal fish species, but many questions remain as to the qualitative aspect of the relationships connecting these species to LEEs and the existence of alternative habitats and nurseries in the coastal environment (Baran *et al.*, 1999).

Many species of continental origin also spend part or all of their lives in an estuarine ecosystem. Some, such as *Schilbe mandibularis* (with a large lagoonal distribution), *Parailia pellucida* and *Schilbe mystus* (limited to low salinity and freshwater sectors) can be observed as being notably abundant there (Albaret, 1994). The relationships between fluvial and lagoonal "populations" remain poorly understood, and the nursery role of the estuarine zone is still hypothetical as far as they are concerned.

Conclusions

Contrary to many preconceptions, the composition and general structure of estuarine fish communities display a high degree of stability and robustness at certain time scales (periods of 10 years or more). A connection must be made between this stability and the adaptability of species comprising these communities, the diversity and efficiency of the vital strategies deployed, as well as the existence within these communities of compensatory mechanisms for species (replacement over time of certain species by others that occupy a similar place and role without altering the general structure of the community). The constant availability of varied trophic resources and the sturdiness of food webs (Moyle & Cech, 1982) also constitute a factor contributing to the stability of fish communities. Such long-term stability and robustness nonetheless has limits, which were seen after monitoring the changes that occurred in certain brackish water systems: hypersalinization of the Casamance (Albaret, 1987), isolation of Togolese lagoons from the sea (Laë, 1992a) or, conversely, an increase in exchanges following the opening of a new channel in the Ébrié lagoon (Albaret & Écoutin, 1989), construction of a dam in the upstream section of the Senegal River estuary, etc. These studies show that communities then undergo major changes in species richness, structure, and the mechanisms that govern their functioning. Baran (1995) stresses that tolerance and adaptability are written in the genes of estuarine species (Schachter, 1969; Battaglia & Fava, 1982), but only within the limits of the "natural" environmental variations encountered during the evolution of the species. The example shows that such tolerance and adaptability do not allow species to adapt to disturbances of an anthropogenic nature when these are of unusual scope, duration, or nature (Livingston, 1984).

Found at the interface of the continent and the ocean, LEEs are among the environmental systems most affected by anthropogenic activity and global changes. They have been sites of human occupation since prehistoric times. Today, with population growth, these systems are under heavy demand from all directions, often in contradictory ways: fishing, aquaculture, transport, protection of fauna and flora, urbanisation, tourism, various exploitations (e.g. mangrove wood, sand), hydro-agricultural works, etc.

While human activities are most often behind the deterioration of LEEs, natural events or changes may also lead to a more or less significant erosion of biological diversity. In fact, quite often the most delicate situations are the result of the combination of the two types of factors and their mutual aggravation. In West Africa, the chronic rainfall deficit in the Sahelian area enters in combination with multiple human interventions, profoundly modifying the biocenoses of estuarine systems without making it possible, at least in the current state of knowledge, to determine the exact degree of "responsibility" of the offending factors.

Species introductions

DIDIER PAUGY

CHRISTIAN LÉVÊQUE

Since antiquity, fish have been introduced and translocated between and within continents. This practice was greatly developed during the 20th century with the primary aim of improving fishing production and fish farming development. Fish have been introduced on every continent, but this chapter focuses only on Africa.

While species introductions have been encouraged more or less throughout the world in order to improve aquaculture production, they have become controversial in recent decades among scientists and aquatic ecosystem managers. The introduction of new species sometimes has enormous consequences on native fish populations. Some believe that humans should not play with fire and that any introduction is causing irreversible damage to native fauna. On the contrary, others think that nature has not necessarily gone in the right direction, and that the introduction of species to improve fisheries production is justified in a number of cases. This debate is far from resolved and should prompt us to adopt a precautionary approach.

Goals of introductions

There have been several introductions of alien fish species to African waters, and many translocations of African fish species within Africa to areas outside their natural ranges (tables 23.I and 23.II) (see also box "Some semantic explanations"). The goals of these introductions are varied, and have been detailed by Welcomme (1988),Moreau *et al.* (1988), Ogutu-Ohwayo & Hecky (1991) and Lévêque (1997b). Nearly 50 species from other continents have been introduced more or less everywhere in Africa.

SOME SEMANTIC EXPLANATIONS (REPRODUCED FROM LAZARD & LÉVÊQUE, 2009)

There is some confusion regarding the use of certain terms.
We propose the use of **introduction** to designate species that have been intentionally or accidentally transported and introduced by humans into a system found outside the natural area of distribution for that species.
Meanwhile, **translocations** (or transfers) correspond to the deliberate or accidental transport of individuals of a species to other sites within the natural area of distribution of the species. The genomes of these translocated individuals may differ from that of the native population, leading to a modification in gene flows.
Species are referred to as **indigenous**, **native**, or **autochthonous** when they originate from the area under consideration. They are **introduced**, **exotic**, or **allochthonous** when they originate from another area of distribution. A **cryptogenic** species is one for which there is no clear evidence whether or not it is introduced.
Acclimatization is the adaptation of a specimen to new conditions. This does not automatically result in the establishment of a population, as reproduction is not necessarily guaranteed. When a population of an introduced species develops in the natural system, that is, it lives and reproduces there, this is called **naturalisation**.

Introduced for sport fishing, the European brown trout (*Salmo trutta*) has now acclimatized in different upland aquatic systems. This is the case as well for the black bass (*Micropterus salmoides*) originally from the United States, now acclimatized in Kenya and Madagascar. Among the Cyprinidae, the European carp (*Cyprinus carpio*), as well as the goldfish (*Carassius auratus*) were also introduced in the 19th century in Madagascar. Asian species such as the gourami (*Osphronemus goramy*), introduced in the mid-19th century, and the snakehead *Channa* sp., (according to Lowe-McConnell, 1987) of more recent introduction, now populate Malagasy waters.

Sport fishing

Among the many reasons to perform introductions, nostalgia of displaced peoples for familiar fauna to surround them would seem to rank fairly high (Welcomme, 1988) and, in the past, fishery officers introduced alien species to improve sport fisheries, such as in Morocco, South Africa, Kenya and Madagascar where bass (*Micropterus salmoides* from North America) (Moreau *et al.*, 1988) and trout (*Salmo trutta* from Europe) (Baglinière & Maisse, 1991) were introduced.

The controversial introduction of *Lates niloticus* (figure 23.1) in Lake Victoria (see box "The case of *Lates niloticus* in Lake Victoria") could have also been partly motivated by the wish to develop sport fishing.

Fish culture

More than a hundred fish species have been introduced for aquaculture purposes around the world, but few of such introductions involve tropical Africa. The carp (*Cyprinus carpio*) is one of the rare non-indigenous species for which farming

TABLE 23.I.

Alien (from other continents) species introduced in Africa. Total: number of countries where the species has been introduced. Species established in the wild (E); species not established in the wild (NE), data unknown (U) (data synthetized from Froese & Pauly, 2010 and Lever, 1996).

Species	Families	Algeria	Angola	Botswana	Burundi	Cameroon	CAR	Congo	Côte d'Ivoire	Egypt	Eritrea	Ethiopia	Ghana	Kenya	Lesotho
Anguilla anguilla	Anguillidae										E			NE	
Astronotus ocellatrus	Cichlidae								NE						
Astyanax orthodus	Characidae														
Barbus barbus	Cyprinidae														
Carassius auratus auratus	Cyprinidae											E			
Carassius carassius	Cyprinidae											U		NE	
Catla catla	Cyprinidae														
Channa maculata	Channidae														
Channa striata	Channidae														
Cichla ocellaris	Cichlidae													NE	
Ctenopharyngodon idella	Cyprinidae	NE	U		NE				E	E		E		NE	NE
Cyprinus carpio carpio	Cyprinidae		U	E	U	E	E		E	E		E		NE	U
Esox lucius	Esocidae	E										E			
Gambusia affinis	Poeciliidae						E		U	E			U	E	
Gambusia hilbrooki	Poeciliidae											E		E	
Gobio gobio	Cyprinidae														
Hucho hucho	Salmonidae														
Hypophthalmichthys molitrix	Cyprinidae	NE								NE		E			NE
Hypophthalmichthys nobilis	Cyprinidae	NE								NE					NE
Ictalurus punctatus	Ictaluridae								U	NE					
Labeo rohita	Cyprinidae														
Lepomis cyanellus	Centrarchidae							NE						U	
Lepomis gibbosus	Centrarchidae							E							
Lepomis macrochirus	Centrarchidae							NE						U	
Lepomis microlophus	Centrarchidae														
Macropodus opercularis	Osphronemidae														
Micropterus dolomieu	Centrarchidae														
Micropterus punctulatus	Centrarchidae		NE												
Micropterus salmoides	Centrarchidae	E		E		NE		NE		NE				E	E
Mylopharyngodon piceus	Cyprinidae									U					
Oncorhynchus mykiss	Salmonidae					U		NE			E	E		E	E
Osphronemus goramy	Osphronemidae	U							NE						
Perca fluviatilis	Percidae														
Phalloceros caudimaculatus	Poeciliidae														
Poecilia latipinna	Poeciliidae													E	
Poecilia reticulata	Poeciliidae													E	
Pseudorasbora parva	Cyprinidae	E													
Rutilus rutilus	Cyprinidae														
Salmo trutta fario	Salmonidae													E	
Salmo trutta trutta	Salmonidae											E		E	E
Salvelinus fontinalis	Salmonidae														
Sander lucioperca	Percidae	NE													
Scardinius erythrophthalmus	Cyprinidae														
Silurus glanis	Siluridae	NE													
Tanichthys albonubes	Cyprinidae														
Tinca tinca	Cyprinidae														
Trichogaster trichopterus	Osphronemidae														
Xiphophorus helleri	Poeciliidae														
Xiphophorus maculatus	Poeciliidae														
Total		**9**	**3**	**2**	**2**	**3**	**2**	**5**	**6**	**8**	**2**	**9**	**1**	**15**	**7**

Species	**Families**	Madagascar	Malawi	Morocco	Mozambique	Namibia	Nigeria	RDC	Rwanda	South Africa	Sudan	Swaziland	Tanzania	Togo	Tunisia	Uganda	Zambia	Zimbabwe	**Total**
Anguilla anguilla	Anguillidae																		**2**
Astronotus ocellatrus	Cichlidae																		**1**
Astyanax orthodus	Characidae					E													**1**
Barbus barbus	Cyprinidae			E															**1**
Carassius auratus auratus	Cyprinidae	E				E				E								E	**5**
Carassius carassius	Cyprinidae																		**2**
Catla catla	Cyprinidae																NE		**1**
Channa maculata	Channidae	E																	**1**
Channa striata	Channidae	E																	**1**
Cichla ocellaris	Cichlidae																		**1**
Ctenopharyngodon idella	Cyprinidae		NE	E	NE		U		NE	NE	E		U		E	NE	NE	NE	**20**
Cyprinus carpio carpio	Cyprinidae	E	NE	E	U	E	E	NE	E	E	NE	U	U	U	E	E	NE	E	**27**
Esox lucius	Esocidae	NE		E											NE	U			**6**
Gambusia affinis	Poeciliidae	E		E						E	E						NE	E	**11**
Gambusia hilbrooki	Poeciliidae	E																	**3**
Gobio gobio	Cyprinidae			E															**1**
Hucho hucho	Salmonidae			NE															**1**
Hypophthalmichthys molitrix	Cyprinidae	NE	NE	E	NE		NE		NE	NE			NE		E		U	U	**15**
Hypophthalmichthys nobilis	Cyprinidae	NE		U	NE														**6**
Ictalurus punctatus	Ictaluridae						U												**3**
Labeo rohita	Cyprinidae	U					NE											U	**3**
Lepomis cyanellus	Centrarchidae	NE		E						U		E					E	NE	**8**
Lepomis gibbosus	Centrarchidae			E															**2**
Lepomis macrochirus	Centrarchidae	E	E	E						E		E					NE	E	**9**
Lepomis microlophus	Centrarchidae			E															**1**
Macropodus opercularis	Osphronemidae	E																	**1**
Micropterus dolomieu	Centrarchidae									E		NE	E				NE	NE	**5**
Micropterus punctulatus	Centrarchidae									E		U						E	**4**
Micropterus salmoides	Centrarchidae	E	E	E	U	E	U			E		E	U		E	U		E	**19**
Mylopharyngodon piceus	Cyprinidae			U															**2**
Oncorhynchus mykiss	Salmonidae	E	E	E	U					E	E	E	E		NE	U	NE	E	**18**
Osphronemus goramy	Osphronemidae	E														NE			**4**
Perca fluviatilis	Percidae			E						E									**2**
Phalloceros caudimaculatus	Poeciliidae		E																**1**
Poecilia latipinna	Poeciliidae																		**1**
Poecilia reticulata	Poeciliidae	E	NE			E	NE			E						E	E		**8**
Pseudorasbora parva	Cyprinidae																		**1**
Rutilus rutilus	Cyprinidae	NE		E															**2**
Salmo trutta fario	Salmonidae	E																	**2**
Salmo trutta trutta	Salmonidae	E	NE	NE						E		E	U					E	**10**
Salvelinus fontinalis	Salmonidae			NE														E	**2**
Sander lucioperca	Percidae			E											E				**3**
Scardinius erythrophthalmus	Cyprinidae	NE		E											E				**3**
Silurus glanis	Siluridae														NE				**2**
Tanichthys albonubes	Cyprinidae	E																	**1**
Tinca tinca	Cyprinidae	NE		E						E					NE		NE	E	**6**
Trichogaster trichopterus	Osphronemidae					E													**1**
Xiphophorus helleri	Poeciliidae	E				E				E							U		**4**
Xiphophorus maculatus	Poeciliidae	E					E												**2**
Total		**25**	**9**	**23**	**6**	**7**	**8**	**1**	**3**	**16**	**4**	**8**	**7**	**1**	**10**	**7**	**11**	**16**	**236**

TABLE 23.II.

African translocated species. Number: number of countries where the species has been translocated. Species established in the wild (E); species not established in the wild (NE), data unknown (U) (data synthetized from Froese & Pauly, 2010 and Lever, 1996).

Species	Families	Algeria	Angola	Benin	Botswana	Burkina Faso	Burundi	Cameroon	CAR	Chad	Congo	Côte d'Ivoire	Egypt	Eritrea	Ethiopia	Gabon	Ghana
Aphanius fasciatus	Cyprinodontidae																
Astatoreochromis alluaudi	Cichlidae							E	E		NE						
Bagrus meridionalis	Bagridae																
Barbus anoplus	Cyprinidae																
Boulengerochromis microlepis	Cichlidae																
Butis koilomatodon	Eleotridae																
Clarias gariepinus	Clariidae						E	E			E	NE				E	
Distichodus nefasch	Distichodontidae										E						
Heterotis niloticus	Arapaimidae							U	E		E	U				E	
Labeobarbus aeneus	Cyprinidae																
Labeobarbus kimberleyensis	Cyprinidae																
Labeobarbus natalensis	Cyprinidae																
Lates niloticus	Latidae										E						
Limnothrissa miodon	Clupeidae																
Microctenopoma ansorgii	Anabantidae																
Oreochromis andersonii	Cichlidae																
Oreochromis aureus	Cichlidae											NE					
Oreochromis esculentus	Cichlidae																
Oreochromis karongae	Cichlidae																
Oreochromis leucostictus	Cichlidae						U										
Oreochromis macrochir	Cichlidae	NE	U	NE		E	U	NE	E		NE	E	E			E	E
Oreochromis mortimeri	Cichlidae																
Oreochromis mossambicus	Cichlidae	E	U	E			U				E	NE	E				
Oreochromis niloticus eduardianus	Cichlidae																
Oreochromis niloticus niloticus	Cichlidae				E		E	E	U		E	E		E		U	
Oreochromis shiranus shiranus	Cichlidae																
Oreochromis spilurus niger	Cichlidae																
Oreochromis spilurus spilurus	Cichlidae			U				U			U	U	U				
Oreochromis tanganicae	Cichlidae						U										
Oreochromis urolepis hornorum	Cichlidae											E					
Pachypanchax playfairii	Aplocheilidae																
Protopterus aethiopicus aethiopicus	Protopteridae																
Sarotherodon galilaeus boulengeri	Cichlidae															E	
Sarotherodon galilaeus galilaeus	Cichlidae										E						
Schilbe mystus	Schilbeidae										E						
Serranochromis robustus jallae	Cichlidae																
Serranochromis robustus robustus	Cichlidae																
Stolothrissa tanganicae	Clupeidae																
Tilapia guinasana	Cichlidae				U												
Coptodon rendalli	Cichlidae		U				E	NE	NE	E	E	NE			E	E	
Tilapia sparrmanii	Cichlidae																
Coptodon zillii	Cichlidae	NE										NE		E	E		
Total		**3**	**3**	**3**	**2**	**1**	**7**	**7**	**5**	**1**	**12**	**10**	**3**	**2**	**2**	**6**	**1**

Species	**Families**	Guinea	Kenya	Lesotho	Liberia	Madagascar	Malawi	Morocco	Mozambique	Namibia	Nigeria	RDC	Rwanda	Sierra Leone	South Africa	Sudan	Swaziland	Tanzania	Togo	Tunisia	Uganda	Zambia	Zimbabwe	**Total**
Aphanius fasciatus	Cyprinodontidae							E																**1**
Astatoreochromis alluaudi	Cichlidae											E										NE		**5**
Bagrus meridionalis	Bagridae																		NE	NE				**2**
Barbus anoplus	Cyprinidae									E														**1**
Boulengerochromis microlepis	Cichlidae																			NE				**1**
Butis koilomatodon	Eleotridae										E													**1**
Clarias gariepinus	Clariidae			E								NE												**7**
Distichodus nefasch	Distichodontidae																							**1**
Heterotis niloticus	Arapaimidae					E						E							E					**8**
Labeobarbus aeneus	Cyprinidae																			E				**1**
Labeobarbus kimberleyensis	Cyprinidae																			NE				**1**
Labeobarbus natalensis	Cyprinidae																			E				**1**
Lates niloticus	Latidae		E					NE										E			E			**5**
Limnothrissa miodon	Clupeidae								E			E	E									E	E	**5**
Microctenopoma ansorgii	Anabantidae					E																		**1**
Oreochromis andersonii	Cichlidae		U									E			E			E					NE	**5**
Oreochromis aureus	Cichlidae		U			E									E						NE	E	U	**7**
Oreochromis esculentus	Cichlidae												E					E						**2**
Oreochromis karongae	Cichlidae						E																	**1**
Oreochromis leucostictus	Cichlidae		U									E	E					E			E			**6**
Oreochromis macrochir	Cichlidae		E		U	E						E	E		U	E		U	U			E	E	**23**
Oreochromis mortimeri	Cichlidae											E										U		**2**
Oreochromis mossambicus	Cichlidae		U			E				E		E			E			E		E	E			**15**
Oreochromis niloticus eduardianus	Cichlidae		E															E			E			**3**
Oreochromis niloticus niloticus	Cichlidae	NE	E		U	E			U			U	E	U	E			E		E		E	E	**21**
Oreochromis shiranus shiranus	Cichlidae					NE																		**1**
Oreochromis spilurus niger	Cichlidae		NE			E			U													U		**4**
Oreochromis spilurus spilurus	Cichlidae					NE			U			E									E			**9**
Oreochromis tanganicae	Cichlidae																							**1**
Oreochromis urolepis hornorum	Cichlidae																							**1**
Pachypanchax playfairii	Aplocheilidae																	E						**1**
Protopterus aethiopicus aethiopicus	Protopteridae												E											**1**
Sarotherodon galilaeus boulengeri	Cichlidae																							**1**
Sarotherodon galilaeus galilaeus	Cichlidae														NE									**2**
Schilbe mystus	Schilbeidae																							**1**
Serranochromis robustus jallae	Cichlidae														E		E							**2**
Serranochromis robustus robustus	Cichlidae																E					U		**2**
Stolothrissa tanganicae	Clupeidae											NE												**1**
Tilapia guinasana	Cichlidae																							**1**
Coptodon rendalli	Cichlidae		E			E	U						E			NE		E			E	E		**17**
Tilapia sparrmanii	Cichlidae					E									E			NE						**3**
Coptodon zillii	Cichlidae		E			E									NE			E			E			**9**
Total		**1**	**11**	**1**	**2**	**12**	**2**	**2**	**4**	**2**	**1**	**12**	**7**	**1**	**9**	**2**	**2**	**12**	**2**	**2**	**8**	**11**	**9**	**183**

was attempted several times in various African countries. Many tilapia species have also been translocated to different sites on the African continent (Moreau *et al.*, 1988; Lazard, 1990a) or introduced more or less everywhere in the world (see chapter *Fish culture*). In the intertropical zone, *Oreochromis niloticus* (figure 23.1) and to a lesser extent *Oreochromis mossambicus* currently account for most of aquaculture production.

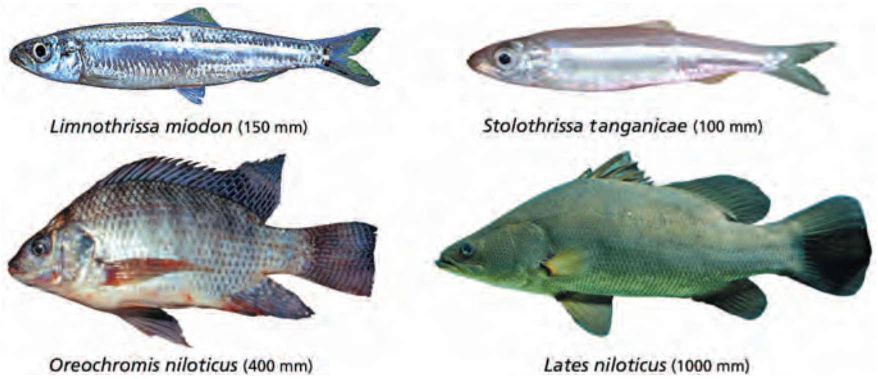
Improvement of wild stocks

Fisheries managers have often attempted to introduce species in order to improve the fish production of an aquatic ecosystem, particularly when they believe that certain ecological niches are vacant and that the resources of a given system are not optimally exploited by indigenous fishes.

Hence, *Limnothrissa miodon* and *Stolothrissa tanganicae* (figure 23.1), two small Clupeidae endemic to Lake Tanganyika, were introduced into Lake Kivu in 1958-1960 where they occupied a vacant niche by exploiting pelagic zooplankton. This introduction is considered a success from the economic viewpoint (Spliethoff *et al.*, 1983) and allowed the establishment of a fishery in the early 1980s (see also box "Genetic evolution of introduced species").

Species introduction has also been justified at times by the creation of new habitats. For instance, fluvial species that prefer running water are not always suited to reservoirs. We can thus seek out species that are likely to colonize these new systems and use their resources more efficiently. This is why *Limnothrissa miodon* was also introduced into Lake Kariba (an artificial reservoir) in order to use the pelagic zone's zooplankton more optimally. It became well-established there and now occupies the entire lake, where it serves as food for *Hydrocynus vittatus* and allowed the development of a fishery (Marshall, 1984b). Fishery production which stood at 1,000 tonnes in 1974 increased to 24,000 tonnes by 1985 (Marshall, 1988).

The introduction of *Heterotis niloticus* and *Oreochromis niloticus* in Lake Kossou, Côte d'Ivoire, was also intended to encourage colonization of this reservoir by fishes that were more suited to lacustrine conditions (Lazard, 1990b) and the two species have become well-established there with no apparent consequences to date on the native fauna.



Limnothrissa miodon (150 mm)

Stolothrissa tanganicae (100 mm)

Oreochromis niloticus (400 mm)

Lates niloticus (1000 mm)

FIGURE 23.1.
Four main African fish species introduced in other environments to improve fisheries: two pelagic zooplanktivorous clupeids *Limnothrissa miodon* and *Stolothrissa tanganicae*, one omnivorous cichlid *Oreochromis niloticus* and one ichtyophagous *Lates niloticus*. In brackets: common size of the species.

To justify introductions, fisheries managers highlight other examples deemed positive for fisheries development. The introduction of different tilapia species of African origin (particularly *Oreochromis mossambicu*s) in natural lakes and artificial reservoirs has made it possible to improve subsistence fishing in many African countries (Fernando, 1991; Fernando & Furtado, 1975; Holcik, 1984). Tilapias (*Oreochromis* sp. and *Sarotherodon* sp.) are very good colonizing species for their biological characteristics (species practicing parental care), their great physiological tolerance, and their ability to feed on seaweed and detritus which are often poorly-used resources in many tropical systems (Philippart & Ruwet, 1982). They have been introduced in Africa in many small agro-pastoral reservoirs that have been constructed over the last two decades.

Another example is that of Lake Kyoga where *Lates niloticus* and *Oreochromis niloticus* were introduced in the 1950s and rapidly thrived (Gee, 1969). In 1977 each species accounted for about 40% of artisanal fishing, estimated at 167,000 tonnes, a far cry from the 4,500 tonnes recorded in 1956. In 1985 the situation had changed with *O. niloticus* accounting for 78% of catches compared with only 17% for *L. niloticus* (Ogutu-Ohwayo, 1990).

Finally, in Lake Victoria improved fishing technology (nylon gillnets and outboard motors) combined with increased fishing effort resulted in a severe drop in catches of the endemic tilapia species by the beginning of the 1970s, well before the Nile perch (*Lates niloticus*) was established (Fryer & Iles, 1972). In this case, as the native species declined, new fisheries were established targeting other newly introduced species (particularly *Lates niloticus* and *Oreochomis niloticus*). The total catch reached 0.9 million tonnes at the end of the 2000s (figure 23.2). The question now is how stable the new fishery, based on non-native species, will be over the longer term as the catch composition appears to be undergoing a period of quite dramatic change (Witte *et al.,* 2007b).

GENETIC EVOLUTION OF INTRODUCED SPECIES

Do species introduced into new systems keep their genetic characteristics, or can an evolution be observed in a relatively short time span? The answer depends in part on the techniques used.

Limnothrissa miodon was introduced in 1959 into Lake Kivu from populations caught in Lake Tanganyika. Hauser *et al.* (1995) have shown that 34 years later, the translocated population differs from the original population both morphologically and genetically. While no allozyme diversity was observed, the Kivu population shows nonetheless poorer diversity of mitochondrial DNA (mtDNA haplotype diversity). This loss of variation which suggests a founder effect may have been caused by high individual mortality (several tens of thousands) after the introduction, such that the current population may come from only a few dozen surviving individuals. This loss of variability in mitochondrial DNA controlling enzymes needed for cell physiology may in theory have consequences on the physiological adaptability of the species.

THE CASE OF *LATES NILOTICUS* IN LAKE VICTORIA

Lake Victoria is the second-largest lake in the world, covering an area of 68,000 km^2. In the mid-1980s, the lake's fish community and fishery changed drastically from being dominated by a few hundred endemic haplochromine species to a catch of basically three species: the introduced Nile perch (*Lates niloticus*) and *dagaa*/*omena* (*Rastrineobola argentea*) in the open waters; and the introduced Nile tilapia (*Oreochromis niloticus*) along the shores. The endemic cichlids (haplochromines) that vanished almost completely as the fish community changed, have been reappearing in catches since 2000 and are probably recovering slowly. The inshore demersal species, originally mainly endemic tilapias (*Oreochromis esculentus* and *O. variabilis*), Nile catfish (*Bagrus docmak*), lungfish (*Protopterus aethiopicus*), the elephant-snout fish (*Mormyrus kannume*), and the *ningu* (*Labeo victorianus*), are all depleted, except the lungfish. Today, the Nile tilapia dominates, its abundance is increasing in surveys and it is considered moderately exploited. *Dagaa* stocks and catches have been increasing steadily. Since 2005, it has been the most important fishery in the lake by weight, but there are no signs of overexploitation (figure 23.2).

The explosion of *Lates* populations associated with the vanishing of small cichlid populations led many scientists to claim that *Lates* exterminated endemic haplochromines. They denounced the ecological disaster following the introduction of the exotic top predator and its impact on the naïve endemic ichthyofauna. In most textbooks *Lates* became the archetype of mismanagement of aquatic systems by man leading to environmental disaster.

The situation is actually much more complex. Detailed analysis has shown that the dynamics of fish production in Lake Victoria are, to a large extent, environmentally driven. Changes in land-use practices and a huge increase of human settlements in the lake basin have led to an increased input of nutrients, resulting in an eutrophication process which poses a serious threat to the entire ecosystem.

Eutrophication began as early as the 1940s to 1950s as revealed by diatom analysis. The timing of the eutrophication means that Nile perch population growth could not be the primary cause. Long-term human population growth, agricultural and urban development, and the associated increases in nutrient pollution and soil erosion are the most likely underlying causes of the recent changes in water quality, with climatic conditions sometimes amplifying those effects.

The main consequences of eutrophication are the deoxygenation of bottom waters and loss of habitat (endemic cichlids built nests on the bottom), and increased turbidity (the benthic cichlids use visual signals for sexual recognition). Meanwhile, eutrophication led to an increased primary production that benefits shrimp (*Caridina)*, and pelagic fish (*Rastrineobola*), whose biomass exploded, providing food to *Lates*. As a result, *Lates* may have contributed to the depletion of small cichlid populations, but the eutrophication was a serious threat to these populations that may have been endangered even in the absence of *Lates*. This is a different story from the one singling out *Lates* as a "devil" fish. It is possible to control eutrophication through water purification plans, but it will be costly. Who is ready to pay?

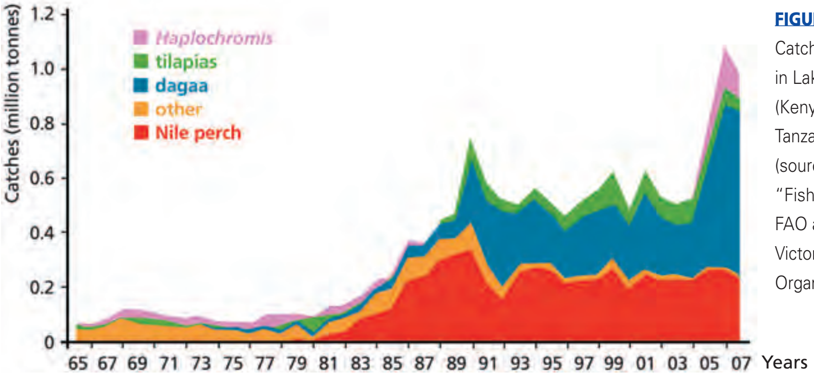


FIGURE 23.2.

Catch evolution in Lake Victoria (Kenya, Uganda, Tanzania) (source: "Fishstat Plus", FAO and "Lake Victoria Fisheries Organization")

Biological control

Fish species introduction was also practiced to control disease vectors. Certain species such as *Gambusia affinis* or *Poecilia reticulata* were used in different regions of Africa in an attempt to control malaria-bearing mosquitoes. There was also a proposal to use the mollusciverous cichlid *Astatoreochromis alluaudi* from East Africa to fight schistosomiasis vectors (Slootweg, 1989). This species was introduced into different locations in Africa without any visible ecological effects, but without proving its effectiveness as a means of disease control either. Finally, African fishes are sometimes used to control aquatic vegetation, with the example of *Coptodon rendalli* which was introduced into irrigation canals in Sudan.

Accidental introductions

Introductions that are accidental (or thought to be) are relatively frequent. Many, if not all, species introduced for aquaculture purposes escaped from fish farms during uncontrolled events such as exceptional floods, whereas their presence was not desired in the natural environment. This is thought to be the case in Madagascar of the snakehead, *Channa striata*, a fish of Asian origin that spread in many aquatic systems after a flood destroyed the fish farming station where the species was stocked.

The transport of fishes via the ballast of vessels is also considered a major source of transfers. This is the hypothesis advanced by Miller *et al.* (1989) to explain the introduction of an Eleotridae (*Butis koilomatodon*) originating in the Indo-Pacific into the mangroves of Lower Guinea.

As transfers of aquarium fishes are not controlled, there are more and more so-called accidental introductions of these species in aquatic systems around the world. These are often individuals released by amateur aquarists into the natural environment.

Consequences of introductions for the aquatic environment

The introduction of new species into an ecosystem is sometimes behind competition phenomena that can lead to the elimination of indigenous or introduced species. But there may also be indirect changes, generally more difficult to observe, via trophic chains. To interpret the impact of introductions accurately, it is necessary to distinguish between several levels of intervention:

- the transplantation of species from one point to another within the same watershed;
- the introduction of species missing from the watershed but present in the same biogeographic area;
- the introduction of species from biogeographically different areas, or even different continents.

Several observations appear to indicate that most species introductions do not have noticeable ecological effect, and that the socio-economic impact has often been beneficial (table 23.III). Nonetheless, despite its highly interesting findings, this widely-disseminated table is not accompanied by the methodology that allowed these conclusions to be drawn, and we cannot verify their pertinence. The discussion remains partially unresolved (Lazard & Lévêque, 2009).

Impact	Fisheries	Aquaculture	Aquarium trade	Biological control	Unknown	Others
Negative	36 (2)	78 (8)	17 (5)	23 (9)	13 (0)	40 (12)
Beneficial	16 (87)	52 (283)	11 (42)	11 (19)	3 (10)	6 (15)
Unknown	28 (16)	76 (49)	9 (9)	8 (2)	21 (3)	
Nil	196 (299)	949 (815)	169 (150)	106 (122)	459	283 (328)

TABLE 23.III.
Effects of introduced fish on ecological (and socio-economic) environments (from Lazard & Lévêque, 2009).

Interaction with native species

Introduced species can compete with indigenous species and eventually eliminate them. This is particularly true when predator species are introduced. One of the most spectacular cases is the introduction into Lake Victoria of *Lates niloticus*, a piscivorous fish that can reach a weight of more than 100 kg. For some scientists, this predator could be the reason for the decline and probable disappearance of several species belonging to a rich endemic fauna of small Cichlidae that it preyed upon (see box "The case of *Lates niloticus* in Lake Victoria"). It is also believed that the introduction of black bass in Lake Naivasha in 1929 for sport fishing could have been responsible for the disappearance of some indigenous species, as well as that of species such as *Gambusia* and *Poecilia* sp. that were introduced to control mosquito larvae.

Non-predator species can also have an impact on indigenous fauna, as was shown in Lake Luhondo (Rwanda) (De Vos *et al.*, 1990). Until 1934, three Cyprinidae species were known in the lake: a small barb, *Barbus neumayeri*, and two large species, *Barbus microbarbis* and *Varicorhinus ruandae*. *Oreochromis niloticus* had been voluntarily introduced in 1935, along with a few *Haplochromis* species that were apparently accidentally introduced. In the 1950s, *O. niloticus* became the dominant species but the *Haplochromis* started flourishing, to the point of being the most abundant fish at present. Meanwhile *B. microbrabis* has disappeared, and the two other Cyprinidae are now restricted to the small tributaries of the lake.

The spread of alien invasive plants and animals is recognized to be a major threat for freshwater biodiversity (Dudgeon *et al.* 2005; Leprieur *et al.* 2009). Until now, only a few true exotic species have been deliberately introduced into African freshwaters, with the exception of Madagascar (Benstead *et al.*, 2003). More often, there have been species translocations from one African water system to another. For example, Nile tilapia, *Oreochromis niloticus*, has been introduced both for aquaculture and fisheries throughout most of inter-tropical Africa where it is reported to have negative impacts on the indigenous fish fauna (Canico *et al.*, 2005). On the other side fish farmers promote the introduction of tilapia species as an important species group for improving fish production in many African water bodies.

In South Africa, alien fishes introduced for angling are a particularly serious threat (Darwall *et al.*, 2009). Smallmouth bass (*Micropterus dolomieu*), together with largemouth and spotted bass (*M. salmoides* and *M. punctulatus*) and bluegill sunfish (*Lepomis macrochirus*), all from North America, and banded tilapia (*Tilapia sparmanii*) from further north in Africa now dominate the fish fauna in more than 80% of the Olifants River system, with indigenous fish often surviving in less than 1 km of river in headwater streams. Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) have had major impacts in cooler headwater streams.

Impact on the aquatic ecosystem

The introduction of a predator into an aquatic ecosystem may have an impact on the system's biological function through its effects on trophic chains. A spectacular example of the trophic cascade (see chapter *Role of fish in ecosystem functioning*) is the one that followed the introduction of Nile perch, *Lates niloticus,* into Lake Victoria, which may be responsible for the near-disappearance in the 1980s of the detritivorous/phytoplanktivorous group of haplochromines (endemic Cichlidae), as well as the zooplanktivorous group that respectively accounted for 40 and 16% of the biomass of demersal fishes (figure 23.3). The detritivorous were replaced by the indigenous shrimp *Caridina nilotica*, and the zooplanktivorous by the pelagic cyprinid *Rastrineobola argentea* (Witte *et al.*, 1992a), with the latter two species becoming the main food source for perch after the haplochromines vanished.

The introduction of planktonic species appears to have consequences on zooplanktonic communities. Green (1985) has noted that *Limnothrissa* introduced into Lake Kariba has reduced zooplankton abundance by 2.4 to 44 times, depending on the taxa under consideration. In Lake Kivu, several species of large planktonic crustaceans are believed to have disappeared because of predation, as indicated by the analysis of zooplankton samples taken prior to introduction and some 20 years after it (de Iongh *et al.,* 1983, 1995). In 1981, *Daphnia* water fleas had completely disappeared and the average size of cyclopoids was found to be much smaller. Meanwhile, ciliates, rotifers, and small water fleas, that is, small species, were abundant. Samples taken in 1986 contained no planktonic organisms that were larger than 0.2 mm (Dumont, 1986).

Hybridizations

The introduction into the same body of water of neighbouring species that do not usually cohabit may lead to a hybridization of the introduced species. Tilapia species are particularly notorious for hybridizing (Trewavas, 1983), which can lead to genetic modifications for surviving species. For example, in Lake Naivasha, *Oreochromis spilurus* introduced in 1925 was abundant in the 1950s and 1960s, then hybridized with *Oreochromis leucostictus* introduced in 1956.

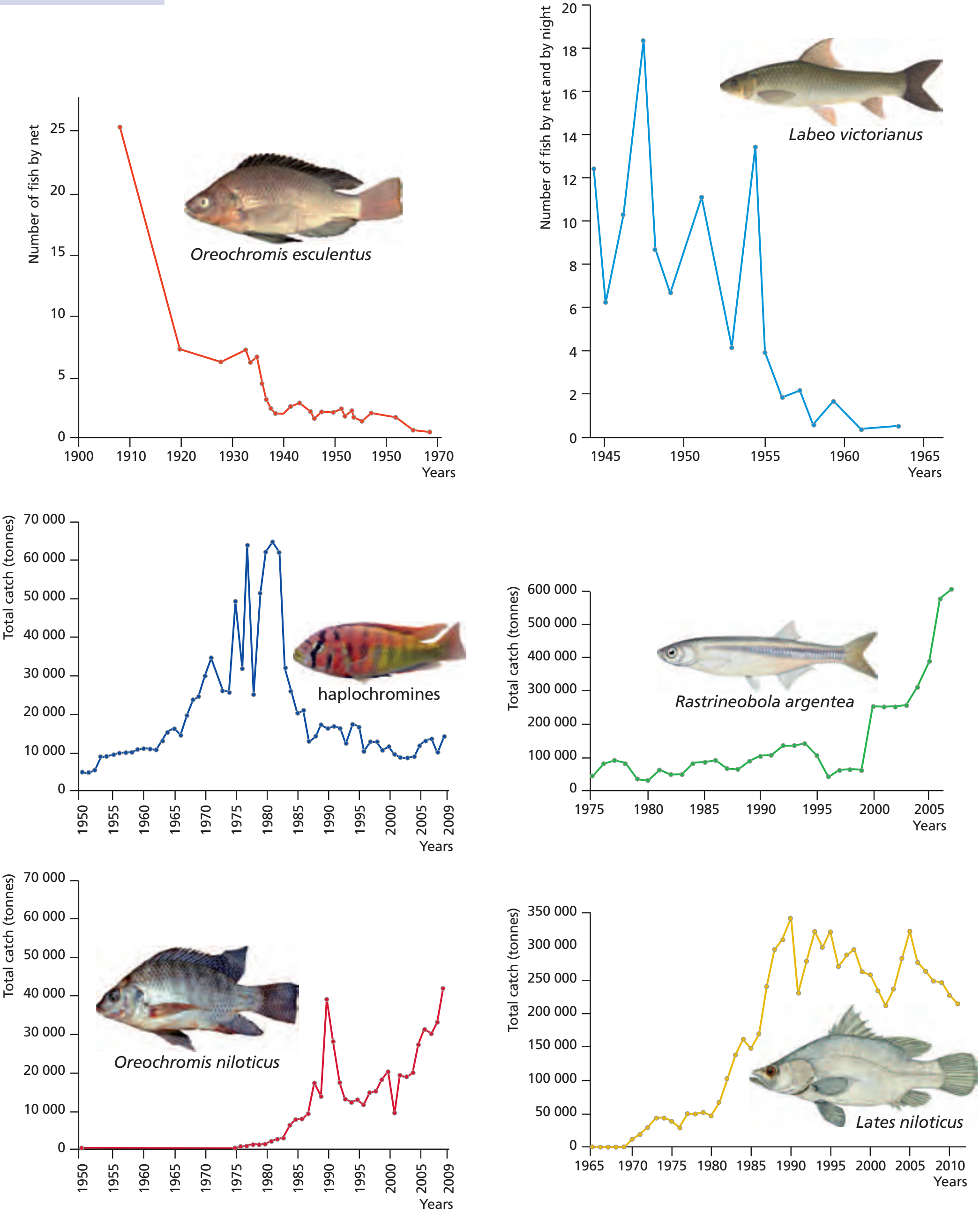
FIGURE 23.3.

Fisheries results for main species from Lake Victoria.

Sources: *Oreochromis niloticus*, *Lates niloticus*, haplochromines (FishStat Plus);

Oreochromis esculentus, *Labeo victorianus* (Ogutu-Ohwayo, 1990);

Rastrineobola argentea (Witte *et al*., 2009, completed by "Lake Victoria Basin Aquatic Biodiversity Meta-Database").



This resulted in the disappearance of *O. spilurus* and hybrids (Siddiqui, 1977, 1979).

The disappearance of the species *O. esculentus* and *O. variabilis*, endemic to Lakes Victoria and Kyoga, may be due to the hybridization and/or competition with introduced species (*O. niloticus*, *C. zillii*). *O. niloticus* x *O. variabilis* hybrids have been observed in Lake Victoria (Trewavas, 1983).

Cumulative impacts of introductions on wildlife and fisheries: example of Malagasy lakes

Malagasy fish fauna is relatively poor but comprises numerous endemic species belonging in particular to the Cichlidae and Bedotiidae families (Reinthal & Stiassny, 1991). The introduction of alien species began in the 20th century (Kiener, 1963; Moreau, 1979) and the current populations of many Malagasy lakes (e.g. Lake Alaotra, Lake Itasy) are made up of species from various continents (tables 23.I and 23.II). These species cohabit very well and are behind a fairly prosperous fishery. But they also eliminated part of the indigenous fauna.

In Lake Alaotra, prior to the introduction of exotic species, the fish community was poor and dominated by *Paratilapia polleni, Rheocles alaotrensis, Ratsirakia legendrei*, and two eels (*Anguilla mossambicus* and *A. marmorata*) (Moreau, 1980). In the beginning of the 20th century, *Carassius auratus* introduced in Madagascar in 1865 was found present in the lake, and in 1925 *P. polleni* as well as *C. auratus* accounted for most of the catches of artisanal fishing (table 23.IV). In 1935, *Cyprinus carpio* introduced in 1925 was a non-negligible component of catches, and in 1954 this species was largely dominant (table 23.IV).

This was followed by a period in which three tilapia species were introduced in succession, and two of these (*Coptodon rendalli* and *Oreochromis macrochir*) proliferated during the 1960s while native species and *C. auratus* markedly regressed. The decrease of tilapias in catches during the 1970s may be due to overexploitation following the introduction of gillnets in the fishery in the

TABLE 23.IV.
Fishing activities, introductions and changes in commercial catches (in %) in Lake Alaotra, Madagascar (from Moreau, 1980).

Years	**1925**	**1935**	**1954**	**1957**	**1960**	**1963**	**1966**	**1969**	**1972**	**1975**
Anguilla spp.	5	5	1	1	1	1	1	1	1	1
Paratilapia polleni	75	40	5	3	2	1				
Carassius auratus	20	25	14	10	4	2				
Cyprinus carpio (1925)		30	80	40	15	14	5	11	21	21
Coptodon rendalli (1954)				46	23	8	10	20	16	16
Oreochromis macrochir (1958)					55	74	85	66	56	50
Oreochromis niloticus(1961)								1	3	7
Micropterus salmoides(1961)							1	1	3	4
Total catches (tonnes)			**1 800**	**2 200**	**2 700**	**3 000**	**3 200**	**2 500**	**2 100**	**2 100**

late 1960s. The black bass *Micropterus salmoides* introduced in 1962 did not develop much, as it only accounted for 4% of catches in 1975. From 1966 to 1972, *Cyprinus carpio* juveniles were reintroduced into the lake, which could explain the slight increase in catches.

More recently, *Channa striata* spread in the natural waters of Madagascar after escaping from fish farms. This predator of Asian origin may have a significant impact on fish fauna.

A similar tale took place in Lake Itasy (Moreau, 1979) which was inhabited by several indigenous species in the beginning of the 20th century: *Anguilla mossambica, Anguilla nebulosa labiata, Anguilla marmorata, Ptychochromis betsileanus, Ratsirakia legendrei*, and *Chonophorus macrorhynchus*. *Carassius auratus* was introduced in 1899, and *Paratilapia polleni* (an endemic Malagasy species) in 1924 but they did not really prosper. In 1930, *Ptychochromis betsileanus* made up 40% of catches, but in 1950-1955, *Cyprinus carpio* which was introduced in 1925-1930, accounted for 80 to 85% of catches compared with only 10% for *P. betsileanus* (table 23.V). *Coptodon rendalli* introduced in 1955, rapidly replaced *Cyprinus carpio*, and in around 1958 represented 70% of catches. But *C. rendalli* itself was replaced by *Oreochromis macrochir* which was introduced in 1958 and accounted for the bulk of catches in 1963. In 1965, the importance of *O. macrochir* went down because of the appearance in catches of a hybrid called *Tilapia* 3/4, and in 1972 *O. macrochir* had disappeared. *Tilapia* 3/4 is the result of natural hybridation between *O. macrochir* and *O. niloticus* which was introduced in 1961. This spontaneous hybridization led to more fecund fertile hybrids of the same size as *O. macrochir*. But populations of *O. niloticus* developed slowly and in 1975 represented 55% of catches, followed by *Tilapia* 3/4 that started showing signs of degeneracy. The contribution of species to captures in 1985 was essentially similar to figures for 1975 (Matthes, 1985).

TABLE 23.V.
Fishing activities, introductions and changes in commercial catches (in %) in Lake Itasy, Madagascar (from Moreau, 1979).

Years	**1930**	**1950-55**	**1958**	**1963**	**1964**	**1965**	**1966**	**1967**	**1968**	**1969**	**1970**	**1971**	**1972**	**1973**	**1974**	**1975**	**1985**
Ptychochromis betsileanus	40	10	0	0													
Anguilla spp	50?			3	2	2	2	1	1	1	1	1	1	1	1	1	
Cyprinus carpio (1925)		80-85		6	6	5	4	4	4	3	3	3	3	3	3	3	1.5
Coptodon rendalli (1955)			70	5	4	4	3	3	2	1	1	1	1	1	1	*	0.4
Oreochromis macrochir (1958)				85	86	78	56	30	10	1	1	0					
Oreochromis niloticus (1961)				1	2	5	8	10	15	18	24	32	39	45	50	55	57
Tilapia 3/4				0	0	5	25	50	66	74	68	61	54	48	43	39	38
Micropterus salmoides (1961)				0	0	1	1	2	2	2	2	3	3	3	3	3	1.5
Total catches (tonnes)				**1200**	**850**	**500**	**300**	**280**	**84**	**830**	**450**	**300**	**290**	**280**	**280**	**275**	**625**

Certain species were also introduced, without apparent success, in Lake Itasy. This is the case for *Micropterus salmoides* introduced in 1962, *Gambusia holbrooki* introduced around 1950, and *Oreochromis mossambicus* introduced in 1961, but these species, along with *O. macrochir*, seem to have disappeared (Matthes, 1985). *Channa striata* was observed in catches in 1985 and we can imagine that this predator species will have a major impact on existing populations.

It should be noted that overfishing or at the very least changes in fishing techniques have probably also played a role in the evolution of fish populations in Lakes Alaotra and Itasy. It is however difficult to make a distinction between the consequences stemming from introductions and those resulting from a shift in the means of resource exploitation.

What can we learn from the lessons of the past?

The invasion of aquatic ecosystems by new species during geological or climatic events is not an exceptional situation on a historical scale. But the current degree and frequency of introductions caused by human activity are worrying to scientists, as we run the risk of obtaining mixtures of faunas from the most diverse origins in only a few decades, something that could not have been achieved over millions of years through geological events alone.

Many believe – not unreasonably – that these species introductions, a true gamble, can lead to ecological disasters in some cases. They thus condemn from the outset, on a more or less intuitive basis, any attempt to introduce a species without a proper evaluation of its potential merits from an economic or ecological perspective.

Can we draw a number of lessons from past experience and put forth some principles that would limit the negative consequences of introductions? First, we must remember that introductions are irreversible and that it is not possible to eradicate introduced species using the means currently available. Moreover, it seems to be well-established through numerous examples in Africa and other regions of the world that the introduction of large predators in lakes where endemic species form the bulk of the fish fauna, has often produced a catastrophic impact on this indigenous fauna. The example of Lake Victoria (see box "The case of *Lates niloticus* in Lake Victoria") is a particularly dramatic illustration of this situation.

When we examine the consequences of various introductions, we too often notice that the information is anecdotal or fragmented and that the effects of introduced species may have been obscured or amplified by environmental changes that stemmed from different causes. It is also possible that in some circumstances, some impacts may have been wrongly attributed to introductions. Conversely, we have probably not always taken into account the consequences of introductions on other aspects of the biological systems involved. In reality, it is often difficult to distinguish the consequences of species introductions from the consequences of human activity on aquatic systems. For instance, in Lake Victoria where *Lates* is accused of causing the disappearance of numerous endemic species, it has been found that the latter had already been undermined by the introduction of new fishing techniques (trawling) and that the lake was also undergoing a process of eutrophication, which meant that an increasingly larger part of benthic habitats was being subjected to periods of anoxia, thereby limiting the space available to indigenous species.

There nonetheless remains a number of examples that tend to show that introductions can have a positive effect, at least on fisheries, in newly-created environments such as reservoirs where riverine species are not well-suited to colonizing pelagic systems (Fernando, 1991). This may also be the case in a number of regions where the fish fauna is poor for historical or biogeographical reasons.

To avoid making irreparable errors while remaining active, better communication is needed between scientists and managers. However, Balon & Bruton (1986) have clearly indicated the difficulties involved. Are managers ready to accept recommendations that run counter to their plans? Do scientists have a good enough understanding of issues to provide clear and unambiguous advice? In reality, scientists have a limited capacity to predict the impact of introductions, and a certain reluctance to tackle these questions or take responsibility. Targeted research would be needed to grasp the consequences of introductions, by drawing on field experience and using all available information. But managers and politicians must also be aware that the lack of regulations, or the absence of controls at the very least with regard the translocation of fishes, leave the door open for the occurrence of ecological changes comparable to what has been observed in Madagascar or some watercourses in South Africa.

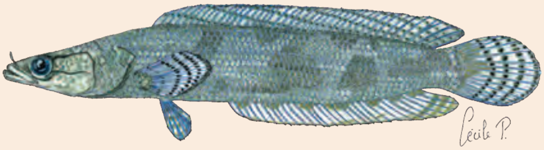
The experience from centuries of introductions and translocations of fishes around the world reveal, in fact, a positive overall outcome, if the analysis is made from both the ecological and the socio-economic perspectives.

Today, the issue of introductions is seen in a new light: the growing preoccupation with the protection of biodiversity, which would tend to favour the development of aquaculture for indigenous species. On the other hand, scientific investigations, increasingly focused on the genome, tend to concentrate on a few model species whose farming is most developed (*Oreochromis niloticus* for example). A happy medium needs to be found in coming years between these two trends which, when not antagonistic, are at least difficult to reconcile in a given environment, by reserving introductions for situations where they are clearly justified (lack of native species of fish farming interest, vacant tropical niche, etc.).

Impacts of human activities

DIDIER PAUGY

CHRISTIAN LÉVÊQUE


Cécile P.

Continental aquatic ecosystems are particularly affected by human activities including the modification or elimination of habitats because of territorial planning works, pollution from different sources, and overfishing. The consequences of these activities, now amplified by population growth and increasingly heavy pressure on natural resources, endanger ichthyological fauna the world over. Long spared these impacts, Africa is now feeling their effects even though pollution, for instance, is still relatively limited in extent.

A number of anthropogenic threats to freshwater ecosystems are recognized to operate at the continental scale, including habitat loss or transformation, water extraction and hydrological disruption, invasive alien species, pollution, and overexploitation (Dudgeon *et al.*, 2006).

Given the unpredictable rainfall, very high evaporation rate (around 65% of rainfall), and low conversion of rainfall to runoff, it is clear that large areas in Africa face water management difficulties. In an effort to meet the increasing demand for water and power, many large wetlands have been affected by developments such as dams, flood control measures, or direct abstraction, and their ecological function has been impaired (Postel & Richter, 2003; Richter *et al.*, 2003). Groundwaters are also being used, most often to provide irrigation for agriculture, at a faster rate than they can be replenished such that the water table is being lowered and wetland areas are disappearing (Darwall *et al.*, 2009; Garcia *et al.*, 2010). Abstraction for agriculture or industry accounts for a large part of the total water consumption from rivers, lakes and aquifers such that an estimated 85% of Africa's total water withdrawals are directed toward agriculture (Aquastat, 2010) with about one-third of its surface area estimated to be under agricultural land use in 2000 (FAOStat, 2010). Such measures impaired the effective functioning of wetlands and floodplains with consequences on their associated biodiversity. Moreover, water runoff from agricultural lands brings sediments, nutrients and pesticides into aquatic systems. Pollution from domestic sewage and industrial facilities is also a large problem in many parts of Africa, where the infrastructure required for water purification is often inadequate or non-existent (Saad *et al.*, 1994; Lévêque, 1997a, UNEP, 2004b).

Changes in habitats

Habitat degradation is one of the greatest threats to aquatic fauna. Changes that can occur have two very distinct origins that nonetheless often act concomitantly:

- climate change and its effect on the water balance and the hydrological function of hydrosystems;
- anthropogenic changes at the level of both the aquatic system and its watershed.

Climate change and water abstraction

We know that at the geological scale, climate has never been stable and that aquatic systems have always fluctuated without humans bearing responsibility for such fluctuations (e.g. the "El Niño" phenomenon). Yet we also know that humans can affect the climate indirectly, either locally through deforestation or on a planetary level through the emission of so-called "greenhouse gases". In recent years, global opinion has been alerted of the possible warming of the planet that may be due to higher atmospheric concentrations of carbon dioxide, methane, and chlorofluorocarbons (CFC), the massive emissions of which are tied to industrial activity. Although we do not know the scope and speed at which this warming will occur, we can nonetheless fear that these changes to the climate will take place in coming decades, leading to a shift in the rainfall regimes of certain parts of the world. In addition to still hard-to-predict consequences on the hydrological front (local increase or decrease of rainfall), we can also expect an increase in insolation and temperature, changes in plant distribution, and a rise in sea water levels. These somewhat catastrophic scenarios will have long-term effects if they become a reality. While it is still impossible at the local level to evaluate the consequences of these expected changes, it seems obvious that regardless of the extent of the phenomenon, aquatic fauna as a whole will be the first to be affected.

Anthropogenic climate change and increasing human water use are widely expected to place great stress on available water resources across Africa (Thieme *et al.*, 2005), but their expected effects on freshwater biodiversity have only just begun to be considered (see www.freshwaterbiodiversity.eu). According to the global hydrologic model, by the 2050s, ecoregions containing over 80% of freshwater fish species and several outstanding ecological and evolutionary phenomena are likely to experience hydrologic conditions substantially different from the present, with alterations in annual discharge or runoff of more than 10% (Thieme *et al.*, 2010).

However, in the Sahelo-Sudanese area, fish populations have long been subjected to long-term climate changes. A typical example is Lake Chad. The levels of the lake have fluctuated over decades, centuries and millennia, responding to changes in the global temperature and regional precipitation. There was a time in history when Lake Chad was so huge that contemporary historians refer to it as Mega-Chad. At other times it may have even come close to disappearing. For instance when it was discovered at the beginning of the 20th century, the lake level was so low that the northern basin was dry.

These long term changes were clearly driven by natural climatic changes. That was also the case for the recent drying out of the lake which started at the beginning of the 1970s and has continued for almost two decades. This drying out was the result of a severe meteorological drought (reduced rainfall for well over a decade) in the Sahelian zone. A recent report on climate change and the hydrologic cycle suggested, that "of all the major basins in the world, probably Lake Chad has been affected most by climate change" (see www.fao.org/docrep/W5183E/w5183e04.htm).

Actually, diversion of streamflow for irrigation remained low until the 1980s when Lake Chad basin countries began to intensify their food production efforts. However, by the 1980s and 1990s, water from the inflowing rivers was increasingly diverted for irrigation purposes. It is estimated that about one-third of the streamflow today is diverted from the Chari River before its flow reaches Lake Chad. According to UNEP GRID about 50% of the decrease in the lake's size since the 1960s is attributed to human water use, with the remainder attributed to shifting climate patterns. (Glantz, 2004; http://www.fragilecologies.com/sep09_04.html). (figure 24.1). In such a situation, the recovery of Lake Chad is becoming difficult.

Virtually all wetlands in the region are either dried up or on the verge of drying up and planned irrigation development of 213,400 ha has been stopped at 33,824 ha (Musa *et al.* 2008). More than 20 million people, most of whom are

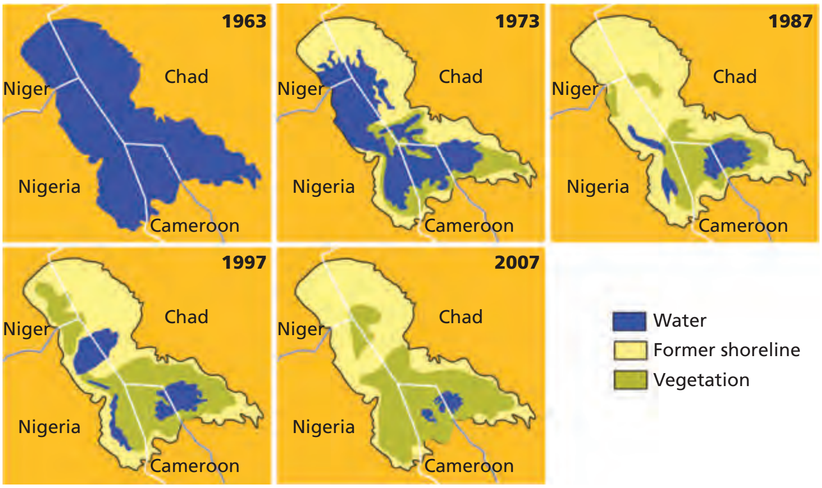


FIGURE 24.1.
Reduction in the size of Lake Chad over the period 1963-2007 (redrawn from Musa *et al.*, 2008).

farmers, fishermen and livestock breeders are dependent upon the lake and its surrounding wetlands for their livelihood (fishery and agriculture). This is so serious that plans are being tabled to transfer water from other rivers in the region.

System managements

The various uses of water for agriculture, power generation, transport, and domestic use lead to structural adjustments of hydrosystems. These constraints modify the water balance but also directly or indirectly change the original aquatic habitats.

Man-made lakes (water fragmentation)

Africa has a large number of dams, particularly in the Maghreb and southern and western Africa (figure 24.2). Most of the largest dams were built after the mid-1950s on large rivers to supply electricity. More recently, probably thousands of smaller reservoirs have been established to meet other water demands including irrigation, pastoralism, water supply (domestic use) or fish production (figure 24.3).

FIGURE 24.2.
Location of 135 large dams (≥ 500,000 m^3) and 1,072 secondary dams (< 500,000 m^3) in Africa (data from Aquastat, 2010).

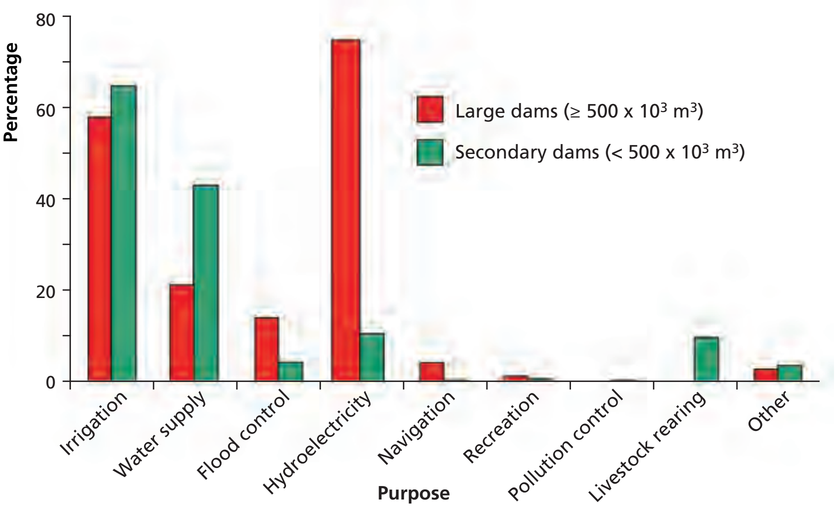


FIGURE 24.3.
Main purposes of dams in Africa (data from Aquastat, 2010).

The impacts of large dams on ecosystem functions and biodiversity are well documented (e.g. McAllister *et al.*, 2001; McCartney *et al.*, 2001; Nilsson *et al.*, 2005). They constitute obstacles for longitudinal exchange of organisms, and nutrient and sediment flows along rivers. They permanently destroy upstream submerged habitats, and block the migration pathways for some aquatic species. Downstream impacts include changes to the flow regime, water temperature and quality. The ecosystem impacts from dams should therefore be treated as costs to society and be considered in decisions taken before building a dam and in the subsequent design of its implementation. The nature of impact is summed up in one of the main conclusions of the Report of the World Commission on Dams (2001) as "On balance, the ecosystem impacts are more negative than positive and they have led, in many cases, to significant and irreversible loss of species and ecosystems. In some cases, however, enhancement of ecosystem values does occur, through the creation of new wetland habitat and the fishing and recreational opportunities provided by new reservoirs… Efforts to date to counter the ecosystem impacts of large dams have met with limited success due to the lack of attention to anticipating and avoiding such impacts, the poor quality and uncertainty of predictions, and the difficulty of coping with all impacts…"

For a few major impoundments in Africa, the sequence after damming has been studied (e.g. Jackson *et al.*, 1988) and, in general, the impacts are important (figure 24.4), but different from those observed in north temperate man-made lakes.

When a watercourse is blocked to create a reservoir, this triggers several modifications to habitats and fish communities (Jackson *et al.*, 1988) which, broadly speaking, can be summed up as follows:

- the new reservoir lake upstream eliminates species that are restricted to running waters. That said, owing to the development of plankton, there is generally an explosion of growth in planktophagic species, closely followed by significant development of pelagic piscivorous fishes. Because of water

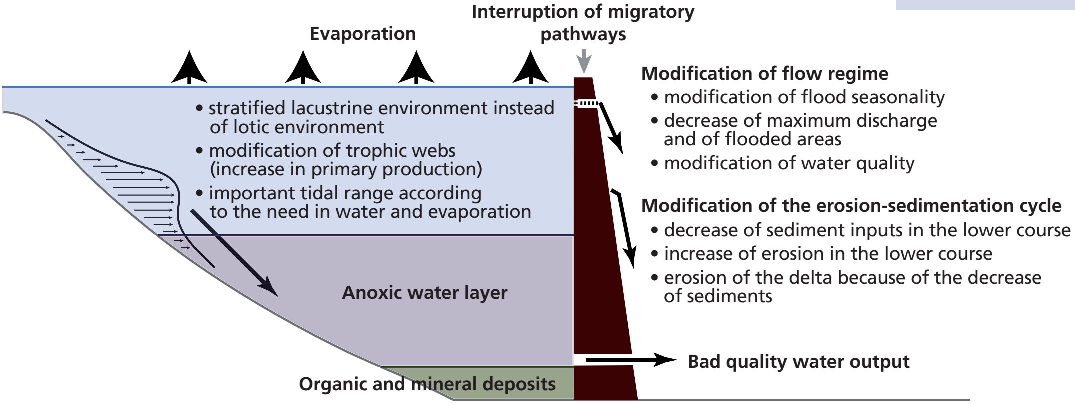


FIGURE 24.4.
Diagram showing the major impacts of the building of a dam on the aquatic environment.

stratification, the benthic zone is generally deoxygenated and unsuited to fish life. Only the littoral and pelagic zones are likely to be colonized by species adapted to lentic conditions. But in the tropical environment, these biotopes are generally brutally exundated, which leads to high mortality in clutches found there. Finally, reservoir lakes are often the site of the uncontrolled development of floating macrophytes (mainly *Pistia stratiotes* and *Eichhornia crassipes* but also *Azolla nilotica* and *Salvinia molesta*) which can favour the establishment, if not the proliferation, of certain fish species, but are also hinder fish capture and movement within the reservoir.

- The modification of the flood regime downstream, and flow regulation in particular, disturbs the biology of species that habitually reproduce in the high waters of flooded areas. This most often results in a simplification of communities, with the disappearance of some species. Moreover, stirring up deep waters that are generally anoxic and methane-rich leads to a more or less pronounced deterioration of water quality downstream. In some extreme cases, this deterioration may reach such an extent that downstream fish production is severely affected. This occurred in Egypt, where the retention of the Nile's organic matter in the Lake Nasser reservoir triggered a decline in the pelagic fisheries of the coastal Mediterranean area.
- In tropical regions, dams are rarely equipped with fish passes. This prevents migrating species from going upstream during floods to spawn in more favourable environments. Likewise, during these migration periods, dams trigger an over-concentration of breeders at the bottom of the dike. This phenomenon is known to local fishermen who manage to make exceptional catches, which could in turn imperil available stocks if they are too intensive.

One of the most well-documented examples for the evolution of fish communities following the damming of an African river is that of Lake Kainji on the Niger (Ita, 1984) where an inventory of fish fauna was carried out before damming (table 24.I). After damming, the most significant changes were as follows:

- A high decrease of Mormyridae, which includes many species that need riverine conditions to reproduce. According to some hypotheses, the disappearance of Mormyridae could come from the submersion of their customary

Fish families	Niger River before damming			Kainji Lake		
	number of species	% of individuals	% weight	number of species	% of individuals	% weight
Mormyridae	19	20.7	19.5	12	1.4	1.4
Alestidae	8	36.3	12.1	8	18.6	10.3
Citharinidae + Distichodontidae	5	6.1	19.8	4	4.7	15
Cyprinidae	5+	3.3	4.3	7	8.6	5.5
Bagridae + Claroteidae	7	7.2	18.2	8	18.5	15
Schilbeidae	3	8	3.6	3	0.1	*
Mochokidae	18	18	18.7	11	2.3	2.5
Clariidae	2	*	*	2	*	2.2
Malapteruridae	1	*	*	1	0.1	2.5
Latidae	1	*	*	1	1.7	1.2
Cichlidae		*	*	7	36.1	43.6

TABLE 24.I.
Relative abundance of fish families caught before and after the closure of the Kainji dam (from Ita, 1984). (*: very low %)

habitats that are now at much greater depths and insufficiently oxygenated. It appears that the rarefaction of species from this family after the damming of Lake Kainji is not a generalized phenomenon, and depends on the species present. Thus the Mormyridae persisted after the damming of Lake Kariba, with the development of both *Mormyrus longirostris* and *Marcusenius macrolepidotus* in particular. These two species also became abundant in the McIlwaine reservoir (Marshall, 1982).

- Extraordinary development in the pelagic zone of small species such as Clupeidae (*Sierrathrissa leonensis*) and Schilbeidae (*Physailia pellucida*, *Schilbe mystus*) during the first year. These species colonized the newly-created pelagic zone, as has also been observed for two clupeids in Lake Volta (*Pellonula leonensis* and *Odaxothrissa mento*). In Lake Kariba, the indigenous pelagic species *Brycinus lateralis* was supplanted by the clupeid *Limnothrissa miodon* introduced from Lake Tanganyika.
- An increase in the stock of fish predators (*Lates*, *Hydrocynus*) consuming the stock of pelagic species. This is also the case in Lake Kariba where *Hydrocynus vittatus* developed particularly well after the introduction of *Limnothrissa*.
- The spectacular increase of *Citharinus citharus* in catches.
- An increase in the proportion of Cichlidae.

Changes continued to take place in the lake in subsequent years, in particular with a decline in *Citharinus* population and a sharp increase in the proportion of Cichlidae in catches. Downstream from the dam, a general decrease in catches was observed in the Niger River.

We were able to monitor the evolution of fish communities in Lake Kariba with the aid of both artisanal fishing and experimental fishing carried out by the Lake Kariba Fisheries Research Institute (Machena *et al.*, 1993; Karenge & Kolding, 1995) (table 24.II).

Taxa / years	1960	1961	1962	1963	1964	1967	1969	1970	1971	1972
Mormyridae										
Hippopotamyrus discorhynchus					13	20	225	318	556	1,090
Mormyrus,longirostris						90	602	294	800	371
Mormyrus anguilloides					4			24	16	68
Marcusenius macrolepidotus					32			6		
Alestidae										
Hydrocynus vittatus	2,900	2,000	2,773	3,258	2,058	1,370	2,876	2,718	5,936	6,042
Brycinus imberi	3,150	2,200	968	1,233	180	110		6	36	50
Distichodontidae	400	650	1,884	109	114	50	5	6		6
Cyprinidae										
Labeo spp	11,650	4,600	2,096	1,384	656		4			6
Siluriformes										
Schilbe depressirostris			46	146	18	80	664	900	1,260	694
Clarias gariepinus	600	1,450	828	667	45	90	209	42	48	172
Heterobranchus longifilis								6		3
Synodontis zambezensis					26		63	18	36	50
Cichlidae										
Oreochromis spp	1,900	50	1,050	408	139	480	915	192	356	1,039
Serranochromis condringtoni		1	50	21	6	140	401	162	312	1,635
Coptodon rendalli		150	23	46	9	40	83	18	80	141

Taxa / years	1973	1974	1975	1976	1977	1978	1979	1980	1982
Mormyridae									
Hippopotamyrus discorhynchus	1,028	532	159	378	389	500	286	565	270
Mormyrus longirostris	324	266	68	96	165	275	112	184	33
Mormyrops anguilloides	141	277	413	460	443	159	91	122	284
Marcusenius macrolepidotus		20	6	11	7	9	8	18	26
Alestidae									
Hydrocynus vittatus	4,466	7,020	4,219	2,906	1,979	1,808	1,332	1,646	2,095
Brycinus imberi	30	206	994	1,093	1,379	827	1,649	1,364	878
Distichodontidae	6	12	2	4	1	4	1		1
Cyprinidae									
Labeo spp	6	4	22	9	45	29	90	87	18
Siluriformes									
Schilbe depressirostris	295	604	212	160	601	299	324	735	162
Clarias gariepinus	104	458	345	231	168	294	73	78	204
Heterobranchus longifilis	4	6	12	12	16	2	1	2	4
Synodontis zambezensis	99	167	88	103	125	80	57	103	84
Cichlidae									
Oreochromis spp	757	2,684	2,046	1,632	1,493	1,178	150	171	332
Serranochromis condringtoni	1,145	1,967	2,439	1,860	1,118	723	571	534	1,567
Coptodon rendalli	64	193	304	314	144	132	248	80	117

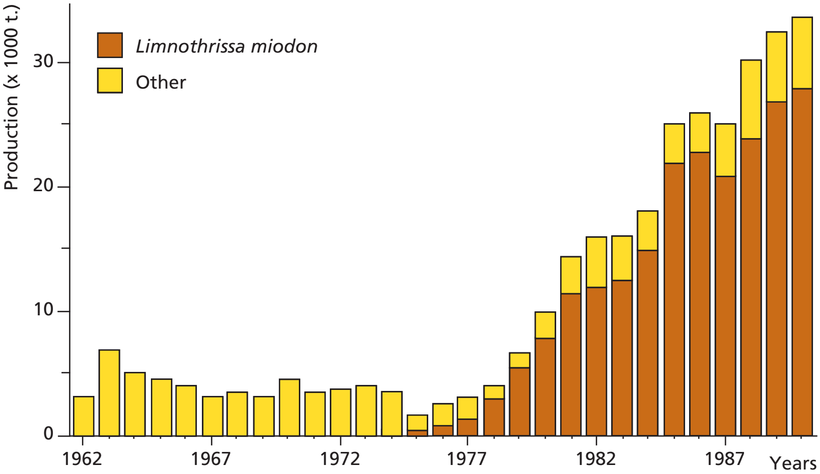
TABLE 24.II.
Lake Kariba: change in the abundance of major fish species (tonnes), lakeside station (from Karenge & Kolding, 1995).

The species composition of catches after damming (early 1960s) was essentially the same as prior to it, and included mostly *Labeo* spp., *Distichodus* spp., *Hydrocynus vittatus, Mormyrops anguilloides* and *Clarias gariepinus*. Afterwards, the community evolved and the most striking features were as follows:

- The maintenance of Mormyridae after damming, contrary to what was observed in Kainji, with the development of *Mormyrus longirostris* in particular.
- After the rarefaction of *Labeo congoro* and *Labeo altivelis* in the early 1960s, the latter reappeared in relatively high quantities during the 1980s.

- The pronounced development of Mochokidae, especially *Synodontis zambezensis* during the 1980s, to the extent that the species does not appear to be exploited much (Machena *et al.*, 1993).
- The clupeid *Limnothrissa miodon*, a species introduced from Lake Tanganyika, has acclimatized well and has been heavily exploited by fishers since the early 1980s (figure 24.5).
- *Hydrocynus vittatus* flourished during the lake's filling phase, particularly after the introduction of *L. miodon* (Machena, 1995). During the 1980s it became less plentiful, but the species continues to be well-represented in catches and there appears to be no sign of overexploitation from fishing (Machena *et al.*, 1993).
- A growing importance of Cichlidae in the early 1970s, but whose stocks seem to decrease as a result of fishery overexploitation (Machena *et al.*, 1993).

FIGURE 24.5.
Lake Kariba: trend in fish production from 1960 to 1990 (from Greboval *et al.*, 1994).



River management

In Europe and North America, many rivers were developed with the construction of dikes, the diversion of watercourses, the construction of navigation locks, and so on. Such engineering works are still limited in Africa, but there are nonetheless a few examples of projects that modified natural systems fairly extensively.

In the Senegal valley, for instance, several engineering projects were conducted in order to manage river water resources more effectively and use them for agriculture. The construction of a downstream dam at the level of the estuary (Diama dam) was intended to prevent sea water from moving to the river's lower course during the dry season, whereas the Manantali dam found upstream allows storage of large quantities of water during the flood and release them as required, in particular to supply vast stretches of irrigated farmland. All of the water resources of the Senegal valley is thus now partially under control, but water management is complicated by sometimes contradictory needs in terms

DEVELOPMENT OF THE LOWER VALLEY OF THE SENEGAL RIVER
(FROM ALBARET & DIOUF, 1994)

The estuary, and more generally the area known as the lower valley of the Senegal River, was particularly affected by a series of construction projects. To address the significant imbalance between food resources and local needs, a development programme that included the construction of two dams (Diama and Manantali) was put in place.

The Diama dam, commissioned in 1986, is located about fifty kilometres from the river mouth. Its main functions are to prevent the entry of saltwater, to create a water reserve for irrigation, and to improve the filling of surrounding depressions.

The Manantali dam, in operation since 1988, was built on the Bafing, one of the major tributaries of the Senegal River. It is located in Mali about 1,250 km from the river mouth and serves to regulate the river flood and manage water releases at relevant moments, either to irrigate farmland areas or to produce hydroelectricity.

These dams, along with numerous dikes built along the main riverbed, have had important effects on the ichthyofauna among other things. In the lower valley of the river, the Diama dam is a physical barrier to fish migration and has also considerably reduced the estuarine zone of the Senegal river. From a length of around 200 kilometres before the Diama was built, it now only stretches over some 50 kilometres, leading to a significant loss of habitat for many species, particularly those of estuarine or marine origin (see chapter *Fish communities in estuaries and lagoons*). A comparison of faunistic inventories taken in the areas downstream of the Diama, made before and after the construction of the reservoir, shows that species composition is generally similar in this part of the river (Diouf *et al.*, 1991). This is most certainly because, in the absence of disturbances owing to off-season freshwater releases, recorded surface salinities are essentially the same as in the past (Cecchi, 1992). Upstream, on the other hand, because of the dam, estuarine and marine species have practically disappeared, although some of them used to be found up to more than 200 kilometres from the river mouth. Moreover, the main breeding area of euryhaline fishes prior to damming was found in sectors where salinity was between 5 and 15‰. With the Diama dam, this area is no longer accessible to euryhaline fishes, leading in turn to a loss of recruitment for lower estuarine fish stocks and some marine stocks.

Flood regulation from the Manantali dam leads to a reduction in fish biomass, as the latter depends strongly on the type of flood. Because of evaporation from the Manantali reservoir, the water volume rendered downstream is less than the natural volume, which also reduces halieutic potential (Reizer, 1984). Moreover, the structure makes the flood subside faster. This only has a slight effect on the reproduction of fish that, in theory, have the time to spawn in such conditions. However, growth is significantly reduced, as it depends mainly on the availability of exogenous nutrients or fertilizing nutrients found in the flooded major bed. The longer the flood is, the better the growth of adults and juveniles in particular.

The massive use of fertilizers that came with the rapid development of agriculture in the Senegal River basin is a potential source of water eutrophication. The spread of floating aquatic vegetation in some areas, especially the southern part of Lake Guiers and the Djoudj Park, may be a telling sign. That said, the proliferation of certain floating macrophytes, particularly *Eichhornia crassipes*, in the downstream part of the basin also depends on the absence of saltwater incursions since the damming at Diama. Moreover, the Côte d'Ivoire authorities attempted to resolve the uncontrolled proliferation of *Salvinia molesta* and *Eichhornia crassipes* by keeping a channel open in the dune belt separating the Ébrié lagoon from the ocean, thus encouraging the circulation of saltwater.

of usage. While this has not been clearly demonstrated by quantitative data, it appears that the fish communities of the Senegal river were significantly disturbed by the simultaneous interruption of connections with the estuary, the elimination of seasonal floods, and the use of vast stretches of floodplains for irrigated farming.

In the Nile basin, the monumental Jonglei canal project was supposed to channel the Nile's course as it crossed the Sudd wetlands in South Sudan, to prevent too much water from evaporating in this huge wetland (Howell *et al.*, 1988). The project began in 1978 but had to be interrupted in 1983 owing to political instability in the region. If such a project had been successfully completed, it would probably have led to shrinkage of the permanent wetlands of the Sudd, with an ensuing significant loss of diversity in available habitats as well as a decline in many species depending on the floodplain.

Reduction of floodplains and wetlands

Wetlands are often considered fertile areas suited for farming. Throughout the world, development projects and dam constructions in particular have had a significant impact on hydrosystems by reducing, sometimes considerably, the surface area of floodplains which serve as sites that promote the development of juveniles of many fish species. Even if traditional floodplains are replaced by profitable irrigated areas for rice crops, for example, they cannot replace the usual biotopes needed by certain organisms such as fish to complete their life cycle normally.

Changes in land-use and their consequences for watershed

The quantity and quality of runoff water inputs to aquatic ecosystems depend on the nature of the watershed and its vegetation. But the elimination of forests, for example, whether for conversion to farmland or for the exploitation of wood for domestic use or trade, immediately increases soil erosion and water turbidity, as well as a modification of the hydrological regime, with shorter but more brutal floods resulting from more runoff.

The problem of deforestation affects Africa as a whole, and available information indicates that its extent is worrying. In Madagascar, the deforestation rate has stood at 110,000 ha annually for the past 35 years, and erosion rates of 250 tonnes per hectare have been reported (Helfert & Wood, 1986). Deforestation is also massive in the Lake Tanganyika basin. Significant erosion on the slopes manifests as considerable sediment inputs to the lake and changes in fauna in some particularly exposed coastal regions (Cohen *et al.*, 1993a). Increasingly, sedimentation from watershed deforestation, road building and other anthropogenic activities is impacting lacustrine habitats, particularly those of rock-dwelling fish communities of East African lakes. In West Africa, the reduction in forest cover is also worrying, especially in Côte d'Ivoire and Nigeria (Barnes, 1990), but also in Guinea and Sierra Leone in recent years (table 24.III). If the current trend persists, future figures are of great concern as it is estimated at that this rate, 70% of West African forests, 95% of East African forests, and 30% of the Congolese forest cover will disappear by 2040.

The increased amount of suspended matter in water, and silt deposits in lakes and rivers, has many consequences for aquatic life (Bruton, 1985). It reduces the transparency of water, with all the implications of that turbidity for planktonic or benthic photosynthesis. Suspended matter can also accumulate in the gill systems of fish or cause irritations, and silt deposits significantly alter the quality of substrates in breeding areas.

Countries	Original forest area (km^2)	mean % deforested (%)	human population density (per km^2) 1980	mean area deforested per million people (km^2)
West Africa				
Côte d'Ivoire	44,580	6.95	25.6	375
Nigeria	59,500	4.79	91.7	34
Liberia	20	2.05	16.8	219
Guinea	20,500	1.76	22.1	66
Ghana	17,180	1.57	48.3	23
Sierra Leone	7,400	0.78	48.8	17
Togo	3,040	0.66	45.4	8
Central Africa				
Cameroon	179,200	0.45	17.8	95
DRC	1,056,500	0.16	12.3	57
Congo	213,400	0.10	4.7	137
Gabon	205,000	0.07	2.5	227
EastAfrica				
Kenya	6,900	1.59	28.6	7
Uganda	7,500	1.33	53.4	8
Tanzania	14,400	0.69	19.7	5

TABLE 24.III.
Annual deforestation rates in 1980 for different African countries (from Barnes, 1980).

Water pollution

While water pollution has long seemed a secondary phenomenon in Africa, it has become increasingly obvious in recent years (Dejoux, 1988). In general, however, we do not have enough data and lack detailed information on the extent of pollution in African waters.

Eutrophication

Nutrients (phosphates, nitrates) are generally present at low concentrations in aquatic systems, and may act as limiting factors for biological production. Any additional input of these nutrients is rapidly assimilated and stimulates primary production. Eutrophication occurs when nutrients (mainly nitrogen and phosphorus) are released in excess into freshwaters. Many examples of eutrophication across inland sub-Saharan Africa are reviewed by Nyenje *et al.* (2010). Most of the nutrients causing eutrophication originate from agricultural and urban wastes.

The effects of eutrophication include increases in macrophytes and/or phytoplankton, replacement of diatoms by cyanobacteria, large scale blooms of algae, and ultimately the eradication of fish species due to the deoxygenation of the water column. The decomposition of this large amount of organic matter uses up much oxygen and often leads to massive mortalities in animal species due to asphyxiation. Eutrophication also leads to wide variations in dissolved oxygen concentrations and pH throughout the day.

Blooms of cyanobacteria can disrupt virtually all of the interactions between organisms within the aquatic community and may produce harmful secondary metabolites which are toxic to humans and animals.

A well-known example is the eutrophication of Lake Victoria. The increase in nutrient inputs to the lake is the result of increased human activity in the lake's watershed: growing urbanization, use of fertilizers and pesticides for crops, use of pesticides to control tsetse flies, etc. The increase in algal biomass here is essentially due to nitrogen inputs (Hecky & Bugenyi, 1992). Symptoms indicative of eutrophication have also been observed in Lake Naivasha (Harper *et al.*, 1993), Lake McIlwaine (Thorton, 1982), and Lake Kivu, but many African lakes are probably threatened by eutrophication sooner or later.

Pesticides

One of the most important sources of contamination in African lakes and rivers is the increasing use of pesticides in public and animal health to curb endemic diseases, or for agricultural purposes (Dejoux, 1988; Lévêque, 1989c). There is an enormous range of products in use, and while some have low toxicity for aquatic organisms, many of them are xenobiotics, that is, substances with toxic properties even when they are present in very low concentrations in the environment. This is the case in particular for pyrethroids (permethrin, deltamethrin) but especially for organochlorides (DDT, dieldrin, endrin, endosulfan, malathion, lindane), which, in addition to their toxicity, also have long persistence times, which accentuates their accumulation and thus their concentration in food chains.

Case study: the Onchocerciasis Control Programme (OCP)

A widespread disease in intertropical Africa, onchocerciasis is both a social and economic bane that can lead to irreversible blindness. Prior to the start of vector control measures, the number of onchocerciasis sufferers in West Africa was estimated at nearly three million. The disease is transmitted by a small blackfly, *Simulium damnosum*, which has aquatic larval and nymph stages. The Onchocerciasis Control Programme (OCP) in West Africa targeted the sites where the larval hosts of the vector are found, in river reaches with strong currents. As with all insecticide-based control programmes, OCP represented a major threat to the environment especially as it was planned for a twenty-year period. The programme thus included an aquatic ecosystem monitoring network, covering the entire zone exposed to insecticide spraying (11 countries, or a surface area of over 1,300,000 km^2, in which 50,000 km of rivers were targets for treatment). In total, nearly ten teams of ichthyologists and entomologists of different nationalities carried out, for twenty years, regular monitoring of aquatic fauna that could be affected by the larvicide treatments. This was the first time ever that such an undertaking was conducted at such a large spatial and temporal scale.

The insecticides (organophosphates, carbamates, pyrethroids, and biological insecticides) used were screened rigorously based on their immediate (table 24.IV) and longer-term toxic effects on aquatic fauna, and criteria were defined in view of their use as larvicide treatments. For instance, all insecticides

Species	Larvicides	Mean lethal concentrations (LC50) (μg l^{-1}) 24 hours	48 hours	72 hours
Pollimyrus isidori	Permethrin 20% ca	40 (30-63)	26 (19-31)	-
Chrysichthys maurus	Cyphenothrin 10% ca	630 (501-800)	220 121-270)	-
Barbus macrops	Cyphenothrin 10% ca	15 (14-17)	12 (11-13)	10 (7-11)
Pollimyrus isidori	Pyraclofos TIA-230, 50% ca	170 (149-184)	70 (41-87)	40 (3-66)
Chrysichthys nigrodigitatus	Pyraclofos TIA-230, 50% ca	150 (113-632)	78 (59-95)	68 (48-82)
Pollimyrus isidori	Carbosulfan 25% ca	82 (71-81)	-	71 (61-82)
Schilbe mystus	Carbosulfan 25% ca	180 (124-269)	140 (105-162)	136 (108-152)

TABLE 24.IV.
Mean lethal concentrations (brackets confidence limits) of some insecticides used on West African fish species (from Yaméogo *et al.*, 1991).

that could have toxic effects on fishes at operational doses were eliminated after the lethal concentrations were determined (Yaméogo *et al.*, 1991) (table 24.V).

Given the weekly application of insecticides and the size of the treated area, the aquatic environment monitoring programme placed special emphasis on identifying the short- and medium-term effects on invertebrate populations and the long-term impacts on fish.

	Permethrin	Cyphenothrin	Carbosulfan	Pyraclofos
Operational dose (μg l^{-1})	15.0	15.0	50.0	100.0
24 hrs - LC 50 (μg l^{-1})	40.0	15.0	82.0	150.0

TABLE 24.V.
Comparison between the mean lethal concentrations observed on *Pollimyrus isidori* and operational doses used in the OCP programme (from Yaméogo *et al.*, 1991).

It was found that when insecticides are sprayed, exposed fishes flee the toxic wave by swimming upstream past it, thus avoiding long exposure (Abban & Samman, 1980; 1982). It was also observed at, in the short term, fishes voluntarily exposed to organophosphates suffered from a decrease in cerebral acetylcholinesterase activity, the duration of which depended on the insecticide, the duration of exposure, and the concentration used (Gras *et al.*, 1982; Antwi 1983). However, after studying the brains of fishes caught in the river immediately or at different times after the operational spraying of organophosphates, no decrease in cerebral enzyme activity was found (Antwi, 1985). This appears to prove that fishes avoid the larvicides one way or another.

Nearly 20 years after the start of larvicide treaments, aquatic monitoring showed that they had noticeable, but not irreversible, effects on invertebrate populations (Crosa, 1996). That said, even if a number of intra- or inter-annual variations have been observed, no clear direct effect of the use of insecticides has been shown on either experimental catches (richness and structure) (figures 24.6 and 24.7) or the biology of fishes in rivers of the treated area (Lévêque, 1990; Fermon & Paugy, 1996) (figures 24.8 and 24.9).

FIGURE 24.6.
Trends in mean catches per 100 m^2 gillnets per night (CPUE: catch per unit effort) at different monitoring sites of the aquatic monitoring programme of the OCP programme in West Africa (from Fermon & Paugy, 1996).

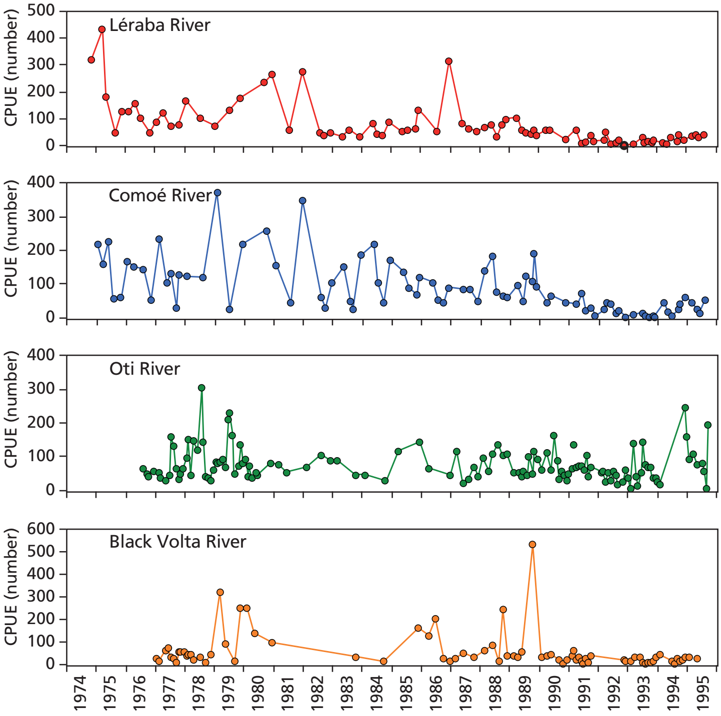
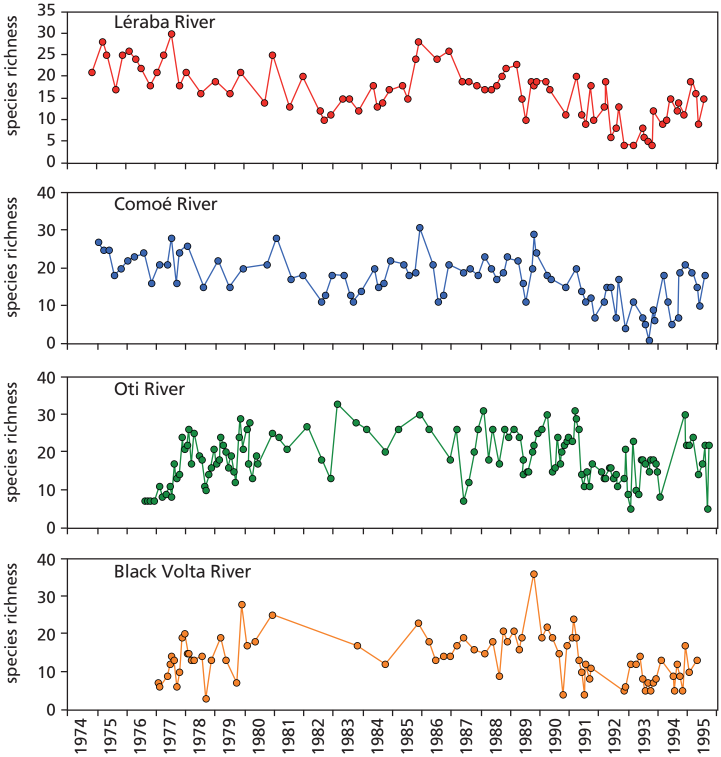


FIGURE 24.7.
Trends in fish species richness at some sampling sites of the aquatic monitoring programme of the OCP programme in West Africa (from Fermon & Paugy, 1996).



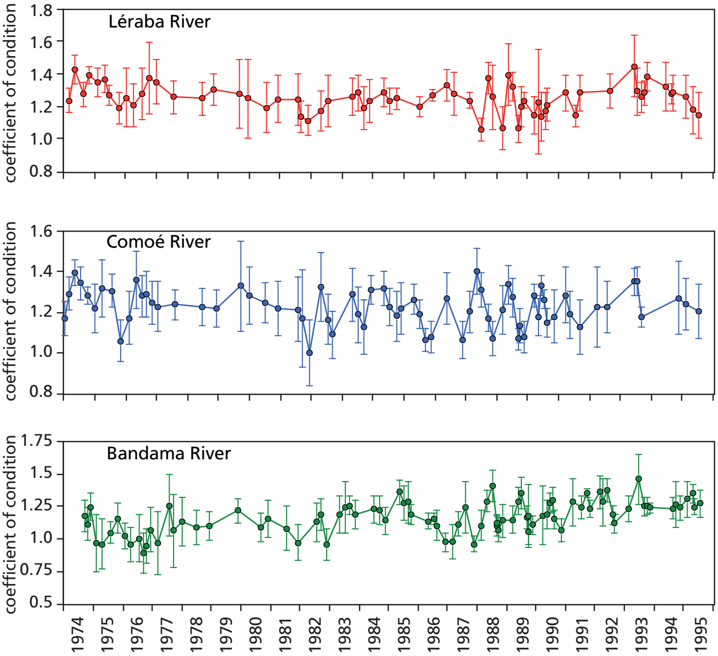


FIGURE 24.8.
Variations of the mean coefficient of condition of *Alestes baremoze* in three rivers from Côte d'Ivoire during twenty years of aquatic monitoring in the framework of the OCP programme in West Africa (from Fermon & Paugy, 1996).

Although insecticide treatments affected the populations of certain invertebrate groups locally, there was no such finding for fish communities. This is a crucial result given that several million children are no longer affected by the endemic disease that is onchocerciasis, and that the resource represented by fishes has been preserved.

Heavy metals

The term "heavy metals" generally includes several groups of substances:

- heavy metals in the strict sense, with a high atomic mass and strong toxicity, and whose presence in small quantities is not needed for life: cadmium, mercury, lead, etc.
- metals with a lower atomic mass, necessary for life (oligo-elements) but which rapidly become toxic when their concentration increases: copper, zinc, molybdenum, manganese, cobalt, etc.

Heavy metals are taken up by both flora and fauna and a few, such as mercury, have been shown to undergo bioaccumulation through the food web. Mercury discharge in freshwater systems is generally linked to gold exploitation, a particular problem in the Congo River system. Nevertheless, in Africa, the occurrence of heavy metal traces is quite low compared with some other parts of the world, like South America for example (Biney *et al.*, 1994; Campbell *et al.*, 2003).

Heavy metals end up in agricultural soils and hydrosystems via the deliberate addition of oligo-elements or pesticides, wastes from refineries or factories treating non-ferrous metals (nickel, copper, zinc, lead, chrome, cadmium, etc.),

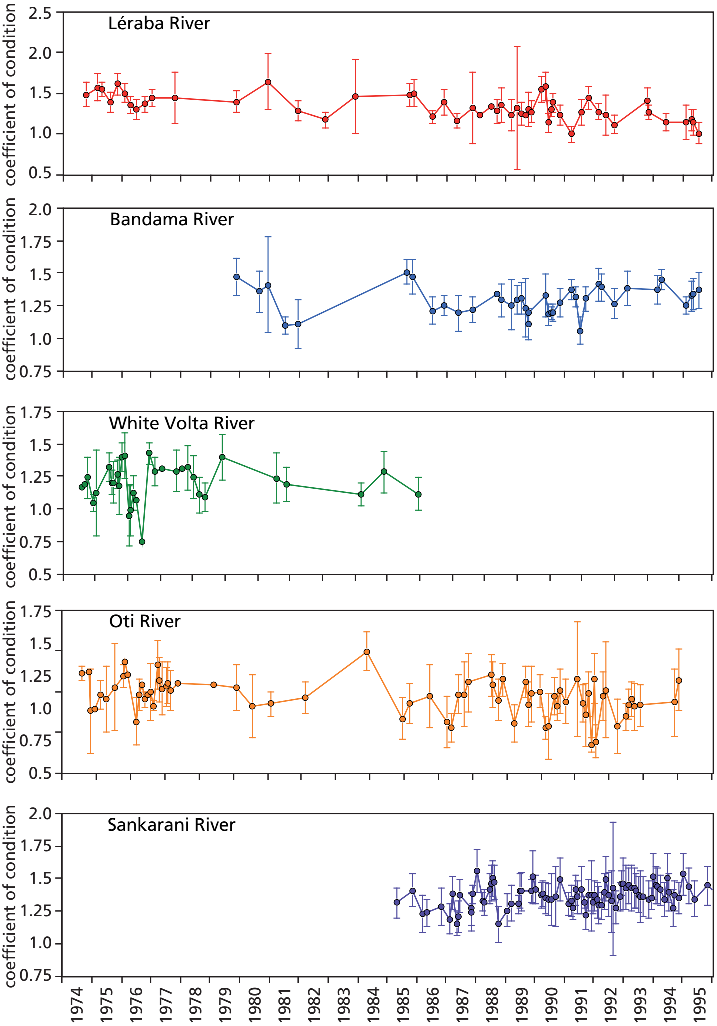


FIGURE 24.9.
Variations of the mean coefficient of condition of *Schilbe mystus* in three rivers from Côte d'Ivoire during twenty years of aquatic monitoring in the framework of the OCP programme in West Africa (from Fermon & Paugy, 1996).

wastes from tanneries (cadmium, chrome) or paper pulp factories (mercury). To these must be added atmospheric deposition of pollutants from human activity (mainly industrial) and household or urban effluents (zinc, copper, lead). Mercury pollution may come from industrial use (paper industry), the exploitation of gold deposits, or the use of organomercury fungicides.

The problems associated with heavy metal contamination result from their accumulation in organisms, sometimes to the point of reaching toxic levels. In general, concentrations of heavy metals in African aquatic ecosystems are low compared with other parts of the world. Nonetheless, some data exist and have been summarized (Dejoux, 1988; Biney *et al.*, 1994). They show that on the whole, concentrations found in the muscles of inland water African fish are below the norms established by the WHO (table 24.VI). Likewise, aside from a few problem areas such as Lake Mariut (Egypt), the Lagos lagoon (Nigeria)

	Mercury	Cadmium	Lead	Arsenic	Copper	Zinc	Manganese	Iron
Lake Mariut, Egypt		0.150			3.70	7.6	0.90	11.2
Lake Idku, Egypt	0.010	0.004	0.67	0.031	1.77	7.4		
Wiwi River, Ghana	0.370	0.190	0.47		0.18	3.0		
Niger Delta, Nigeria	0.034	0.030	0.48		0.70	4.8	1.10	5.4
Lake Nakuru, Kenya	0.044	0.050	0.17	0.360	2.00	22.0	1.80	
Lake Victoria, Kenya		0.04-0.12	0.4-1.1		0.15-0.53	2.21-7.02	0.22-0.74	0.53-4.65
Lake MacIlwaine, Zimbabwe		0.020	0.17	0.280	1.08	9.6	5.40	
Hartbeesport Dam, South Africa		0.020	<0.02	0.400	0.30	6.6	0.24	
WHO limits	0.050	2.0	2.0		30	1000		

TABLE 24.VI.
Mean metal concentration in inland water African fish ($\mu g\ g^{-1}$ fresh weight) (from Biney *et al.*, 1994)

and the Ébrié lagoon (Côte d'Ivoire), the concentrations measured in sediments and some aquatic organisms do not yet pose serious environmental problems (Biney *et al.*, 1994).

Bioaccumulation

A worrying phenomenon with certain contaminants – whether heavy metals or pesticides – is that of bioaccumulation, which leads to the accumulation of a toxic substance in an organism at concentrations that are sometimes much higher than those observed in the natural environment. This phenomenon occurs for various contaminants.

Organisms that have high concentrations of pollutants can in turn enter the food chain, and if the product has not been degraded or eliminated, it will become more and more concentrated at each level of the food chain, for instance from seaweeds to piscivorous fishes. This phenomenon, known as bioamplification, shows that the pollution of a system by substances that are found only in tiny quantities in water can have unexpected consequences at the higher levels of the food chain.

Impact of fishing

Depending on the fishing gears used, the impact of fishing on fish communities manifests mainly as selective pressure on adults or on juveniles of certain species. It is widely believed that fishing activity alone, when practised with traditional fishing gears, cannot be responsible for the extinction of fish species. Indeed, it is hard to imagine that a population can be totally eliminated by catches done blindly, unlike what can occur in hunting. That said, strong pressure associated with changes in habitat can rapidly lead to the rarefaction of certain species.

The effects of fishing are especially clear on large species with low reproductive capacity. One example is the near-disappearance of *Arius gigas* in the Niger basin (Daget *et al.*, 1988). In this species, the male is a mouth brooder of a few large eggs. While captures of 2-metre long specimens were mentioned in the early part of the 20th century, the species seems to have become very rare since the 1950s.

Many observations also seem to show that species of the genus *Labeo* (Cyprinidae) are particularly vulnerable. This is the case in Lake Chad where *L. coubie* has practically disappeared from the fishery of the northern basin in the few years that followed the establishment of a fishery (Durand, 1980). The rarefaction of *Labeo mesops* in Lake Malawi (Turner, 1994) and of *Labeo altivelis* in the Luapula River (Jackson, 1961) is also attributed to overfishing.

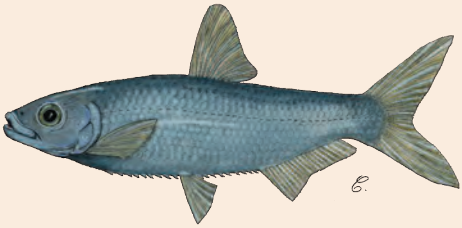
Generally speaking, the establishment of a fishery in systems that were hardly exploited up to that moment leads to a considerable modification of the composition of fish communities. We have seen for instance that large predators (*Lates, Hydrocynus*, *Gymnarchus*, etc.) were particularly vulnerable to gillnets even though this fishing gear almost never caught individuals of other species (*Synodontis*, *Alestes*, Mormyridae, etc.) (Bénech & Quensière, 1989).

The introduction of a benthic trawling fishery in Lake Malawi 1968 could be responsible for population reductions, if not the outright disappearance of certain endemic cichlid species (Turner, 1994), and the same phenomenon has been observed in Lake Victoria (Witte *et al.*, 1992a). A rapid decline in the populations of large cichlids (individuals of more than 190 mm) in Lake Malawi was observed after trawling began in 1968, and about 20% of species from this family disappeared from catches after a few years. In the early 1990s, the benthic species *Lethrinops macracanthus* seemed to have completely disappeared, while *Lethrinops microdon*, which accounted for 16% of catches by weight in 1970, now represents less than 2%. In the south of Lake Malawi where intensive fishing occurs, three large haplochromine species have been eliminated while eight others have seen a steep decline.

According to Coulter *et al.* (1986), the experience acquired in the East African great lakes shows that the existence of a mechanized fishery is incompatible with the maintenance of highly diverse Cichlidae populations, mainly owing to the mode of reproduction of the majority of species, characterized by low fecundity and territorial behaviour. Tweddle (1992) holds a different opinion, saying that benthic species rapidly reintegrate the area after the passage of a trawler and that commercial fishing is currently managed well in Lake Malawi.

One of the most marked effects of fishing can be seen demographically, with a reduction in the average size of species and the disappearance of large individuals. Indeed, while fishing generally begins with the use of large-meshed gears, they become smaller as large individuals become rarer. In some cases the mesh is so small that gears capture immature individuals and the populations of species that can no longer reproduce drop drastically. In Lake Malombe for example, *Oreochromis* (*O. karongae, O. squamipinnis*) fishing was done using gillnets. In the 1980s, an increase in the use of small mesh size seines and a concomitant collapse of *Oreochromis* catches was observed. This mode of exploitation is also thought responsible for the disappearance of nine endemic large cichlid species (Turner, 1994).

Fisheries



RAYMOND LAË

CHRISTIAN LÉVÊQUE

The continental waters of Africa are generally rich in fishes, and fishing has long been practiced there as a subsistence activity, like hunting and gathering. To face growing demand after the Second World War, the development of aquaculture was seen as a way of satisfying the human need for animal protein. In practice, there was little development of fish farming in Africa, whereas the use of natural fish communities grew at a spectacular rate for reasons both direct (high demographic growth leading to an increased demand for protein; use of new environments and species) and indirect (development of road networks and transport; improvement of trading circuits; use of newer and more resistant materials such as nylon, which reduced the manufacture and repair times for equipment, leading to a significant rise in individual fishing efforts; introduction of more powerful fishing equipment) (Daget, 1988b; Laë, 1994). In addition, there were changes in the food behaviour of certain ethnic groups such as pastoral societies that formerly did not eat fish owing to customs or taboos.

Consequently, African waters are extensively used. For many countries, fresh or frozen marine and freshwater fish constitute a basic food product. As food, fish is more or less identical to meat in terms of protein content (17 to 20%) and nutritional value. Moreover, fish flesh is rich in minerals and oligo-elements, as well as vitamins A and D, which are often deficient in the diet. In these countries, fish is usually cheaper than meat.

The "fisheries system"

For a long time, the study of fisheries was confined to specialists, fisheries biologists who focused their efforts on the dynamics of the resource and its use. This approach turned out to be inadequate, and the current trend is to take a more holistic approach to the problems arising from the use of natural resources by including fishing behaviour along with other natural and man-made constraints encountered by the system. We thus speak of studying socio-eco-systems, an approach that integrates the tools and knowledge of several disciplines such as ecology, geography, anthropology, economics, and so forth.

Fisheries is, indeed, a complex system of interactions between a biological resource with its own dynamics in an environment that is itself evolving, and diverse predation strategies that are carried out differently in time and space on this resource. In such a system, the main elements are thus:

- the resource composed of different compartments: phytoplankton, zooplankton, molluscs, shells, and different fish species of variable trophic levels, with interspecific relationships that determine the dynamic of the whole;
- exploited fish stocks and those that are hardly or not used, where the trophic cascade phenomenon can lead to variations in abundance that are independent of fishing pressure;
- the environment in which the resource is found. Changes that occur in this environment (climate change, impact of human activity) can significantly modify the resource renewal rate, the abundance of stocks used, as well as their specific composition, and thus fisheries production;
- fishing techniques and modes, as well as fish conservation methods. Not all species are fished, even if subsistence fishing in Africa concerns a majority of them. Moreover, species vulnerability varies according to the fishing equipment used;
- fishing communities and their socio-economic strategies that are conducted in the context of regional trade. Demand for fish can fluctuate according to season, availability of the resource and thus its price, and possible trade circuits. Fishers try to adapt to these different constraints by choosing different forms of fish processing and sale (fresh, smoked, dried). We often note the absence of a strategy, which manifests as day-to-day crisis management due primarily to poor catches.

For Beverton (1983), the "fisheries system" is composed to two main parts: on one hand, the resource and its environment; on the other hand the fishers and their activities, techniques, and modes of organization. The interaction between these two sub-systems is found at the level of catching operations, that is, the removal of a biomass that has consequences on the ecosystem as well as the economy.

Indeed, fisheries is now studied as a complex whole where we must distinguish flows (of materials, currency, information), levels and centres of action and decision-making (production, sale, management, administration, research), as well as behavioural rules for each level of decision or action. These elements may change over time (Chaboud & Charles-Dominique, 1991; Quensière, 1994; Bousquet, 1994).

Ecosystemic approach to fisheries and biological indicators

The state of generalized overexploitation of aquatic resources is worrying, and preserving the ecosystem requires the implementation of management methods that ensure responsible fishing (Reykjavik Conference of October 2001; World

Summit on Sustainable Development in Johannesburg on September 2002). Global catches appear to have reached their limit in a context of growing demand: 60 to 70% of marine stocks are fully or overexploited (Garcia *et al.*, 1999), and the average trophic level of catches has been going down for the last fifty years (Pauly *et al.*, 1998). Such fishing pressure is sure to affect the structure of trophic networks, with probable consequences in terms of the diversity and productivity of aquatic ecosystems (Bœhlert, 1996). This major disturbance is compounded by profound changes – stemming from natural or manmade causes – in ecosystems that lead to stressful situations for the species that inhabit them. Some of the species respond to these disturbances using remarkable physiological adaptations, such as resistance to pollution or high salinity. They may also adapt by modifying their reproductive or growth mechanisms, in order to thrive in areas where other, less adaptive species are doomed to disappear. Cases of dwarfism and early sexual maturity have thus been observed. The effects of these disturbances occur at various levels of organization, individuals, populations, and communities. As such, their composition and structure end up being profoundly transformed. Although these adaptive responses are often noted, they remain poorly understood.

We now recognize that exploited populations are an integral part of the ecosystem rather than units that evolve independently of their environment, hence the need to prioritize ecosystem-based fisheries management (Daan *et al.*, 2005) and define indicators that provide an accurate picture of the state of aquatic ecosystems. To do so requires developing new tools that take into account the multiple and interactive ways we use ecosystems. In terms of exploitation, we need to consider not only the target species but also their effects on prey species or competitor species, as well as the habitats shared by these species (Cury & Christensen, 2005). In terms of organization, the measures applied to a species can have significant consequences on the exploitation of other species that may, moreover, be the target of other fisheries.

In this context, the use of biological indicators of the state of communities and populations should allow an assessment of both the state of fish communities and the ecosystem in which they evolve. Indeed, many authors find that the community level and the fish compartment are particularly suited to this type of study (Soto-Galera *et al.,* 1998; Whitfield & Elliot, 2002). They favour an ecosystemic approach and the development of biological indicators for the state of health of ecosystems using fish communities and populations (Lévêque, 1995b; Blaber *et al.,* 2000).

The advantages of the use of multispecific ichthyological data in decision-making systems for rational ecosystem management have been reviewed and discussed by several authors including Whitfield & Elliott (2002):

- fish are present in all aquatic systems,
- the life traits of many species as well as their response to environmental changes are known,
- compared with many invertebrates, fishes are relatively easy to identify and most samples can be processed in the field (sometimes with the possibility of releasing the individuals),

- fish communities usually include a range of species that are found on various levels of the trophic network and that use sources of nutrition from both terrestrial and aquatic environments,
- compared with other aquatic organisms, fishes have a longer lifespan and can thus record the length of environmental stresses,
- they comprise a large variety of life forms and functional guilds that can cover all elements of aquatic ecosystems that are affected by disturbances,
- some species are sedentary while others are mobile, making it possible to assess the effects of disturbances at various spatial and temporal scales,
- they are known to a wide audience and are more representative than invertebrates or aquatic plants, especially in Africa where they are of major economic, social, and cultural importance.

Using fishes as biological indicators nonetheless has certain limitations, such as the selectivity of sampling tools, movement-related bias, high tolerance to certain chemical substances compared with other organisms, the capacity for escape, etc. Nonetheless, most of these drawbacks are largely compensated for by the many advantages cited previously.

Although it is based on already old concepts, the use of biological indicators to evaluate the state of aquatic ecosystems gained much traction over the past ten years (Adams, 2002). Today there is a growing interest in the use of biological communities in order to evaluate aquatic resources (Paller *et al.,* 1996; Simon *et al.,* 2000). Most of the work done has focused on defining and using biological indicators in interior freshwater bodies (lakes, rivers, streams) in the United States (Environmental Protection Agency) and Europe (Water Framework Directive). There is a very large number of potential indicators which can be classified into broad categories:

- **environment**: temperature, salinity, turbidity, biotic capacity, primary production indicator, habitat indicator;
- **fisheries**: at population scale, the maximum sustainable yield (MSY), CPUE(catch per unit effort), yield per recruit (Y/R), fishing effort, maximum rate of fishing mortality (FMSY), the rate between exploited/potential area, distance of fishing sites, captures/biomass, rate of fishing mortality on total mortality (F/Z), capturability q. At community scale, total landings, proportion of exploited areas, total captures per zone, distance of fishing sites, effort per km^2, yields per km^2;
- **biology**: gonado-somatic index, sex ratio, growth variations, early maturity, fecundity, migration index (Sr/Ca);
- **species**: at the population scale, occurrence, abundance, biomass, extinction risk. At community scale, total biomass, total abundance, species richness, K-dominance curves, ABC curves, Spatial Biodiversity index;
- **trophodynamics**: at population scale, the trophic level. At community scale, Fishery is Balanced (FIB index), trophic level of catches, trophic level of communities, trophic spectrum
- **Fish lengths**: at population scale, average length, maximum length, proportion of large lengths, length spectrum, lengths slope. At community scale, average length, maximum length, length spectrum (slope and order at origin, diversity of length structures, proportion of large lengths).

BIOLOGICAL CONSEQUENCES OF HYPERSALINITY IN WEST AFRICAN ESTUARIES

(FROM LAË *ET AL.*, 2004; ALBARET *ET AL.*, 2004; PANFILI *ET AL.*, 2004A, B; VIDY *ET AL.*, 2004)

Estuaries, which are interface zones between continental and oceanic hydrosystems, play an important role for ichthyological communities. An estuary serves as a nursery zone for fish juveniles, as it offers them favourable trophic conditions (abundant phyto- and zooplanktonic resources), and refuge zones from predators (turbid waters and profuse vegetation). Yet these estuaries are also historically sites of human occupation, originally serving as shelters and providing a wealth of halieutic resources. The space is increasingly coveted (exploitation of living and mineral resources, urbanization, harbour use, construction of reservoirs in upstream areas) and its nursery function is threatened. The comparison of two West African estuaries has highlighted significant differences in the composition and structure of fish communities that cannot be attributed to fishing activities.

The Gambia estuary is a preserved estuary system that receives large amounts of fresh water, leading to a seasonal fluctuation of salinity between 0 and 40 psu. Meanwhile, the Sine Saloum in Senegal is a "reverse" estuary that receives no feeders, with rainfall accounting for most of its freshwater supply. Salinity there is generally higher than that of the ocean, and increases from downstream to upstream, where it can reach very high levels of up to 135 psu, or four times the salinity of sea water.

In these conditions, species that have their full biological cycle in brackish water are more numerous in the Gambia estuary than species of marine origin. The latter, which reproduce in sea water and whose juveniles use the estuary as a nursery, are hardly diverse and rather scarce. Meanwhile, the Sine Saloum estuary appears to be more accessible to juveniles of marine species, except in its saltiest parts. When we consider adult stages, significant differences are also seen in the fish communities of the two estuaries, in terms of composition (specific diversity, ecological category) and trophic structure as well as in the life traits of the individuals comprising them. Such differences are heightened in the hypersaline area in upstream Sine Saloum, above the 60 psu threshold. The diversity of biological cycles and ecological categories of these fish communities could therefore serve as a good indicator of biodiversity to assess the ecological state of West African estuary environments.
In addition, few species are able to survive in the saltiest zones of hypersaline estuaries. In the Sine Saloum estuary, at least two species, *Tilapia*, *Sarotherodon melanotheron,* and *Ethmalosa fimbriata,* can live in these extreme conditions by modifying their life traits, particularly reproduction and growth.
In the most saline zones of Sine Saloum, size at sexual maturity of both male and female fishes is smaller than that of individuals in the Gambia estuary. Moreover, other life traits such as relative fecundity and oocyte size also vary according to the environments. Growth, evaluated through otolith analysis, is found to be limited in hyperhaline systems (salinity above 60 psu). It is nonetheless comparable in both estuaries in the first year of growth, during which the fishes achieve sexual maturity. In the most saline environments, the reduced size at sexual maturity can thus be explained by a phenomenon of early maturation rather than dwarfism. Based on results of research conducted on the bonga shad, there is no genetic differentiation between the "upstream-downstream" sub-populations of Sine Saloum and Gambia. Modifications in biological characteristics are thus a phenotypic response to environmental constraints rather than the result of genetic isolation.

Recent work has discussed the evaluation of the state of ecosystems by characterizing fish communities. In Mali, the comparison of two artificial reservoirs, lakes Sélingué and Manantali, was made using only ecological indicators related to the specific composition (Kantoussan *et al.*, 2007), structure size

(Kantoussan *et al.*, 2009), trophic spectrum, (Kantoussan *et al.*, 2010), and catch-per-unit-effort and yields (Kantoussan *et al.*, 2014). Similar work has already been carried out in marine ecosystems (ICES/SCOR, 2000), but they often lack scientific rigour and are missing reference values obtained using reproducible protocols. These shortcomings preclude all possibility of making comparisons between observed situations and initial states. Such deficiencies have been pointed out by different authors in their assessments of MPAs (marine protected areas) based on a set of ecological, economic, and social indicators (Halpern 2003; Pomeroy *et al.*, 2005; Lester *et al.* 2009). Software tools have nonetheless been developed for estuary and lagoon systems (Habasque *et al.*, 2012) which allow joint analysis of these groups of indicators that thus serve to evaluate the extent of disturbances suffered by communities as well as the repercussions in terms of economics or ecosystem management. Ultimately, fisheries management using multidisciplinary indicator tables should make it possible to establish a diagnosis of the state of fish populations and communities, their production potential, and their renewal capacity, and take into account the multiple-use component of ecosystems.

State of fisheries in Africa

Quantity of fish landings

Between 1.5 and 2 million tonnes of fish are captured in African continental waters. This production is unevenly divided according to country and the size of aquatic systems in its territory (table 25.I). With the exception of Egypt, aquaculture production is negligible in comparison to the fishing exploitation of natural resources.

While overall results (tables 25.I and 25.II) give an indication of the extent of fishing, they must nonetheless be analysed with care because the share of captures that do not enter the trade circuit is often not known. Yet this share represents more than 60% of total captures in some West African countries.

Continental fishing represents nearly 80% of total production in East Africa (table 25.II). Lake fishing developed considerably over the past ten years, primarily due to the significant increase of production in Lake Victoria following the introduction of *Lates niloticus* in the 1960s. However, the increase in productions, as observed through fishing statistics, does not depend solely on the level of exploitation of stocks or on more efficient fishing activity, but may simply reflect better coverage of fishing activities. Thus, the end of interior conflict (as in the case of Eritrea or Mozambique) is often followed by resumed monitoring of fishing activity by the relevant authorities and the inclusion of these data in national statistics, thus giving a misleading impression of an increase in captures.

It is interesting to note the significant differences that exist between East and West Africa (tables 25.I and 25.II). Although the annual total captures are comparable (> 1,000,000 tonnes), fish come from different sources: continental in East Africa, where the great lake ensembles are found; marine in West

TABLE 25.I.

Fish catches and fish aquaculture production in inland waters of Africa (from Van den Bossche & Bernacsek, 1990; 1991).

Country	Fisheries inland capture (tonnes)	Aquaculture inland capture (tonnes)	% inland fish to total fish production
Angola	8 000	0	10
Benin	31 973	14	76
Botswana	1 900	0	100
Burkina Faso	6 964	36	100
Burundi	4 984	25	100
Cameroon	19 863	137	24
Central African Republic	8 800	88	100
Chad	110 000	0	100
Congo	13 385	115	43
Côte d'Ivoire	27 353	847	27
Democratic Republic of the Congo	163 300	700	99
Egypt	141 700	60 000	81
Equatorial Guinea	400		10
Ethiopia	3 500	0	87
Gabon	1 897	3	9
Gambia	2 700	0	19
Ghana	53 614	386	14
Guinea	1 999	1	7
Kenya	124 096	210	95
Liberia	3 997	3	21
Madagascar	45 806	194	72
Malawi	88 485	103	100
Mali	55 690	12	100
Mozambique	246	21	0,7
Namibia	150	0	0,03
Niger	2 386	14	100
Nigeria	103 209	5 528	44
Rwanda	1 565	65	100
Senegal	14 966	34	5
Sierra Leone	15 982	18	30
Sudan	22 757	43	95
Tanzania	265 735	35	85
Togo	705	9	5
Uganda	200 000	387	100
Zambia	66 980	1 020	100
Zimbabwe	17 344	156	100
Total	**1 632 431**	**70 204**	

Africa where continental aquatic ecosystems are less developed. We can also note a stabilization of captures in the continental system in this part of the continent, whereas maritime fishing grew significantly in the same period (figure 25.1).

TABLE 25.II.
Trends in production of fisheries in inland and marine African waters between 1970 and 1989 (from Greboval et *al.*, 1994).

Year	**Catches marine water fisheries** (tonnes)	**Catches inland water fisheries** (tonnes)	**% lakes**	**Total** (tonnes)
1970	76.7	601.3	50.0	678.0
1971	82.0	605.2	48.1	687.2
1972	84.1	576.3	49.6	660.4
1973	66.0	621.8	48.3	687.8
1974	77.3	593.5	51.4	670.8
1975	94.0	614.0	52.4	708.0
1976	87.9	696.0	49.9	783.9
1977	77.8	750.4	48.5	828.1
1978	75.9	692.2	46.9	769.1
1979	64.0	631.7	52.1	695.7
1980	86.0	667.7	47.8	753.7
1981	83.2	644.9	49.3	728.1
1982	70.3	700.1	50.0	770.4
1983	79.6	734.8	54.8	814.4
1984	80.4	843.7	60.4	924.1
1985	134.4	847.6	66.7	982.0
1986	140.9	917.8	74.3	1 058.7
1987	136.8	954.2	74.0	1 091.0
1988	145.8	1 044.0	74.6	1 189.8
1989	143.7	1 034.3	78.7	1 178.0

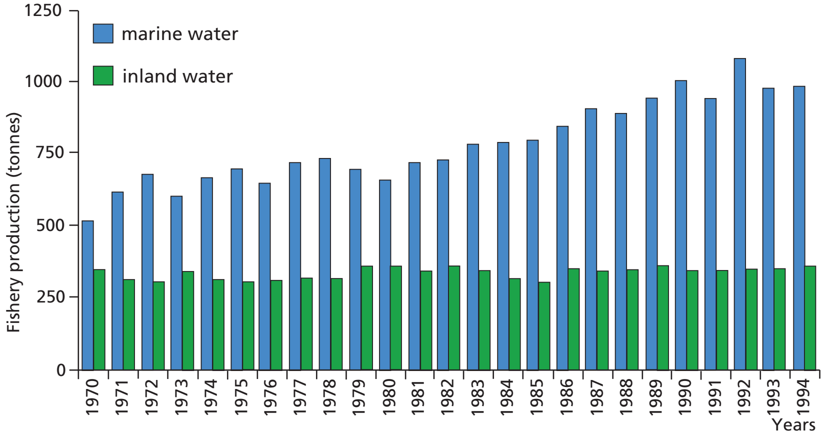


FIGURE 25.1.
Trends in production of fisheries in inland and marine waters of Western Africa between 1970 and 1994 (source: FIDI, 1996).

Major fish species caught

In Africa, continental fishing involves a large number of species. In fluvial environments, there is significant spatio-temporal variability in continental ecosystems that has led to the definition of fisheries based on the existence of a biotope, a season, a species, and a gear (Fay, 1989). In these conditions, fishing pressure can be strong and the variety of gears used makes it possible to capture most of the species found in the system, given that few species are currently subject to a ban.

In the lakes, however, a large portion of commercial catches is composed of a small number of species (table 25.III). These are Cichlidae which are most often demersal fishes, Latidae, and pelagic Clupeidae. In West Africa, pelagic Clupeidae represent just a small portion of captures. In some East African lakes such as Kivu, Kariba, or Victoria, the bulk of total catches is represented by introduced species.

TABLE 25.III.

Major commercial species groups by lake in East and West Africa (from Greboval *et al.*, 1994; Laë, 1995; Van den Bossche & Bernacsek, 1990).

Water body	Species or family	Family	Contribution to present catches (%)	Origin
Lakes				
Albert	*Hydrocynus forskalii*	Alestidae	40	endogenous
	Lates niloticus	Latidae	20	endogenous
	Oreochromis niloticus	Cichlidae	20	endogenous
Rwemu	*Oreochromis niloticus*	Cichlidae	70	*introduced*
	Oreochromis macrochir	Cichlidae	0	endogenous
Edward	*Oreochromis niloticus*	Cichlidae	60	endogenous
Kivu	*Limnothrissa miodon*	Clupeidae	80	*introduced*
Malawi	*Engraulicypris*	Cyprinidae	20	endogenous
	Cichlidae	Cichlidae	40-60	endogenous
Mweru	*Oreochromis macrochir*	Cichlidae	25	endogenous
	Microthrissa moeruensis	Clupeidae	50	endogenous
Tanganyika	*Stolothrissa tanganicae*	Clupeidae	70-80	endogenous
	Limnothrissa miodon	Clupeidae	0	endogenous
	Luciolates stappersii	Latidae	5-15	endogenous
Turkana	*Tilapia* spp.	Cichlidae	15-20	endogenous
	Lates niloticus	Latidae	30	endogenous
Victoria	*Lates niloticus*	Latidae	60	*introduced*
	Oreochromis niloticus	Cichlidae	15-20	*introduced*
	Rastrineobola argentea	Cyprinidae	20-25	endogenous
Reservoirs				
Sélingué	*Labeo senegalensis*	Cyprinidae	16	endogenous
	Chrysischthys nigrodigitatus	Claroteidae	15	endogenous
	Schilbe niloticus	Schilbeidae	9.5	endogenous
	Tilapia spp.	Cichlidae	14	endogenous
Ayamé	*Oreochromis niloticus*	Cichlidae	50	*introduced*
	Heterotis niloticus	Arapaimidae	0	*introduced*
Volta	*Tilapia* spp.	Cichlidae	38	endogenous
	Lates niloticus	Latidae	16	endogenous
	Labeo sp.	Cyprinidae	10.5	endogenous
	Alestes	Alestidae	6	endogenous
Manantali	*Sarotherodon galilaeus*	Cichlidae	37	endogenous
	Tilapia monodi	Cichlidae	12	endogenous
	Lates niloticus	Latidae	9	endogenous
Kainji	Cichlidae	Cichlidae	44	endogenous
	Bagridae	Bagridae	15	endogenous
	Citharinidae	Citharinidae	15	endogenous
	Alestidae	Alestidae	10	endogenous
Kariba	*Limnothrissa miodon*	Clupeidae	85	*introduced*

Table 25.IV provides an overview of the evolution of fish production on both quantitative and qualitative levels between 1970-1972 and 1988-1990 for some natural and artifical East African lakes. Cichlidae (tilapias and haplochromines) as well as pelagic species comprise about a quarter of captures in 1970. Some twenty years later, total production had nearly tripled and catch composition had changed significantly, dominated by *Lates* and small pelagic fishes. If Lake Victoria is not taken into account, we can observe the growing importance of small Clupeidae that represent nearly half of total captures. At the same time, the share of tilapias and haplochromines is decreasing. These changes are mainly the result of the introduction of *Limnothrissa miodon* and *Lates niloticus* in certain East African lakes. In West Africa, chronological data of such length is not available, and it is impossible to track the evolution of captures over time. Nonetheless, species introductions were rare, which explains why Cichlidae still represent between 35 and 50% of total captures depending on the environment in question.

TABLE 25.IV.
Relative importance of major species groups in fish production from some natural or artificial African lakes (1970/72–1988/90) (1,000 tonnes) (from Greboval *et al.*, 1994).

Lakes		1970-1972					1988-1990				
		small pelagics	*Lates*	*Tilapia*	*Haplochromis*	others	small pelagics	*Lates*	*Tilapia*	*Haplochromis*	others
Albert	natural	1	3.3	1.6		10.6	0.8	4.8	4.8		13.5
Chilwa	natural			1.3		3.9					
Edward	natural			7	*	3.1					
Kariba	reservoir			0.5		3					
Kivu	natural			0.2	0.7	*					
Malawi	natural	3.3		23	29.5	9.9					
Mweru	natural	*		10		2.7					
Tanganyika	natural	62	4	1		10.5					
Turkana	natural		0.7	0.3		3.3					
Victoria	natural	12	*	23	36.3	25					
Total		**78.3**	**8**	**76.6**	**66.5**	**72.4**	**240.8**		**97.3**	**29.9**	**114.9**
Total %		**25.9**	**2.5**	**25.3**	**21.9**	**13.9**	**29.2**	**41.2**	**11.8**	**3.6**	**13.9**
without Lake Victoria											
Total		**66.3**	**8**	**53.6**	**30.2**	**47.4**	**144.9**	**18.7**	**41.8**	**24.6**	**84.3**
Total %		**32.3**	**3.9**	**26.1**	**14.7**	**23.1**	**46.1**	**5.9**	**13.3**	**7.8**	**26.8**

Dynamic of the resource

Biomass (fishery scientists often use the term stocks) is the quantity of fishes present in an environment at a given moment, expressed as a unit of weight per unit of area (such as kg/ha). The production of this biomass is the quantity of biological matter produced during a given time period. Biomass tends to increase with growth and reproduction (arrival of fry and juveniles) of individuals, whereas it tends to decrease as a result of natural mortality or mortality from fishing activity or other causes related to increased anthropization of ecosystems (pollution, transformations, etc.). This biomass has its own dynamics in the absence of fishing, which depends on the biological characteristics of species, and the seasonal and inter-annual dynamics of the aquatic environments in which these species live.

Resource, and more specifically fishing resource, refers to the set of species that may be captured in fishing activities. In effect, the biomass produced by the ecosystem is only a resource inasmuch as it is used.

Relation between biological production and biomass

Biological production is the total quantity of organic matter produced by a given biomass in a given period. The ration between production (P) and biomass (B), or P/B ratio, given per unit of time, expresses the biomass turnover rate of the population under study in the absence of exploitation.

The higher the P/B, the faster the turnover of biomass. There is in effect a relationship between P/B and species longevity. The longer the average lifespan, the lower the P/B and thus the biomass turnover rate (Lévêque *et al.*, 1977). In fact, for exponential mortality, it has been shown that P/B was equivalent to the instantaneous mortality coefficient (z) (Allen, 1971), which is tantamount to saying that biological production per unit of time is a function of biomass and mortality rate. For example, observations show that P/B is around 1 for fishes with a lifespan of 4 to 5 years. This means that biological production is equivalent each year to biomass. For annual species, P/B is between 4 and 6, while for species that live around ten years, P/B is about 0.5-0.6.

In an outlook of long term biomass equilibrium, biological production serves in part to compensate for natural mortality, and possibly for fishing-related mortality. Fluctuations (ΔB) of biomass (B) can be schematically represented by the following equation:

$$\Delta B = B + C + R - M - F$$

where B is biomass, C is biomass growth from weight gain of individuals in the biomass, R is recruitment of fry and juveniles, that is, entry into the biomass of individuals yielded by reproduction, M is natural mortality due to predation, disease, etc., and F is mortality from fishing.

The quantity of fishes that can be captured, or fishery production, is necessarily a fraction of biological production. This capture should remain limited enough to ensure that the productive potential represented by the biomass is not affected, as this would eventually lead to a reduction in the fraction of biological production that can be used for fishing. In extreme cases, overexploitation can lead to the disappearance of a stock. The art of fisheries management lies entirely in the capacity to determine what amount of biomass can be removed without undermining the stock, which must essentially remain identical year-on-year in order to maintain its productive potential.

Stock assessment

The assessment of fish stocks, *i.e.*, their biomass, is a highly difficult exercise for which no simple methods exist.

For African continental environments, some estimations (table 25.V) have been carried out using various methods. For shallow lakes, one can use purse seines, as was the case for Lake George or Lake Nakuru. For a few Great African lakes, the use of acoustic methods made it possible to estimate fish stocks. In Lake Tanganyika, the biomass of pelagic fishes was estimated at various periods, and the values observed were between 1,200 kg ha^{-1}, which seems an exceptionally high value for a lake, and 200 to 300 kg/ha (Coulter, 1991a). The differences can be ascribed to seasonal and inter-annual variations in the abundance of *Stolothrissa*. Acoustic prospecting in Lake Malawi yielded lower figures: 168,000 tonnes of pelagic fishes, or around 70 kg/ha (Menz *et al.*, 1995). In Lake Kainji, the biomass of pelagic fishes is relatively low (18 kg/ha) compared with Cichlidae (105 kg/ha) or Bagridae/Claroteidae (36 kg/ha).

TABLE 25.V.
Assessments of the average fish biomass in various types of African inland aquatic environments.

Water body	**System**	**Biomass** (kg/ha)	**Source**
Shallow lakes	Nakuru	300-400	Vareschi, 1979
	George	290	Gwahaba, 1971
Deep lakes	Malawi, pelagic zone	70	Menz *et al.*, 1995
	Tanganyika, pelagic zone	200-300	Coulter, 1991
	Kainji	240	Pitcher & Hart, 1995
	Kariba	31-650	Pitcher & Hart, 1995
Rivers and floodplains	Kafue Flats		
	- peak flood	338	Kapetsky *et al.*, 1971
	- low-water	435	Kapetsky *et al.*, 1971
	Bandama		
	- peak flood	125-175	Daget *et al.*, 1973
	- low-water	305	Daget *et al.*, 1973
	Nile, Sudd	306-433	Mefit-Batbie, 1983

As for rivers and floodplains, estimates are even more difficult to carry out given the spatial and temporal variability of these physical systems. A few attempts to qualify them were made (table 25.V). These must be taken as estimates and orders of magnitude that should not be used to extrapolate.

Aquatic environment and fisheries

Fish population dynamics are controlled by the dynamics of the environments inhabited by these populations. The available habitat (see chapter *Diversity of fish habitats*) will influence, at all stages of development of a species, the quantity of fishes that the environment can host and which constitutes the stock from which fishes will be captured.

In this context, any change to water regime or volume will have direct repercussions on stocks, and therefore on fishing. Such changes may result from natural phenomena related to climate fluctuations or human activity, to the extent that freshwater is used in a variety of ways such as irrigation, domestic consumption, and the production of hydroelectric energy, which all can be factors. These different forms of water use, often given priority in the context of national economies, lead to disturbances in water regimes which have consequences on fish populations. In this situation, fishing activities are often marginalized owing to the inadequate assessment of their social and economic importance.

Historically speaking, interest in the relationships between fisheries resources and their environment only began for tropical systems in the 1970s. Prior to that, in many countries, the water and forests services were in charge of fisheries management, relatively independently of limnologists who studied the aquatic environment, its components, and its productivity (Rigler, 1982). The convergence between these two areas of activity has proved to be particularly fertile, but the question of sustained cooperation between fisheries management and environmental specialists is still relevant (Magnuson, 1991).

Hydrological variability and variability of fisheries

In many fluvial environments associated with floodplains, flood duration and extent are deciding factors for the abundance of fish stocks (Welcomme, 1979). During floods, plains provide plentiful and varied nutrition to fishes that leave the minor bed of rivers as well as the permanent pools where the fall of water levels forced them to take shelter during the dry season. The larger the water surface, the longer the flood duration, and the more fishes are able to find favourable conditions for their reproduction and growth. Vegetation also allows them to escape the many predators hunting them. A good flood thus signifies low natural mortality, low fishing mortality in floodplains, strong individual growth, and high captures as the flood recedes and water flows out.

There is thus a close relationship between yearly fluctuations in hydrology and captures. Fisheries production for a given year *n* depends on the intensity of floods in years *n*-1, *n*-2, or *n*-3, with decreasing weight. In rivers, most captures involve 1- or 2-year-old fish. By taking into account the hydrological indices (HI) of years *n*-1 and *n*-2, Welcomme computed the following relationships:

- for the Kafue River: $P = 2962 + 70.54\ (0.7\ HI_{n-1} + 0.3\ HI_{n-2})$ (1969-1973 period) (Welcomme, 1979).
- for the Niger: $P = 151.73 \log (0{,}7\ HI_{n-1} + 0.3\ HI_{n-2}) - 4281.26$ (1966-1984 period) (Welcomme, 1986).

In the central Niger delta, Laë (1992b; 1994) showed that there was a good correlation between total fish catches expressed in tonnes and water loss (m^3) from one year to another for the 1966-1989 period (figure 25.2). The estimate of flooded surfaces is indirectly obtained by calculating a flood index expressed as the volume of water that is lost through evaporation or infiltration of the lake basin (difference between inflows and outflows). These water losses are related to flood intensity and are proportional to the extent and duration of the flood. Thus, when the average annual flow of the Niger is cut in half (1972-1973 or 1977-1978), the flooded surfaces are divided by four and represent only 5,000 km^2. The calculated ratio is:

$$P = 780.95\ (\text{losses})_n + 770.71\ (\text{losses})_{n-1} + 32304\ (R^2=0.93)$$

Annual catches and the flood index for the same year are well correlated as the first term alone of this relation accounts for 77% of the variation. This strong correlation is explained by the composition of catches, which concerns some 60 species, primarily at younger stages as it is estimated that about 69% of fish catches are individuals less than a year old (Laë, 1992b; 1994).

In the Cross River, Moses (1987) also showed good correlation between catches and the flood index of the two previous years.

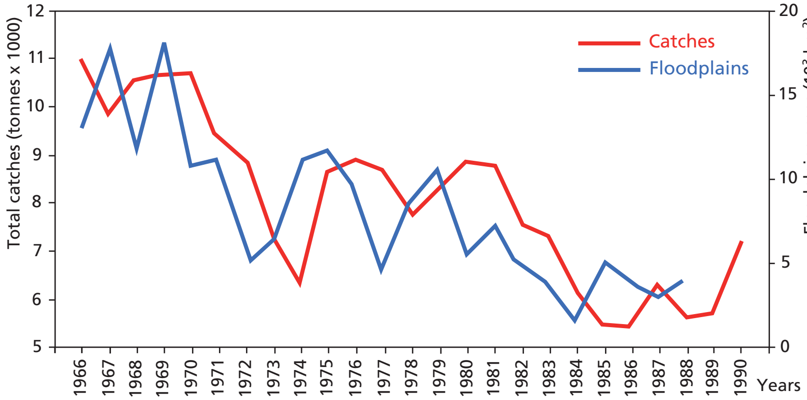


FIGURE 25.2.
Relation between lost water (floodplains areas 10^3 km^2) and total fish catches (tonnes) in the Inner Delta of the Niger River from 1966 to 1990 (from Laë, 1992b).

Types of aquatic ecosystem and fisheries production

From the standpoint of fisheries production, lacustrine systems have been studied the most (table 25.VI). For a majority of them, fisheries production is between 50 and 100 kg/ha, but there may be significant variations locally, with values reaching as high as several hundred kg/ha.

In rivers and floodplains, fisheries production is highly dependent on the seasonal cycle, as well as the extent and duration of the flood. Overall, catch by unit area is lower than in lakes (table 25.VII), but the surface area occupied is much greater. The difficulty of obtaining reliable statistics for this hard-to-access area should not fool us into underestimating their role in African fisheries production.

Effects of dams on the environment and on fisheries

Controlling river flooding is important for watercourse regulation, agriculture, and livestock farming. Production of hydroelectric energy in Africa began much later than in Europe and North America, thus benefiting from technologies that had been tried and tested in developed countries. The 1960s were marked by the construction of large reservoir such as Lake Volta in Ghana, Lake Nasser in

System	Max. area (km^2)	Mean depth (m)	Catch (tonnes)	Yield (kg/ha)	Period	Source
Reservoirs						
Kossou	900	18	4 700-9 300	67-147	1972-1978	v.d. Knaap, 1994
Lagdo	700	11	7 700-13 400	175-340	1985-1991	v.d. Knaap, 1994
Maga	360		700-3 600		1984-1992	v.d. Knaap, 1994
Manantali	500	20-25	1 500	30	1995	Laë & Weigel, 1995a
Sélingué	400	5.3	4 000	100	1995	Laë & Weigel, 1995b
Jebel Aulia	1 500	2.3	7 000-8 000	50	1975	v.d. Knaap, 1994
Mtera	600	6	3 250-5 000	80	1986-1991	v.d. Knaap, 1994
Mwadingusha	1 000	2.6	674-8 000	50	1953-1983	v.d. Knaap, 1994
Kafue Flats	4 300	2	2 450-10 850	6-25	1957-1982	v.d. Knaap, 1994
Kainji	1 270	11	4 500-6 000	35-47	1974-1978	Crul & Roest, 1995
Kariba	5 300	29	30 700	30-41	1990	Greboval *et al.* 1994
Nasser	6 200	25	15 600-31 200	6-25	1981 -1991	v.d. Bossche & Bernascek, 1990
Volta	7 400	19	40 000	55	1970-1979	v.d. Bossche & Bernascek, 1990
Lakes						
Turkana	7 560	31	350-22 000	9-16	1962-1988	Greboval *et al.* 1994; Kolding, 1994
Baringo	130	5.6	152-600	10-50	1964-1986	v.d. Bossche & Bernascek, 1990
Naivasha	115-150	11	44-950	5-60	1964-1986	v.d. Bossche & Bernascek, 1990
Albert	5 270	25	23 900	47-65	1989	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Chilwa	750	2	13 700	77	1989	v.d. Bossche & Bernascek, 1990
Chiuta	200		1 100	75	1989	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Edward	2 300	34	14 400	61 -70	1989	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Kivu	2 370	240	4 600	27-42	1991	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Malawi	30 800	426	69 400	35-45	1991	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Mweru	4 650	7	20 200	60	1990	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Tanganyika	32 900	700	133 900	90	1990	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994
Victoria	68 000	40	562 900	29-59	1991	v.d. Bossche & Bernascek, 1990; Greboval *et al.*, 1994

TABLE 25.VI.
Estimation of the fisheries production (total catches in tonnes and average yield in kg/ha) in different lakes and reservoirs of Africa.

River	Area at peak flood (km^2)	Catch (tonnes)	Number of fishermen	Catch per unit area (kg/ha)
Niger (Benin)	242	1,200		49.6
Niger (Inner Delta)	20,000	90,000	54,112	45.0
Niger (Nigeria)	4,600	14,340	4,600	31.2
Benue	3,100	9,570	5,140	30.9
Pongolo	104	400		38.5
Shire (1970)	665	9,545	2,445	143.5
Shire (1975)	665	7,890	3,324	118.7
Yaérés (Cameroon)	7,000	17,500		25.0
Logomatia	600	300	70	5.0
Kafue (1970)	4,340	6,747	670	15.6
Kafue (1982)	4,754	7,400		15.6
Ouémé (1957)	1,000	10,400	25,000	104.0
Ouémé (1968)	1,000	6,500	29,800	65.0
Senegal	5,490	30,000	10,400	54.7
Barotse	5,120	3,500	912	6.9
Cross	8,000	8,000	4,000	10.0
Nile (Sudd)	31,800	28,000		8.8

TABLE 25.VII.
Maximum flooded area, total catch and number of fishermen for some African floodplains. (from Welcomme, 1989).

Fish and fisheries in the Senegal River

"When it rains, the bush fills with water that spills into bodies of water called marigots. The flooded marigots rise and join the river. At this point the fishes go up into the marigots."

"When they go up to the bush, the fishes fill the marigot, both where it is narrow and where it is wide. It's like a herd of cattle heading for fresh grass. You see the fishes in the grass like cattle passing by.

At this time, grass grows in the pools.
The grass isn't very high, just up to the knees.
You can see the grass move.
The fishes moving it as they swim.
Fishing in the ponds yields a good catch."

"As soon as the water level begins to rise, fishes also start going to the bush.
What will they look for there?
They will look for *jaaje* [wild fonio] seeds that have fallen into the water because of the flood. They eat this and fatten up.
For them, it's a time of plenty; for us, those are lean times, when we have to venture out in dugouts to find food."

"The fishes spawn in the bush, in the pools. The eggs of some fishes hatch two or three months after they are laid, but for all the eggs to hatch, you need to wait for the end of the rainy season. By then, the fishes will have stopped breeding and all the hatchlings will have been released.

But it would be wrong to say that as long as the water rises then recedes, the fishes can reproduce. Two months aren't enough for fish reproduction. The water has to remain in the bush for three or four months."

"When the river begins to recede, some of the fishes know it. They leave the bush to go back to the river. The fishes then split up in two groups. All of them, young and adult alike, want to join the river.
But in some places, when the water goes down, the water is cut off. Those fishes have no way of joining the river, and they stay where they are, in what we call pools."

"Sometimes, when the water falls, the fishes return to the river like a flock of birds.
It's like when you throw a stone at a tree where birds are perched: they all fly off at the same time. When the fishes go to the bush, they go up one by one.
But when they all leave together,
when they leave at night, at dawn
there won't be a single adult fish in the bush.
All of them will be gone.
If they leave in the daytime, at sunset
no adult fish will be left in the bush.
They will all be gone.
Only the small fishes are left, the ones who aren't smart and didn't leave in time.
Those fishes are the ones people will catch until the water in the pools has dried up."

Excerpts from Poissons et Pêches du fleuve Sénégal. Fédération des paysans organisés of the Département de Bakel. Dakar (Adams-Sow, 1996)

Egypt, or Lake Kariba in Zimbabwe and Zambia, along with many other reservoirs that are more modest in size (Anne *et al.*, 1991). The construction of these artificial reservoirs obviously had major repercussions on the ecosystems found upstream and downstream (Ward & Stanford, 1979; Petts, 1984). The main effects on fisheries were as follows (Welcomme, 1985):

- changes to river water flow. These lead to changes in the fish reproduction process due to inappropriate stimuli or brief artificial floods.

Consequently there are changes to the composition of fish communities, since species with flexible reproduction are more resistant than ones that reproduce seasonally. There is also a decrease in productivity within communities triggered by the shift from an irregular system to a stable dynamic system. The increase in the speed of water flow that follows river channeling encourages the emergence of rheophilic species, whereas the slowing of currents in reservoirs favours lentic species;

- habitat loss. The absence or reduction of floodplains downstream following the construction of a reservoir, or conversely, the flooding of spawning substrates found upstream or the channelling of watercourses lead to a decrease in biodiversity and generally a decrease in the ecosystem's productivity;
- closure of rivers. Unequipped reservoirs (as is usually the case in Africa) interrupt fish migration circuits and lead to the elimination of diadromous species by preventing adults from joining upstream spawning sites and slowing down the downstream movement of juveniles;
- changes in sedimentation processes. The creation of dams leads to more deposits in the reservoir, which in turn brings about a decrease in suspended matter and a deficit in sediments downstream from the dams. This leads once again to decreased habitat and biodiversity, changes in plant density, modifications in available food and the benthos, leading to a reduction in biological diversity and productivity;
- increase in phytoplankton and zooplankton in the reservoirs or downstream from the dams owing to reduced flows and increased transparency. This encourages the development of planktophagous fishes;
- changes in temperature. This can lead to a stratification of reservoirs and hamper the migrations of certain fishes. They may also lead to deaths upstream from the dam owing to the release of anoxic or H_2S-rich water.

Thus, according to Lelek & El Zarka (1973) and Adeniji (1975), changes in the fish fauna of the Niger followed the construction of the Kainji dam. Captures between Jebba and Lokoja went down by 50% in a space of three years from 1967 to 1969 (Otobo, 1978b). This was accompanied by changes in the composition of communities, with a decline in Alestidae, Mormyridae and Clariidae and an increase in predatory species such as *Lates* or certain Bagridae/Claroteidae (Sagua, 1978). Also downstream, the fisheries of the Anambra basin decreased by 60% owing to the exundation of traditionally flooded plans following the dam's construction (Awachie & Walson, 1978).

For some dams, a highly localized increase of predator fishes was noted below the structures. This is the case for the Nile just after the Owen dam, where populations of *Barbus altianalis* and *Lates niloticus* are particularly abundant. The same phenomenon has been observed below the Kainji dam with Mochokidae, Alestidae and Cyprinidae. It can be accounted for by the enrichment of reservoir water which, when it passes through locks, transports zooplankton, insects, and fishes (Whitley, 1974). This enrichment is only felt locally.

Finally, we should note the significance of the contributions of rivers to ecosystems found downstream. The retention of nutritional matter in Lake Nasser led to a decline in pelagic fisheries in the eastern Mediterranean, whereas yields increased sharply for the lake.

Laë (1992c, 1994) described the repercussions of the Markala and Sélingué dams in Mali on fishing activities in the Central Delta of the Niger River found downstream from the dams (figure 25.3). These repercussions can be felt at different levels.

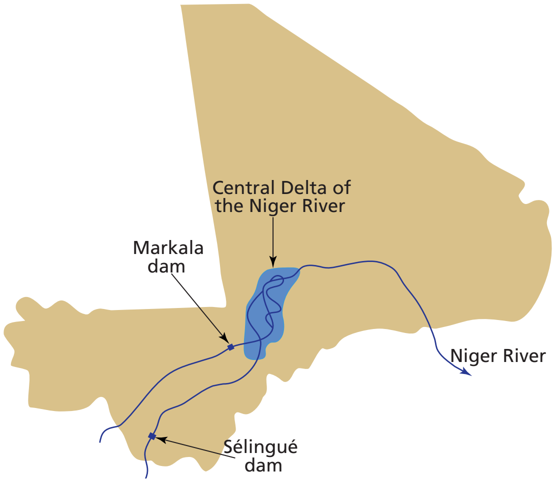


FIGURE 25.3.
Location of the two dams on the upper Niger upstream of the Central Delta of the Niger River.

Perturbation of longitudinal migrations

It is generally thought that dams disturb the spatial distribution of fish fauna and interrupt the breeding migrations of certain species, leading to their disappearance and/or a change in stock composition (Welcomme *et al.*, 1989). This situation does not match the case of the Central Delta, as the Markala dam, build upstream of the floodplains, is not an obstacle to species seeking to join the spawning grounds downstream of the structure (Daget, 1959c).

Longitudinal migrations observed at the approaches of the dam are not related to the fish reproduction process as these are triggered and maintained by external stimuli related to the progressive and regular decrease of available water during the recession period (Daget, 1949). Schools of juveniles from floodplains thus find themselves trapped at the bottom of the dam, and the possibilities of taking the fishway constructed in 1946 are limited, as the pass was designed for the anadromous migrations of a few breeders rather than the much larger migrations, in terms of fish quantities, of juvenile schools. Schools are thus dispersed downstream of the dam, leading primarily to a significant decrease in fishing yields upstream of the dam.

Reduction of the flooded area and the duration of the flood

During the flood, the filling of the two structures leads to a suppression of the flood, which manifests as a decrease in flows entering the lake basin found downstream, and a reduction in the extent and duration of the flood. The action of dams thus reduces the hosting capacity of floodplains, which in turn leads to a decrease in recruitment, slower increase in weight, and ultimately, a poorer fish catch. The loss of captures that is ascribed to the two dams is estimated at 5,000 tonnes per year. Welcomme (1985) also points out that in Nigeria a loss of 6,000 tonnes of fish resulted from the construction of the Kainji dam on the Niger. On the Mekong River, the Pa Mong dam prevents the flood over approximately 700 km downstream, causing a loss of 2,150 tonnes (Petts *et al.*, 1989).

Decrease of activities during low water

The impact of dams is also palpable during periods of low water, and in an even more pronounced manner during droughts in Africa. At times, some spaces no longer receive water while others are flooded for short periods only, although traditionally fishing was deferred for part of the year as the waters were kept undisturbed, and then subjected to collective fishing once the "master of waters" lifted the deferral (Fay, 1989). This results in a considerable reduction of customary fishing activities during low water.

In the same vein, fishing is not allowed in certain parts of the river when waters are low. This measure allows fishes to move past thresholds and become concentrated in the deeper ares of the minor bed, where they are easier to capture once the fishing ban is lifted (Daget, 1956). Currently, large volumes of water are used to run turbines during low water periods to ensure the production of electricity, such that currents in March, April, and May are much faster downstream from the dam (100 to 150 m^3/s higher than their normal rate). Meanwhile, the successive releases of water often hamper fishing considerably, as the artificial floods trigger fish dispersion and makes them less vulnerable to fishing gear.

Indirect protection of the spawning stock

Authors such as Welcomme & Hagborg (1977) and Welcomme (1979) also emphasise the importance of the severity of low water levels in stock renewal. Adult fishes that will be spawning at the next flood need to find refuges that do not dry out during periods of low water.

As average water outflow rates have not changed much over the years, no relationship has been established between fisheries production and water levels during this period. It appears that the reserve of breeders is sufficient at the end of the period to ensure good recruitment levels in the case of the central delta. In other words, low water conditions are not a limiting step. For several years, water releases from the Sélingué dam also reinforce natural water outflow rates. This additional water, which disturbs fishing in pools, thus has an indirect positive effect on fisheries by encouraging the survival of breeders and decreasing their fishing mortality at low water periods.

Fishing gears employed and fishing practices

There is an enormous variety of fishing gears and an exhaustive list cannot be provided (figure 25.4). They come in different forms and show numerous variants that each correspond to precise usages (biotope used, target species, hydrological season). Subsistence fishing has long been practiced using artisanal gear, such as fish traps, harpoons, and so forth. These capture techniques have been grouped according to the main categories established by Nédelec *et al.* (1979) and Moal (1981), following the basic means of construction, size, and use.

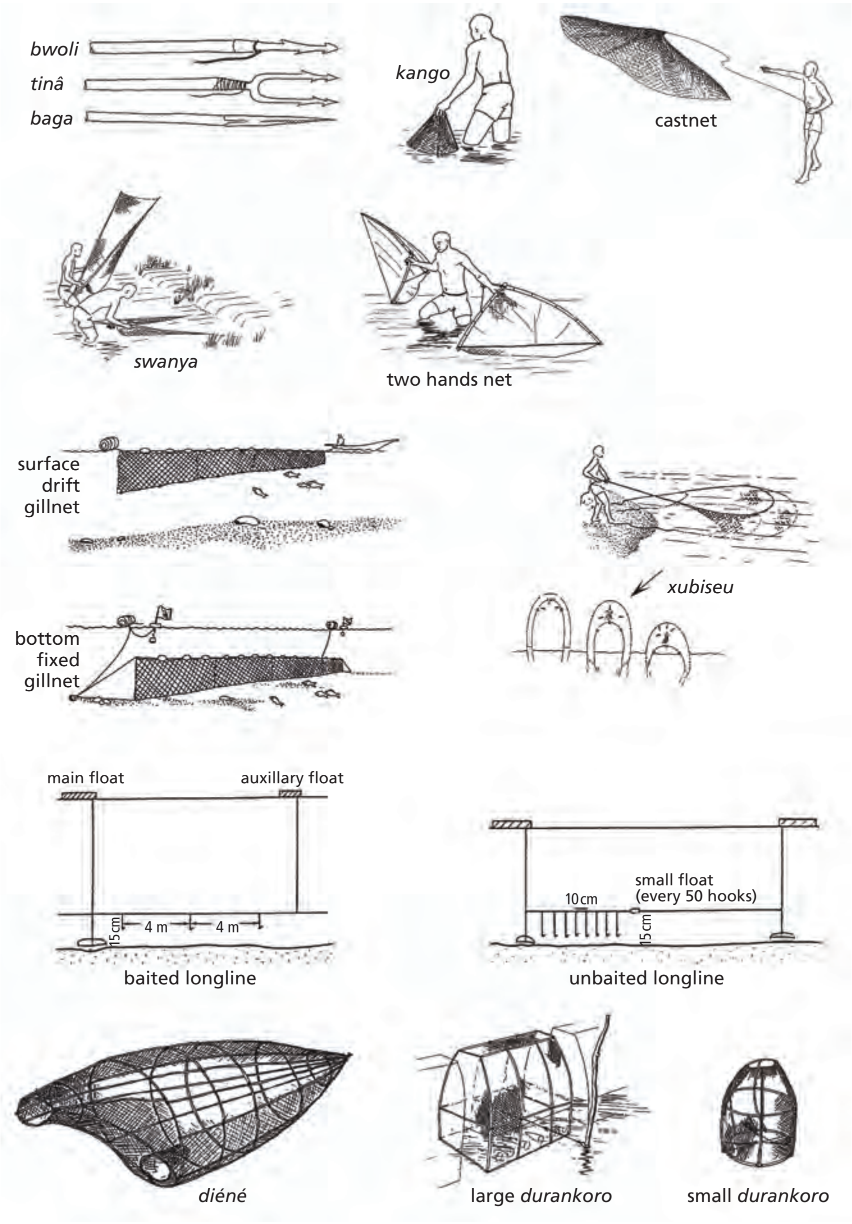


FIGURE 25.4.
Schematic illustration of the main gears used in the Central Delta of the Niger River (from Laë *et al.*, 1994).

Fishing gears

In Africa, the pirogue is often the preferred means of transport. Aside from fishing, it is used to transport people or merchandise. In forested areas, pirogues are carved out of a hardwood trunk. They are monoxylon boats propelled using oars or paddles, or more recently, though this is still rare, motors.

In the Sahelian zone where wood is rarer, fishing pirogues used to be built in two halves made from planks of African mahogany that were nailed together and connected by an enormous transverse seam (Gallais, 1967). Nowadays they are built as a single piece using wood planks from sawmills, making them more watertight and more solid. The use of outboard motors has not become widespread as their price, maintenance, and operation are often too costly compared with the expected benefits. Fishers prefer to set up temporary campsites near fishing areas instead.

Active fishing practices

- Individual fishing

– Wounding gears, such as harpoons, are designed for capturing large fishes, mainly in pools that are drying up, flooded plains, and during collective fishing.

– Cast nets are circular and have lead weights at their perimeter. Once fish are located, nets are casted and capture the fish by falling and closing in on them.

– Different types of push nets include: triangular nets fixed in a "V" and used during dam fishing or collective fishing by a fisher who is waist-deep in water; two-hand nets consisting of two pockets that are held open then closed once the fish has been spotted; and nets used to cover fish on the bottom, which can be clapped over the prey thanks to a large conical frame found on its base.

- Collective fishing

– Beach seines are operated from the shore and used in shallow waters near the shore or on shoals. Some are several hundred metres long (up to 1 km) and require much manpower, of up to twenty people. The use of seines became widespread with the invention of nylon netting. These fine-meshed nets (15 mm) are equipped with large floats and weights. They are set out in a wide arc to surround the fish. Two teams found on the same shore then pull in the ends of the net until the fishes are trapped inside the net. Manipulating the seine is a long and arduous task, and is only carried out once a day.

– Purse seines have a purse line at the bottom of the net which can be drawn in to close the net and retain fish. They are used in deep waters, and the fishing operation mainly consists of surrounding a previously-located fish aggregation. Smaller (300 m) and with a greater drop (50 m) than the previous type, they require the use of a motorised pirogue so that the fish can be encircled rapidly. The operation can be carried out several times a day and targets primarily pelagic species that move in schools.

- Industrial fishing practices

– Semi-industrial fishing techniques have developed significantly in the East African great lakes since the late 1960s (table 25.VIII). The largest fleet by far is the one on Lake Kariba with 213 vessels (rigs/liftnets units). The second-largest fleet is on Lake Tanganyika where 52 seine net boats currently target small pelagic species.

TABLE 25.VIII.
Evolution of small-scale and semi-industrial fleet size in East African lakes (from Greboval *et al.*, 1994).

Lakes	1969	1979	1989
Albert	20	8	1
Edward	5	1	
Kariba		65	213
Kivu			1
Malawi		17	22
Mweru		14	1
Tanganyika	14	35	52
Victoria		5	22

In Burundi and Tanzania these possibilities are limited, and given the efficiency of artisanal fishing, semi-industrial fishing is not highly viable and currently on the decline (Horemans, 1992).

Passive fishing practices

Passive gear are generally fixed, though some mobile types exist (drift gillnets), and take advantage of fish movements to capture them.

- Fixed or drift gillnets

– Fixed gillnets are generally set out in the late afternoon. They are stretched between two poles and remain in place overnight before being retrieved in the morning. As fishes move, they become entangled in the netting. Depending on the type of mesh, the ballasting, and buoyance, the nets may be used near the surface, midwater, or at the bottom, and they have a high degree of selectivity for species. Throughout the year, a net's design may be modified according to the target species and biotope.

– Meanwhile, drift gillnets are not anchored to poles but drift between two pirogues or a pirogue and a float. During an expedition, the fisher drifts with the current for an hour or two, hauls in the net, removes the fish and then goes against the current to return to the starting point. This operation may be repeated several times in a single night. Drift nets have few weights and are used heavily during periods of strong currents.

- Fish traps

– There are numerous variants throughout Africa. In the Ébrié lagoon (Côte d'Ivoire), we can cite the case of fisheries that are located along the shore in locations where waters are barely deeper than 1.50 m. A screen starting from the bank blocks off the lagoon over a distance of about fifty metres. This screen, perpendicular to the shore, leads to a capture chamber in which fish traps are placed. In the lagoons of Benin, barriers are made from screens fashioned from braided Raphia palm or oil palm leaf midribs, gathered together at the bottom and reinforced with stakes. These barriers are arranged in a zigzag manner, forming a broken line with open angles acting as funnels, and each with a fish trap at their end (Pliya, 1980).

– In Mali, in the Central Delta of the Niger, these traps are also placed parallel to the banks or perpendicular to channels or river branches. They are fashioned from branches and fish traps of different shapes depending on water level and surrounding vegetation. The fish traps may be cylindrical (*papolo*) and used when water levels rise in the marigots or flow out of floodplain channels. Other, more recent (1980) traps (*durankoro*) are shaped like truncated cones and installed in low waters (plains, river branch). They may be baited and are used practically throughout the year. Considerably larger in size, *diéné* traps (5 m long and 2 m in diameter), are used in the period when flood waters abate, to create barriers across entire river branches. Traps are made using a bamboo or rônier frame and nylon netting.

– Aside from these fish traps, traps may take other forms, such as 1 m-long hollowed-out bamboo sections placed at the bottom of Ivorian lagoons. These traps target mainly *Chrysichthys* that seek cavities where they can spawn.

LOW WATER FISHING IN LOGONE GANA

The Yaérés (flooded plains) of inland middle Logone are trained by the Ba-Illi which empties into the Logone at Logone-Gana. This area is the heart of intensive fishing at periods of water outflow. This "outflow" fishing takes advantage of fish movements out of the floodzone, particularly *Alestes dentex* and *A. baremoze*. To do so, the Kotokos set up at the river opening, on a natural threshold of sorts, a grid barrier, upstream of which they place 400-500 fish traps with their openings facing downstream, to capture *Alestes*. Downstream from the barrier, and attached to it, about a hundred pirogues are ready to meet the *Hydrocynus* and *Alestes* that have managed to traverse the barrier. Fishing lasts about a week, with yields of 36 tonnes in 1955 and 34 tonnes in 1956 (Blache & Miton, 1962). Upstream from the barrier and for about fifteen kilometres along the river, fisher folk set up camp with unbaited longlines.

The great traditional fishing event of Logone-Gana (North Cameroon, 1969)

1. Transport of basket traps from the village to the fishing site.
2. Start of barrier construction.
3. Establishment of basket traps behind the wooden fences.
4. Hundreds of basket traps are arranged upstream of the fishing area, their opening facing downstream in front of the wooden fence.
5. View of the basket traps during the fishing period.
6. Establishment of stakes used to build the capture compartments.

7. Construction of the of the capture compartments barrier. Fishermen bring the wooden fences.
8. Capture compartments barriers.
9. Dozens of canoes use drift gillnets, downstream of the basket traps and barriers.
10. Overview showing in the foreground numerous basket traps attached to a wooden fence barrier upstream.
    These are followed by canoes collecting fish that have jumped over the barrier. Capture compartments barriers are seen next. Finally, in the background, canoes located downstream use drift gillnets to catch fish.
11. Basket traps with fish (*Alestes*).
12. *Alestes baremoze* is the most abundant caught fish during the great traditional fishing event. This species makes long migrations from Lake Chad to breed in the floodplains.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– There are also crab traps fashioned from a section of netting affixed to a wooden hoop about 30 to 40 cm in diameter. A piece of meat or rotten fish is used as bait.

- Baited or unbaited longlines

The two most common forms are baited longlines placed above the bottom, with spaces of 4-5 metres between hooks, and unbaited longlines consisting of a horizontal main line from which hooked snoods spaced at 5 cm intervals are attached. They are placed just above the bottom and form a barrier for the targeted prey, primarily catfish. Hooks used can vary in size depending on the desired species.

Seasonality of fishing practices

Many fishing gears and their variants are designed to meet specific use norms: hydrological season, target species, type of biotope used. The use of different fishing gears can thus be considered a true adaptive strategy addressing spatiotemporal variations in the systems and in species availability, particularly in rivers and their floodplains.

As such, the activities of fishers in the central Niger delta vary considerably in space and time, as they are dictated by the annual hydrological cycle that is the deciding factor for fish breeding and migration dynamics, and consequently, of fish availability (abundance and vulnerability) (Laë & Morand, 1994). During the flood fishes spawn and spread in nutrient-rich floodplains that are not just areas favourable for their dietary needs, but also safe zones against numerous predators. Transfers from the river to the floodplain occur via channels and marigots that permit the lateral spread of the flood. In low water periods, fishes that stayed for four to five months in the floodplains enjoyed rapid growth (larger size), and return to the river when the current is reversed in the channels and marigots. Other fishes engage in longer longitudinal migrations in schools, going back against the current to the river while being followed by numerous predators. As the current weakens when the water runs out, fishes find themselves concentrated in the minor bed and in the many crevices that follow its course. In some sections, they are once again trapped between sandbars and thresholds owing to the significant drop in water level. The variations of the water level make it impossible to use the same fishing gears throughout the year. This connection between time, space, and fishing activities form the basis for the exploitation of halieutic systems. By combining mobility and diversifying fishing gears, the fisher takes advantage of changes in the system. During the flood and high water periods, halieutic activities are reduced because fishes are dispersed in the water mass and thus less vulnerable, and fishing gears are difficult to use owing to abundant vegetation and low depths. Barrier fishing is practised when water level goes down in river branches and channels, by using different types of fish traps depending on water depth. In the rivers, during water outflow, driftnet fishing is practised, as well as collective fishing using push nets in residual pools during low water levels. Fixed gillnets are used in the period from high to low water levels (October to April).

In the lower Ouémé River, Welcomme (1985) also showed that different gears are used throughout the year depending on the hydrological cycle to capture different species (figure 25.5).

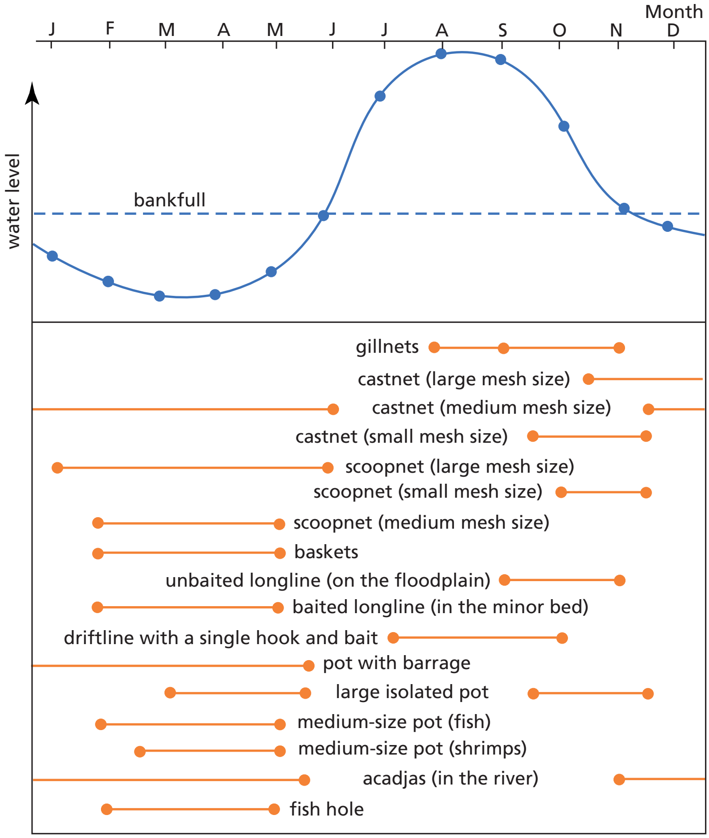


FIGURE 25.5.
Fish gear utilization in the Lower Ouémé River during the course of one year (from Welcomme, 1985).

Evolution of the practices

Subsistence fishing began with locally-manufactured artisanal gear such as fish traps, etc. But significant progress has been made in fishing techniques since the early 20th century. The introduction of gillnets in Lake Victoria in 1905 by Aarup, from Norway (Worthington & Worthington, 1933) was a major technological innovation that spread slowly to other regions of Africa. Nets were initially made locally from cotton or other cheap local materials, but they took a long time to make and the cotton was very fragile. After the Second World War, they were rapidly replaced by nets made from woven nylon, then partially in the 1980s by monofilament nets, more efficient but also more fragile.

The use of synthetic materials makes it possible to keep nets in good condition and use them for several consecutive years. Freed from the arduous work of preparing and maintaining gears, fishers can now devote their time to the activity of fishing itself, while benefiting for a greater number of fishing gears. Because fishers are better equipped nowadays, effective fishing effort continues to grow.

Industrial marine fishing techniques were also introduced in the East African great lakes. Trawling was practiced on an experimental basis in Lake Malawi as early as 1965 and this technique was rapidly adopted by fishers (Jackson & Ssentongo, 1988).

Biomanipulations and improvement of the fishing production

Biomanipulation of natural environments

Capture methods based on the exploitation of natural stocks have been completed by traditional techniques intended to improve production of natural fishing environments. This is the case for the *acadjas* in Benin (Kapetski, 1981) or the "*garse system*" in Cameroon (Stauch, 1966) and the *hoshas* of Egypt (Hem, 1991) (figure 25.6).

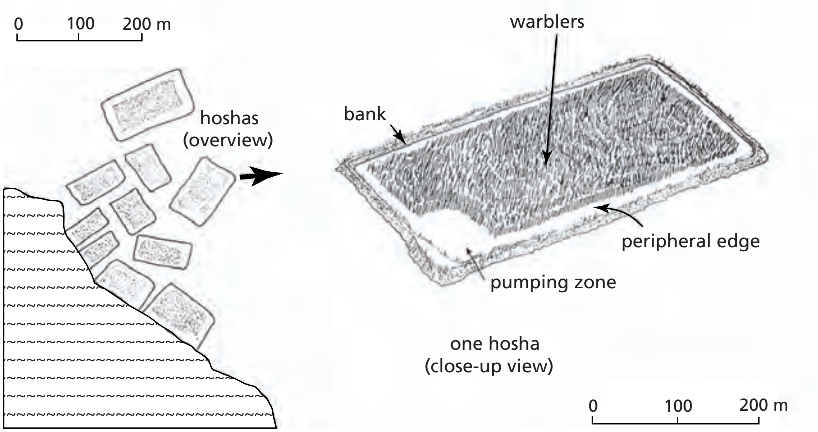


FIGURE 25.6.
Overview and close-up view of *hoshas* (from Hem, 1991).

The principle behind these different techniques is to promote the development of natural food in a fisheries environment, thereby reducing the need for providing artificial food supplements and thus significantly reducing the costs of fish production (Hem *et al.*, 1994). For example, the *acadjas* used in Benin are a pile of branches placed in lagoons in shallow areas. These *acadjas* promote the concentration and multiplication of fishes in natural environments through an attractive effect that is caused by the increase in the surface area for microfauna and epiphytes to develop, which provide fishes with food, and by the shelter provided by the structures themselves. The average annual productivity varies from 5 to 10 tonnes/ha (Welcomme, 1972b), a figure that is much higher than commonly observed figures in West African lagoons that barely reach 200 kg/ha at best.

Introductions of species in aquatic ecosystems

Fish communities in tropical waters are generally diverse enough for most ecological niches to be used. In some hydrosystems, however, fauna may be poor for historical reasons. Moreover, large reservoirs create new lacustrine habitats that are not always colonized by riverine fauna. To justify introductions, fisheries managers provide examples that are seen as positive for fisheries development (see chapter *Species introductions*).

One example of species introduction involves pelagic systems. *Limnothrissa miodon* and *Stolothrissa tanganyicae* are small pelagic zooplanktivorous Clupeidae in Lake Tanganyika, where they are major fisheries targets. *L. miodon* was introduced in 1967 and in 1968 in Lake Kariba, a large reservoir lake on the Zambezi, where it flourished (figure 25.7) to the point of supplying a fishery as well (Marshall, 1984a). The species then colonized another dam, Cahora Bassa, downstream from the Kariba. *L. miodon* and *S. tanganyicae* were also introduced in Lake Kivu in 1958-1960. Here, they also occupied the vacant niche of pelagic zooplanktivores, and the introduction is deemed an economic success, with no negative impact identified (Spliethoff *et al.*, 1983).

Oreochromis niloticus was introduced in numerous natural and artificial water bodies in Africa, Asia, and South America, particularly in many small dams that were built in recent decades. Several tilapia species are currently established throughout the intertropical belt. In Africa, *Lates niloticus* and *Oreochromis niloticus* were introduced in Lake Kyoga in the 1950s and rapidly flourished. In 1977, each species represented around 40% of artisanal fishing estimated at 167,000 tonnes, compared with 4,500 tonnes in 1956. In 1985 the situation had changed, with *O. niloticus* representing 78% of captures compared with only 17% for *O. niloticus* (Ogutu-Ohwayo, 1990). These introductions were accompanied by a sometimes significant regression of native species.

In Lake Victoria (see chapters *Fish communities in East African rift lakes* and *Species introductions*), the introduction of *Lates* was also behind a spectacular growth in fisheries production.

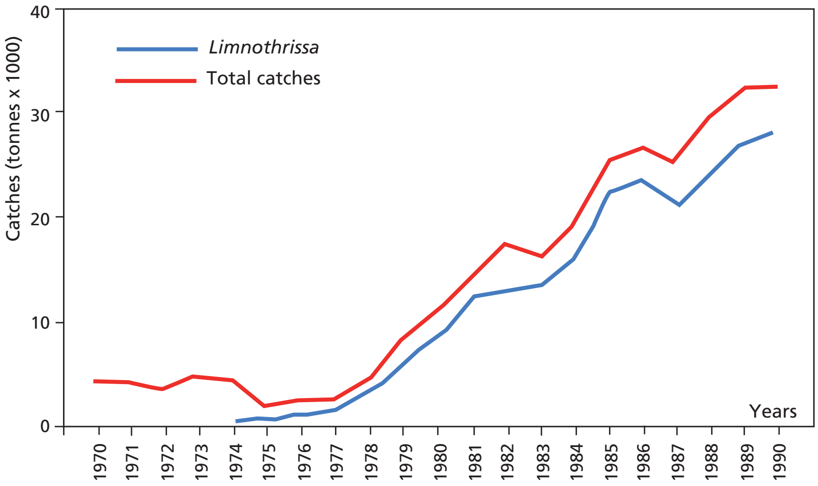


FIGURE 25.7.
Evolution of catches in Lake Kariba after the introduction of *Limnothrissa miodon* (from Marshall, 1984a).

Marketing and processing of fish

Generally speaking, three major fish markets can be identified in relation to fishing locations:

- wholesale markets that centralize production and redistribute it to distant areas;
- semi-wholesale markets found in production and consumer centres;
- retail markets in towns and villages (Breuil & Quensière, 1995). Wholesale markets can be bypassed by sales to local consumers.

Products are brought from fishing sites by the fishers themselves or their representatives, by traders who go from site to site, or by wholesalers. The means of locomotion used are generally large pinnaces, lorries, or vans.

The circuits between fishing sites and wholesale markets are short and require few intermediaries, whereas redistribution to retail markets requires the participation of a large number of intermediaries.

Fish that is not consumed fresh is processed using traditional or modern techniques that are designed to retard the natural process of decomposition and thereby increase shelf life. It is in effect necessary for fish to be processed for storage in one way or another when fishing takes place in areas that are poorly accessible or located far away from major trading and consumer centres.

In some cases, when the road network is sufficiently developed and the country is likely to acquire the needed facilities, it is possible to use cold rooms to preserve fish that are then transported in refrigerated lorries or on ice. Marine fish are in fact most often traded in this form in inland areas.

In Africa, however, a large proportion of fish must be processed for marketing because of inadequate road infrastructure. Moreover, in a continental setting, it is rare for fishing pirogues to be equipped with isothermic crates containing ice. Depending on the length of fishing expeditions, it becomes necessary to process fish as soon as it reaches the site. In these cases, fishers resort to traditional techniques of fish processing.

Drying is one of the most common techniques in Africa. The simplest method is sun-drying. Once fish are gutted and opened, they are placed on mats or grills, or hung on drying racks. This type of traditional processing is efficient in a dry climate, but nonetheless leaves fish vulnerable to insect attacks. For pelagic species of lesser market value, sun-drying is often done directly on the ground, exposing products to all sorts of contaminants carried by dust, insects, and sand. Fish lose three-quarters of their weight.

Drying is often associated with smoking. This consists of partially eliminating the water contained in the fish while imparting a flavour that is obtained when smoke is absorbed by the flesh. However, despite it being the main artisanal processing method in most African countries, smoking is often badly performed: fish are sometimes charred on the surface, badly smoked, and shelf life is short. Many studies have been carried out with moderate success to improve smoking methods and conditions (GRET, 1993). The FAO in particular has improved the *chorkor* oven and encouraged its spread, and it has been accepted by women fish processers. Finished products have a better golden colour and quality than those processed using traditional round ovens. Smoking in the Sahelian area is also responsible for deforestation and in current conditions, it is becoming increasingly difficult to find the wood needed for this type of processing. Women often use dried cow dung. After smoking, fish lose two-thirds of their weight.

The technique of burning can also be used, although it is rarer than the two previous ones. Fish are laid out on a layer of dry grass or rice stalks which is then set on fire.

Salting is a proven effective technique that has not met with much success, probably because of costs but also of dietary habit.

Processed fish are often treated with chemical products (K'Othrine or Gardona) to stave off deterioration by mould or ichtyophagous insects. However, because of the fish storage time (several months depending on distance from trading centres), losses can be as high as 20% of total production (Coulibaly *et al.*, 1992).

The choice of processing method partly depends on the species. In the Sahel area, species that are preferably smoked are the *Clarias* as well as many species of the Bagridae and Claroteidae families (*Chrysichthys*, *Bagrus*, *Auchenoglanis*), *Synodontis,* and *Labeo*. Species that are exclusively dried are the Alestidae except for *Brycinus leuciscus* which is used to produce oil, the *Citharinus,* and the Mormyridae. Those that are preferably dried belong to the Schilbeidae family. Certain species, such as *Lates* or tilapias, are either smoked or dried. In this case, the method selected depends on situational factors such as price or demand.

Empirical models for evaluating the fishing potential

It is difficult to collect fisheries statistics in a continental setting because of the nature of fisheries themselves: use of a large variety of fishing gears, significant annual and inter-annual fishing effort and captures depending especially on hydrology, extensive scattering of fishing points and loading sites, highly variable individual strategies and behaviour of fishers. For these reasons, which are compounded by the lack of training for personnel in charge of fisheries management, we have little reliable data on fishing statistics in African continental waters (and more specifically the large riverine systems). Obtaining more reliable figures will require the definition of clear methodologies, better personnel training, and more organized collection of statistical data and information processing. Such a data-gathering system is, in principle, quite compatible with the means available to fisheries authorities, as long as basic funding is provided for.

Given the aforementioned difficulties, several scientists think that rather than seeking to improve the collection of fishing statistics for a given system, it is a more useful exercise to focus on the research and development of even just rough empirical models that would make it possible to predict the fishing potential of an aquatic system based on simple ecological parameters. According to Rigler (1982), an empirical theory's purpose is to generate forecasts based on a comparative approach of different systems. An empirical model should make it possible to predict complex biological effects from simple ecological parameters. Given a variable that we wish to predict, we try to establish correlations between this variable and other ecological variables or combinations thereof.

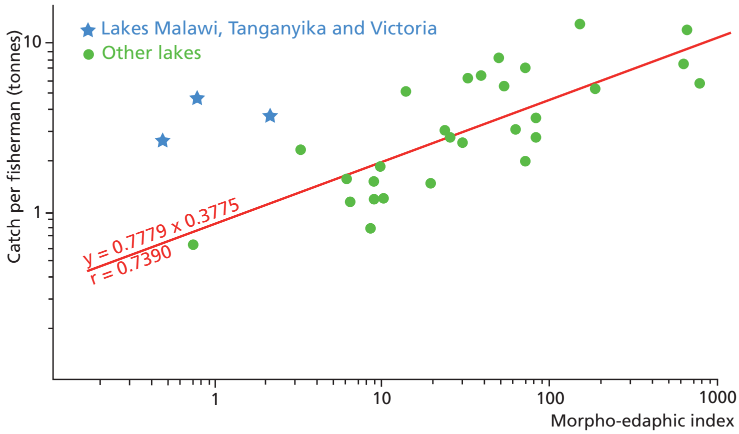
One of the first empirical approaches was to establish a relationship between fish production in a lake and its average depth (Rawson, 1952). This rather simplistic yet interesting approach led to a series of studies afterwards.

Henderson & Welcomme (1974) calculated, for 31 African lakes whose level of exploitation is close to maximum, a relationship of the type:

$$P = 14.3136\ MEI^{0.4681}$$

Where MEI (morpho-edaphic index) is a synthetic index corresponding to the ratio of water conductivity expressed in $\mu S\ cm^{-1}$ by average depth expressed in metres (figure 25.8).

FIGURE 25.8.
Relationship between the morpho-edaphic index and catch per fisherman in 31 African lakes (from Henderson & Welcomme, 1974).



This model was later modified by Toews & Griffith (1979) who introduced lake area (A in km^2):

$$P = 1.4071 + 0.3697 \log MEI - 0.00004565\ A$$

Later, Schlessinger & Regier (1982) proposed an estimation model of the maximum sustainable fishing production (P) based on a multiple regression involving annual average air temperature (T in°C), and the morpho-edaphic index (MEI) which is dissolved salt content divided by average depth:

$$\log P = 0.0236 + 0.280 \log MEI + 0.050T$$

For rivers with no large floodplains, and based on a data series, Welcomme (1985) calculated for Africa an empirical model of fish production (P in tonnes) based on the area of the river's drainage basin (A in km^2):

$$P = 0.03\ A\ 0.97\ (r = 0.91)$$

If we replace the basin area by the length of the principal channel (L in km), we obtain:

$$P = 0.0032\ L^{1.98}\ (r = 0.90);\ \text{or approximately: } P\ (\text{in kg}) = L^2 / 300$$

Laë (1997) showed that these empirical models were highly imprecise when used for a predictive purpose (table 25.IX). The use of abiotic data for 65 African lakes shows that adjustments with previous models making use of the morpho-edaphic index and yields (not statistically significant), the total area and total captures ($R^2 = 0.76$), or fishing effort and yields (not statistically significant) are quite inexact and insufficiently reliable for predicting potential captures. The confidence interval of estimates can vary from a relationship of between 1 and 10 whereas on average, African lakes have yields of between 50 and 200 kg/ha/year.

Relationships using yields and lake latitude or altitude do not render statistically significant results. Those that use average depth, surface area, or volume are significant, but only account for a small percentage of variance (respectively 13, 11 and 17%). The morpho-edaphic index remains the least poor parameter ($r^2 = 0.42$) when fishing effort is greater than 2 fishers per km^2. The search for empirical relationships must be conducted from complete and reliable databases. This type of approach has been the target of many attempts in countries of the North (Cyr & Peters, 1996; Havens *et al.*, 1996; Persson *et al.*, 1996; Mavuti *et al.*, 1996; Bachmann *et al.*, 1996). In Africa, the data needed for this type of modelling are not currently available and it is urgent to remedy the situation by establishing permanent fisheries observatories. These should make use of several models, including physico-chemical and hydrological monitoring, as the estimation of primary production is a complement to regular, structured information on the biological, economic, and social components of fishing. This step is necessary for the comprehension of the ecosystems and the fisheries-system under investigation. Under no circumstances can they be replaced by the use of empirical relationships, even if the reliability of the latter were to improve, if the ultimate goal is fisheries management.

Explanatory variable	Value of the explanatory variable	Expected yield	Confidence interval 95%
		(kg/ha)	(kg/ha)
MEI (Henderson & Welcomme) (µS/cm)	6.3	32	7 - 126
	39.8	74	23 - 282
	158.5	144	36 - 1000
		(tonnes)	(tonnes)
Surface (Crull) (km^2)	10	70	18 - 271
	100	585	152 - 2 253
	1 000	4 908	1 264 - 19 055
	10 000	41 523	10 441 - 165 214

TABLE 25.IX.
Confidence intervals of expected yields computed with models of Henderson & Welcomme (1974) and Crul (1992), (from Laë, 1997).

Expected yields and their confidence intervals are provided for different values of the explanatory variables. These intervals are very large: between 36 and 1,000 kg/ha for an expected yield of 144 kg/ha, between 10,441 and 165,214 tonnes for expected total captures of 41,523 tonnes.

Fisheries management

The term "management", now often accompanied by the adjective "sustainable", means that we are no longer content to simply extract a given amount of an exploitable resource, but that we are also concerned about the long-term maintenance of the resource in question. Fish is a renewable resource for fisheries, but it may run out if its exploitation is not controlled by implementing a number of regulations.

Fisheries management at the basin scale

Continental fisheries management must be designed within a larger context of drainage basin water management. Water is put to diverse uses: household use, irrigation, energy in particular which leads to occasionally significant changes in the appearance and function of aquatic systems. Dams create new types of systems while interrupting upstream-downstream connections. Water withdrawals for dams or irrigation modify river currents and the annual flood cycle. Sometimes they can even interrupt the flood cycle entirely, as is the case in the lower Nile valley.

Water management for agricultural use and energy generation has long been given priority over other uses of water. In particular, the many interventions carried out on African continental aquatic systems rarely took into account the biological resource represented by fish. Consequences on fish populations and fisheries are mixed. On one hand, the disappearance of floodzones led to the rarefaction of certain species that use these physical systems to breed. Meanwhile, the creation of reservoir lakes has made it possible to develop populations of other fish species, whose exploitation can underlie new fisheries, without necessarily compensating, qualitatively or quantitatively, for losses suffered downstream.

The future of continental fishers is tightly bound up with the choices made in terms of hydrosystem management. Depending on the preferred goals or the technical choices made, live resources will either obtain or be deprived of the conditions for their maintenance or development.

Fisheries models

Most continental fisheries are either artisanal or subsistence fisheries, which makes their management particularly complex. In the 1950s and 1960s, in a bid to implement rational stock management, there was an attempt to use stock management models developed for maritime fishers to the management of continental fish stocks. At the time, fish biologists believed that the fishing activity-resource interaction was measurable and manageable.

In this context, fisheries is viewed as a biomass extraction industry, which can result in the depletion of this biomass (overexploitation) if the pressure on stocks increases with little consideration. The intervention of a manager is thus necessary to regulate this predator-prey relationship. To do so requires measurable indicators such as fishing effort and total catches, and management tools such as halieutic models postulating that the size of the future population can be determined from information on the biological characteristics of the exploited stock and the extent of exploitation (Schaefer, 1954; Beverton & Holt, 1957; Ricker, 1954). Two types of models were developed: global models which established empirical relationships between the exploitation rate and overall production, and analytical models which analyse the effects induced in the demographic structure of the resource by changes in its mode of exploitation.

These models, and in particular the principles from which they were established, are not suited to continental waters. We now know that they make use of two debatable assumptions:

- the assumption that it would be possible to manage wild animal populations by simply regulating the exploitation rate of the said populations;
- the presumption of an equilibrium state of exploited populations, which assumes that the environment has a negligible influence on the dynamics of the resource.

In fact, the same criticisms emerged for the management of fisheries in marine environments (Rothschild, 1989). Much work then focused on the variability of marine populations (Bakun, 1989), the deciding factors for recruitment (Lasker, 1989), or the variability, instability, and changes in pelagic marine fisheries (Cury & Roy, 1991). These models nonetheless remain difficult to use in a continental context because:

- fisheries is studied as a whole and covers a large number of species (around 50 for example in the Niger) that do not all have the same behaviour, biologically speaking or with regard to fisheries;
- generally, they only take into account the direct impact of resource exploitation on stock, but not the indirect impact resulting for the natural variability of the ecosystem and its consequences in terms of resource fluctuation;
- they are totally inapplicable in many countries, given the difficulties encountered for gathering information: global models require long data series on effort and total captures, and these are rarely available in developing countries. Analytical models, meanwhile, require biological data on the different exploited species (growth, reproduction, natural mortality, etc.) as well as fisheries data (capture by fishing gears and corresponding size structures, fishing mortality, etc.), which are often difficult to gather given the number of species involved;
- these models ignore the motivations and strategies of fisheries stakeholders.

Even aside from these models, the proposed solutions for improving fisheries conditions often depend on reducing fishing effort or modifying it (increasing mesh size, banning certain gears) that would initially lead to a decrease in captures. It is thus very difficult to implement decisions that run counter to the immediate interests of fishers. Although laws have been passed on the nature and size of fishing gears or the start of fishing season, they are not enforced owing to a lack of means (personnel, transport, etc.) to the point that fishers are not always informed of their existence (Thomas *et al.*, 1993).

While the concept of maximum sustainable yield has been largely contested, it *de facto* remains high on the list of preoccupations of managers attempting to make plans in terms of fisheries development. Yet many observations have shown that the influence of environmental factors often carries the greatest weight. Inter-annual variability can be considerable, and is often tied to hydrological variability which itself is difficult to predict from one year to another.

However, the exploitation of natural resources has ramped up considerably over the last two centuries, sometimes exceeding their regenerative capacities and leading to changes in ecosystems. In this context, estuary and lagoon ecosystems have been hit especially hard, as they are at the convergence of demographic, economic, and ecological pressures. Given the deterioration of habitats, the overexploitation of resources, climate change, and an overall increase in natural and anthropogenic constraints, we are experiencing a catastrophic collapse in biodiversity even though it is a key factor in the resiliency of these living systems. One of the options under consideration to combat biodiversity loss in aquatic environments consists of establishing Protected Areas.

Marine Protected Areas (MPA)

In this context, a Marine Protected Area (MPA) is defined as "an area within or adjacent to the marine environment, together with its overlying waters and associated flora, fauna, and historical and cultural features, which has been reserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings" (Kelleher, 1992). Following initial experiments with establishing MPA, there has been great enthusiasm for this approach whose applications should multiply in coming years.

In the field of biology, research has concentrated on MPA as instruments for halieutic management (Sanchirico, 2000), showing that they may serve as a means for protecting and even increasing the income of fishers when fishing pressure is high.

From this point of view, MPA are a major tool for the protection of habitats essential to breeding and the growth of juvenile ecophases (Gell & Roberts 2003). They can play a dominant role in biodiversity conservation (figure 25.9). Their effectiveness for halieutic purposes is based on the following hypotheses:

- Effects inside the MPA: the suspension of fishing in the MPA and the preservation of habitats lead to a drop in natural mortality and fishing mortality, and an improvement in growth and reproduction. All these phenomena work together to produce a significant increase in biomass (Lester *et al.* 2009).
- Effects outside the MPA: the increase in biomass within the MPA leads to greater competition between the individuals present, pushing part of the community to leave the MPA. In addition, aside from these density problems,

the biological cycle of some species which cannot breed in estuary areas is the reason for ontogenic migrations and the departure of pre-adult individuals that join the marine environment (Harmelin-Vivien *et al.* 2008).

- Effects at the ecosystems level: the displacement of eggs, larvae, the departure of juvenile or adult stages depending on the species may have beneficial effects in areas located far from the MPA (Nowlis & Roberts, 1999; Claudet, 2006).

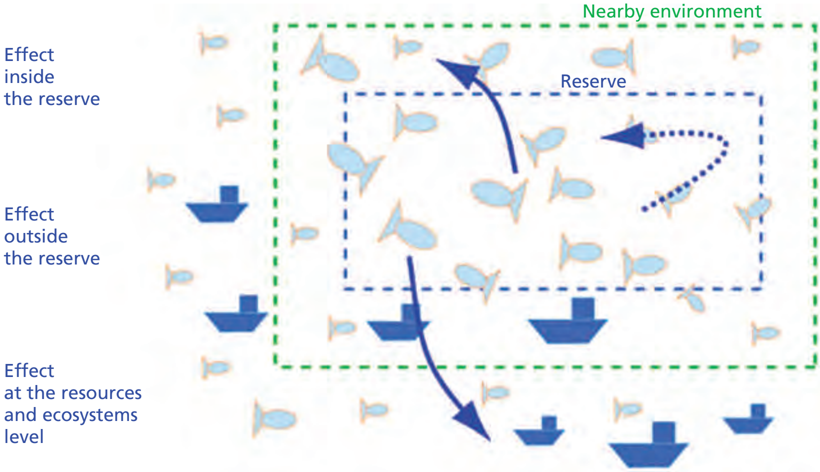


FIGURE 25.9.
Expected effects after the creation of a marine protected area (from Henichart & Gascuel, 2011)

While these different effects appear logical, at this stage many hypotheses still need to be verified, in particular the speed at which such processes are established as well as the time needed for an MPA to mature.

Hence, as part of the AMPHORE project (2008-2011) designed to test MPA as tools for biodiversity conservation and sustainable management of halieutic resources, monitoring was carried out in the Bamboung bolon (channel), located in the estuary of the Sine Saloum in Senegal. There, waters are shallow and the area is highly biodiverse, particularly for birds, fishes, and marine mammals (dolphins and manatees). Fishing has been banned there since 2004 (Breuil 2011) but remains very active in the rest of the estuary and on the maritime front. A number of changes have been observed in the reserve (Écoutin *et al.*, 2013; Écoutin *et al.*, 2014; Laë *et al.* 2015):

- increase in the number of species present,
- increase in the percentage of large and/or emblematic and highly sought after species,
- modification in the community structure characterized by:

– more small fish

– more large fish (new large fish species and/or larger individuals in species already present)

– fewer midsized fishes

- change in trophic structure (greater percentage of predators),

- change in the community in terms of representation of different ecological categories,
- no significant increase in total biomass in the MPA.

While some indicators suggest that the creation of the Bamboung MPA has had a positive effect, this is not an obvious conclusion on the scale of the community as a whole for the 2004-2011 period. At this scale, only four indicators provide positive information on the fishing ban: the average trophic level and three indicators describing the evolution of maximum sizes and the presence of large individuals. These observations appear to be confirmed by trophodynamic modelling (Colleter *et al.*, 2012) which yields relatively constant biomass before and after a fishing ban, but an increase in the number of predators by a factor of 2.5 and a drop in the number of their prey by a factor of 1.7, illustrating the MPA's role as a refuge zone or a "pantry" zone for some predator species. These observations were also made in the OSMOSE model (Brochier *et al.*, 2013) which shows relative stability in biomasses but a sharp change in populations within the MPA leading to an increase in trophic level and an estimated spillover of 30% of interior biomass. These results explain the change in CPUE outside the MPA and matches similar observations showing an increase in the biomass of some target species in the area adjacent to the reserve, leading to a concentration in fishing effort in the bordering zone (Alcala *et al.*, 2005; Russ & Alcala, 1996; Russ *et al.*, 2003 and 2004; Goñi *et al.*, 2008).

Finally, the coastal area is strongly influenced by the presence of essential habitats such as estuaries, rias, lagoons, grass patches, and mangroves, all of which contribute to the conservation and renewal of a resource containing at least one ecophase that is bound to the interfacing physical systems. The spatial distribution of a resource composed of migrating species which cross borders and the mobility of users, particularly fishermen, thus makes it necessary to consider conservation and management measures at the regional level. This was the case in West Africa, with the establishment in 1996 of a coastal planning regional network. A Regional Strategy for the MPA in West Africa was developed on 2002 and based on the creation of a coherent MPA network in West Africa, managed in a participative manner by strong institutions, that put natural and cultural diversity to work in contributing to the region's sustainable development. Hence, in Mauritania, Senegal, Cape Verde, Gambia, Guinea-Bissau and Guinea, a substantial proportion of habitats that are critical for the reproduction of renewable natural resources or act as significant sites for biodiversity currently enjoy protected status. In the wake of these initial measures, the concept of MPA networks is often put forward to improve the protection and management of aquatic ecosystems (Hansen, 2003) with the creation of environmental corridors to ensure the protection of the most sensitive ecophases. The MPA regional network in West Africa (RAMPAO) was created in 2007 to ensure, at the marine ecoregion level for West Africa, the maintenance of a coherent set of critical habitats necessary for the dynamic function of ecological processes that are necessary for the regeneration of natural resources and the conservation of biodiversity in the service of society.

At the international level, by 2020, 10% of marine and coastal zones should either be designated as protected areas or have conservation measures applied to them. The notion of efficiency seems to be a priority of the strategic plan, as the conservation measures should be in place and protected areas managed effectively (Bonnin *et al.*, 2015).

In summary, the goals of MPA are (Claudet & Pelletier, 2004):

- To conserve and protect natural resources in areas that are important for ecological diversity.
- To restore altered or overexploited areas that are considered indispensable for the survival of species or that play a significant role in the life cycle of economically important species.
- To improve the relationships between humans, their environment, and economic activities while maintaining traditional practices and the balanced exploitation of resources, by protecting them from outside activities that are harmful to MPAs and by protecting and managing historical, cultural, and aesthetic sites.
- To improve fish yields by protecting breeding stocks, encouraging the dissemination of recruited and post-recruited stages in adjacent spaces, restoring the age structure of natural populations, and acting as a safeguard against the mismanagement of exploited areas.
- To resolve past and present conflicts between users of coastal areas.
- To improve the state of knowledge of the marine environment by promoting research and awareness-building for stakeholders.
- To assess the value of these ecosystems for local authorities through tourist and economic activities that are profitable for residents.

Social environment and fisheries management

To understand the dynamics of fisheries, it is necessary to take the social dimensions of fishing into account. Fishing strategies developed by fishermen change according to the socio-economic context, and the conditions for access to resources have changed drastically over the past few decades.

Fishing in the African continent is practiced by different groups of individuals with different degrees of investment in both equipment and activity in their fishing practices. Several investigations in the West African lagoons (Laë, 1992a) or in river-floodplain systems (Laë & Morand, 1994) have shown that three modes of behaviour can be distinguished schematically. In practice few groups are exclusively devoted to fishing. Most of these cases involve migrant fishermen that are very well-equipped and specialized, and whose main strategy is to go to where fish are found to capture them. In the majority of cases, fishing and farming are complementary activities and many sedentary fishermen split their time between the two. Some are also traders.

The organization and management of continental fishing has evolved along similar lines over the 20th century in many regions of Africa. The broad lines of such progress can be described schematically.

In the early part of the century, customs and lineage-based rights codified access to fishing areas and resources. Modes of fishing, mostly collective (such as fishing weirs) required significant manpower.

FISHERMEN TYPOLOGY

Around Lake Togo, three distinct classes emerge in fishermen typology (Laë, 1992a):

- A group practicing fishing regularly throughout the year.
These "professional" fishermen for whom fishing is the primary activity use sophisticated gear (gillnets and longlines) that require solid experience and relatively heavy investments in relation to their revenues.
- A second group appears to limit fishing activity to the wet season and flood season. There is less pronounced specialization in fishing gear.
These "seasonal" fishermen are also farmers and modulate their fishing activities according to their agricultural activities and fishing yields.
- A third group comprises fishermen whose activities are minimal or sporadic throughout the year, and the most commonly used fishing gear is the cast net.
Fishing is only a supplementary activity for this group which includes farmers, civil servants, students, and so on.

Towards the middle of the century and the technological advances that were made, individual fishing gears began spreading: gillnets, cast nets, longlines, etc. Fishing became a source of profit and speculation. Production increased with the diversification of captured species and a reduction in the size of captures.

As countries achieved independence in the early 1960s, the state replaced traditional rights. Under the influence of western ideas, there was much talk of rational resource management, which implied a regulatory arsenal, good knowledge of stocks, and the means to apply and control regulations. In practice, the state lacked the means to perform this role, which led to many conflicts between fishermen and fierce competition for access to the resource. The system often led to fragile compromises between the fishermen and the new masters of the water embodied by representatives of the public authorities, and such compromises were regularly called into question.

To illustrate these changes in the modes of resource management, let us take two examples that were the object of well-documented studies: the Central Delta of the Niger River in Mali (Quensière, 1994) and the coastal lagoons of Côte d'Ivoire (Durand *et al.*, 1994).

Case study: the Central Delta of the Niger River

The management of waters and fishing among the Bozo (group of Malian fishers) has been the subject of much investigation (Daget, 1949; 1956; Gallais, 1967; Fay, 1994) owing to the multiple technical and social modes of fishing.

The so-called traditional mode of water management is based on the alliance made by the founding ancestor of a community of fisherfolk with divinities or "genies" of the water, an alliance that allowed the group to fish under the aegis of the "water master", the eldest of the founder's descendants. Each year, this water master renewed the initial pact with the genies through a series of appropriate sacrifices, and established the general conditions of fishing (date of large-scale collective fishing, suspension of fishing, bans of fishing in certain areas, etc.). Some fishing was granted to all members of a given group, within the bounds of the authorized fishing periods. Some fisheries, such as weirs, came under a collective lineage-based appropriation. A third of the production was turned over to the owners of the fishery by outsiders who wanted to fish there, a proportion that was referred to as "the water's share" among the Bozo (Daget, 1956; Fay, 1994).

In traditional fishing rights, the resource is not shared, as uncaptured fish belongs to no one (Daget, 1956). Rights are granted for fisheries exploiting, at certain moments of the hydrological cycle, specific aquatic systems with a given set of fishing gears. "Traditional" access to fisheries was thus not generally free, but was based on lineage.

From the time of colonization to independence, the monetarization of the sector would push fishermen to increase yields, even in defiance of traditional regulations, and the appearance of new fishing gears would lead to migrations, the arrival of new stakeholders, and a technological differentiation between groups according to their means of financial investment. Between 1935 and 1950, cotton lines appeared, then nylon, then netting, cast nets, lines with steel hooks, etc. which would lead to a fishing boom. In about twenty years, fishing production tripled and became one of the main sources of revenue. In 1963, the Malian state proclaimed its sovereignty over the waters and declared traditional regulations illegal. Access to waters was officially "open", and determined by the acquisition of a fishing permit as from 1975. In practice, the resource now belonged to the state which was its sole proprietor. It distributed temporary exploitation rights as it deemed fit. These rights authorized the use of one or several fishing gears and/or the access to a portion of fishing territory. Such a management style would require a knowledge of stock status and the application of measures to limit fishing as decided by the managing authorities. However, in the absence of a service tasked with tracking the evolution of resources, and suitable legislation for regulating fishing, the spirit of the law was not respected. It would have also been necessary to create a body of officials in charge of inspecting fishing practices and sanctioning infractions. This type of inspection becomes merely hypothetical and expensive when the fishing in question involves large, poorly accessible areas, as is the case for the Central Delta.

In the early 1970s, the state attempted to establish the rules for rational management, based on a technological approach of the solutions that needed to be implemented, with the help of input from international experts. It reaffirmed its sovereignty over all continental waters, made regulations regarding gears stricter, and created fisheries councils and committees. These were composed of administrative officers and representatives of fishermen, and their role was to manage conflicts. Meanwhile, laws also granted residents use rights, which conferred legitimacy but also led to territorial conflicts and disagreements with migrant fishermen. The arrival of a drought in the early 1970s would lead to the stepping up of administrative inspections.

In 1986 then 1995, new fisheries legislation was put in place, representing an important step forward in opening fisheries management to fishing communities. This was intended to promote decentralized management of halieutic resources. In this framework, the national piscicole domain was divided into three distinct domains placed under the authority of the state (public waters), decentralized territorial communities (hydraulic or piscicultural arrangements made by the community), and individuals (arrangements of their property). The new legislation reflected a desire to protect halieutic resources, including initiatives from professional categories other than fishermen. Its new provisions made it possible to establish sustainable management of fishers by a vision of planning that favoured ecological management as well as by giving a sense of responsibility and agency to the future decentralized territorial communities. Nonetheless, it shows some gaps (Breuil & Quensière, 1995):

- each entity responsible for a halieutic area was tasked with adopting measures to protect the resource, but the law did not provide any general rule for management that would allow local communities to orient the measures that they need to take;

- in terms of the environment, the law stated a few general principles but did not take into account the full scale of the function of productive hydrosystems, whereas the conservation of halieutic species cannot be entirely carried out at the local level.

Aside from the mode of management, it must also be noted that fishing pressure has increased considerably in the Central Delta of the Niger over the past thirty years (increase in population, progress in fishing techniques and gears) and that this trend has been compounded by the shrinkage of water spaces. Confronted with the same problems, traditional authorities would probably have encountered the same difficulties as the Malian state. The survival of the fishing sector depends on controlling fishing pressure, which is extremely difficult to do in traditional societies that replicate themselves. This will no doubt be a major challenge for decentralized management.

History of fisheries management in Côte d'Ivoire lagoons

The history of halieutic exploitation of the lagoon systems in Côte d'Ivoire also illustrates the transformation of relationships between societies and their environments since the start of the 20th century. Forms of access to the field, to different fishing techniques, to certain sites or spaces, and consequently, to the resource itself, vary and combine differently depending on the period (Verdeaux, 1994). Three configurations have succeeded each other chronologically since the early 1900s (table 25.X).

Before 1930

Up to the early 20th century, organization of fishing around the Aby lagoon (Côte d'Ivoire) was handled by lineage-based authority. This authority mandated and imposed rules regulating fishing activities and ensured, partly to its

Fishing gear	**before 1910**	**1910-1914**	**1935-1950**	**1960-1967**	**1970-1975**	**1979-1982**
Fixed fisheries	**rainy season**		**gradual abandonment**		**disappeared**	
beach seine (ali)						
length (m)	60	150	300-600	800-1000	800-1200	800-1200
mesh size (mm)	50	40	40 puis 25	14	14	14
width (m)	1.5	2	4.5	6 à 12	12	12
“syndicat”						
length (m)			100-150	250-300	400-500	400-500
mesh size (mm)			20-25	14	14	14
width (m)			10	15		12
purse seine						
length (m)					400-650	500-650
mesh size (mm)					14	14
width (m)					15-20	15-20
Individual gears	**dry season**		**all seasons**		**‘sardine’ net**	

TABLE 25.X.
History
of the management
of fisheries
and the fishing gear
used in the Aby
lagoon, Côte d’Ivoire
(from Verdeaux,
1994).

benefit, control of the environment (Perrot, 1989). The effectiveness of the regulation was guaranteed by religious faith; breaking it was tantamount to violating the prohibitions of the lineage’s protective genie. Indeed, the area was ruled by a pantheon of “genies” that guarded access and guaranteed productivity, and it was necessary to seek their intercession in order to fish. Each main lineage had special relationships with local genies whose influence generally extended to a shoal on which a fixed fishery was established. The elder of the line was the favoured interlocutor with this genie, and the group of “relatives” for which he served as interpreter respected the precepts and prohibitions of the divinity (Verdeaux, 1994). By domesticating the power of genies, appropriation procedures could be controlled.

During this historical period, we can distinguish, in the course of a year, two major periods in terms of the intensity of fishing activity and the types of social cooperation or techniques that came into play. The main fishing season began with the main rainy season (May), and ended at the end of the minor rainy season (October-November). The panoply of fishing techniques was used, though with a preponderance of fixed traps built collectively by the lineage or the villages. In the 19th and early 20th centuries, fisheries were characterized by the use of fixed gears, such as the *atterre*, a vegetable barrier that formed labyrinths from which fishes could not escape. Some of these could be hundreds of metres long, requiring for their construction and handling considerable manpower and, consequently, forms of cooperation that required the input of entire lineages and even villages. During the main dry season from November to April, halieutic activity was reduced, with a preponderance of individual and selective techniques: traps, hollow woods, longlines and cast nets. The prohibition of access to fixed fisheries from October to May the following year was a means of encouraging the renewal of stock. In case of infractions, sanctions were severe and acted as deterrents.

The shift from one period to another was marked by religious manifestations. In May, priests and chiefs of the lineage solemnly closed the "door of the genies" and in October, they "opened their door", inaugurating the cycle of celebrations and sacrifices related to the beliefs of the lineage (Verdeaux, 1986; 1994). In one of the villages of the Ébrié lagoon, according to popular belief, the "whale" genie nestled against the bottom of the lagoon kept fishes in its belly until the opening ceremony of the fishing season in late April to early May. Thanks to these offerings, the genie would then be attracted to the surface, thus freeing the fishes that it had kept captive during the dry season. Only then could the main fishing season begin.

Aside from the explicit attribution of fixed sites for fisheries, the spatial and seasonal combination of different techniques made it possible to determine, at the lagoon level, the spaces and territories that could be exploited by different groups — villages, clans, lineages. This partly symbolic distribution had the advantage of controlling and limiting the most predatory techniques and codifying access during the main fishing season.

From 1930 to 1960

In the 1930s and up to the 1960s, large fixed fisheries (*atterre*) gradually disappeared, to be replaced by other types of fishing gears. The "*ali*" net introduced shortly before the first World War was small and originally handled by two men. Fishing was done close to the shore or on shoals by surrounding a small area. The dimensions of the "*ali*" net gradually increased and gave way to beach seines that spread in the lagoon in the mid-1930s. This type of gear was preferred over fixed traps as it was more profitable and could be used for several seasons. Morever, fishing gears became more diverse with the adoption of a series of gillnets and lines that could be used throughout the year. This period was thus marked by the shift from the passive mode of controlled access to the fishing area, mainly owing to fixed fisheries, to a direct and active access to the resource with the development of beach seines and new gears. In particular, the proliferation of gillnets occurred with the importation of cotton lines at the instigation of the authorities.

Simultaneously, we witnessed a transformation in trade circuits. Fishing became a lucrative activity that allowed urban centres to be supplied. In addition, authorities introduced territorial organization, and the lagoon became a strategic point with the definition of village territorial waters.

From 1960 to 1982

Starting in the 1960s, an increase in the size of beach seines can be seen, with some reaching over a kilometre in length and supplanting the traditional "*ali*" net. Another type of fishing mode appeared: the "syndicate net", a purse seine used in open water rather than near the shore, hunting mainly pelagic species such as bonga shad. It is operated by associations of fishermen (hence the name) that form each year during bonga shad season, then break apart afterwards.

Broadly speaking, the evolution of fishing techniques during this period is marked by the transition of fishing for demersals (bottom fish) to pelagic fish (especially

FISHERIES IN BENIN (BASED ON PLIYA, 1980)

In Benin, prior to the colonial period, access to water and fishing was controlled by religious authorities, and lakes were the joint property of villagers.
There were many prohibitions, religious beliefs, and local customs that forbade access to certain areas or banned the use of some types of fishing gears.
These protected areas, often sacred sites, were important locally for fish reproduction.
Societies had thus developed a number of mechanisms that led to a balanced use of the shared resource.

During the colonial period up to the Second World War, changes in social structures contributed to weakening traditional authority in favour of the central administration. But the Water and Forests service did not put new legislation in place, and traditional rules were gradually transgressed.
This led to the chaotic development of fishing that rapidly resulted in overexploitation and conflicts.

Between the Second World War and the country's independence, there were various attempts to improve the role of the Fisheries service, which added to the weakening of traditional authorities and control of access to shared resources.
By the late 1970s there was no control at all.
With the accumulation of conflicts, fishermen proposed a reinstatement of traditional management methods, but the government paid no heed to these proposals.

bonga shad) as dominant target species (Verdeaux, 1990). In the 1960s, seine mesh diminished in stages, making it possible to catch other species and new size classes. As seines were no longer selective and their number increased, this ended up in a competition with the captures of individual gears.

This led to a first crisis in 1969, known as the "war of nets", with several coastal villages in the lagoon refusing to grant fishing rights to seines. After the intervention of authorities, seines were limited to the territorial waters of villages willing to accept them. Nonetheless, by the end of the 1970s, seines accounted for three-quarters of captures. Seines did not always follow regulations, and the unfavourable bioclimatic conditions of the early 1980s contributed to a collapse of halieutic resources. Numerous incidents took place between seine fishers and individual fishers who felt dispossessed as a result of the disappearance of their basic resource, building up to a major crisis in 1982. Several villages demanded a ban on seines, and after several – sometimes violent – incidents, this measure was approved by the administration in 1985. This decision was a departure from a type of relationship with the system that had ended up being reduced to a dynamic of competing for stocks. Free access to the system that was initially obtained by individual fishermen morphed little by little into the cornering of the sector by economic groups who were able to fund seines.

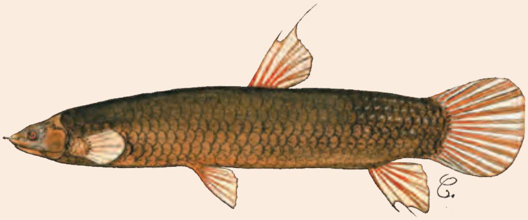
The crisis in the 1980s shone a light on the state's inability to serve justice in the public realm. Introduction of a domanial system was accompanied by free access to the environment, initially well-received by individual fishers. But such free access rapidly turned into differential access to the resource (Verdeaux, 1994). This thus led in 1985 to a situation that was similar, but not comparable, to the one prevailing in the early part of the century: regulation of access to the resource by controlling access to the environment.

Conclusions

For a long time, fishing in Africa was simply an activity that consisted of removing a portion of a natural resource that was controlled as best as could be by traditional practices or the adoption of the western method of centralized management. Demographic pressure as well as the consequences of anthropogenic activity gradually changed the original situation. Unfortunate practices, such as the pouring of large quantities of insecticides into a river to capture fish, developed in many countries.

It seems likely that the exploitation of natural fish stocks has reached its peak in Africa. The increase of catches, in fishing statistics, is often the result of better data on captures rather than the discovery or exploitation of new resources. In these conditions we can predict that, in the absence of proactive measures that are always difficult to apply in countries where fishing is an important component of local economies, captures will stagnate or even fall in the coming years. One of the major issues at stake is without a doubt finding the right balance between the participation of local societies and that of the state in the sustainable management of water resources and live resources.

Fish culture



JEAN-FRANÇOIS AGNÈSE

RANDALL BRUMMETT

MARC LEGENDRE

CHRISTIAN LÉVÊQUE

Although Egyptians were rearing the tilapia *Oreochromis niloticus* in artificial ponds nearly 4,000 years ago, the African continent, unlike Asia, has no tradition of fish culture. In the early twentieth century, aquaculture was still virtually unknown there. The first attempts to develop it date back to the 1940s.

These initial attempts were part of a broader goal to diversify the sources of animal protein in order to promote the food self-sufficiency of rural populations. When pilot tests with tilapia at the Kipopo station created in 1949 in the former Belgian Congo yielded promising results, colonial administrators proceeded with expanding these activities. By the end of the 1960s, there were a number of such research/demonstration stations dotted across the continent: Djoumouna (Congo), Landjia (Central African Republic), Foumban (Cameroon), Bouaké (Côte d'Ivoire), Sagana (Kenya), Anamalazaotra & Ampamaherana (Madagascar), Kanjasi (Uganda), Chilanga (Zambia), Henderson (Zimbabwe), and Domasi (Malawi).

The first tests conducted at these stations involved species that have now been abandoned because of poor yields: *Coptodon zillii, Coptodon rendalli, Sarotherodon galilaeus, Oreochromis mossambicus* and *Oreochromis macrochir*. It took until the 1970s for breeders to take notice of the zootechnical performance of *Oreochromis niloticus* and its hybrids with various neighbouring species, as they far outclassed that of most other tilapias. It was also during this time that other species with fish culture potential began to be identified: *O. aureus, O. andersonii, Sarotherodon melanotheron*, the African sharptooth catfish (*Clarias gariepinus*), the African boneytongue (*Heterotis niloticus*) and the alien common carp (*Cyprinus carpio*).

Despite massive aid to promote fish farming in Africa to mirror the Asian example, results were disappointing. In 2013, estimated aquaculture production was only 1.4 million tonnes for sub-Saharan Africa whereas global production stood at 66.6 million tonnes (FAO, 2014).

Following the FAO report (FAO, 2014) the sub-Saharan Africa region continues to be a minor player in aquaculture despite its natural potential. Even aquaculture of tilapia, which is native to the continent, has not developed significantly. Nigeria leads in the region, with reported production of 278,000 tonnes of catfish, tilapia and other freshwater fishes (source: FishStat Plus). In North Africa, Egypt is by far the dominant country in terms of production (providing 943,000 tonnes) and is now the second biggest tilapia producer after China and the world's top producer of mullets.

Although it is very difficult to obtain reliable figures for actual production, in a context where the trade of aquatic products is often done informally, we are just beginning to realize, in the early 21st century, the continent's vast potential for aquaculture development.

Two reviews (Moehl *et al*. 2006; Brummett *et al.* 2008) distinguished between several types of fish culture on the basis of development criteria: extensive, artisanal, small/medium-scale commercial and large-scale commercial. All categories of aquaculture have the potential to be profitable and sustainable but it is necessary to evaluate which category must be promoted or assessed against the overall objectives defined for this sector.

Different types of African fish culture

Extensive aquaculture

All over the continent, rural communities utilize waterbodies, either temporarily or permanently, for fish production. Often, this simply involves the periodic capture of wild fish, but increasingly, productivity is being enhanced through the use of stocking or other aquaculture practices. In the Guinea rainforests, for example, controlled stocking of small dams (2,000-10,000 m^2) with or without fertilization is being used to increase typical background productivity of normally no more than 100 kg/ha up to between 600 and 2,500 kg/ha/y (APDRA-F, 2007) (see box "Extensive fish culture in the Guinea forest region: a model of integrated development and of rice-fish production"). In the Lower Shire River valley of Malawi, local communities stock otherwise fishless temporary waterbodies, locally known as thamandas, with fingerling tilapias and catfishes, producing an average of 600 kg/ha (range 300-1,575 kg/ha) in a 2-3 month growing season (Chikafumbwa *et al.*, 1998). Acadjas have been used for centuries in West and Central Africa for attracting and nourishing fish (see box "Acadjas").

In Burkina Faso, traditional reservoir management systems have evolved in the direction of restocking after annual drying with fingerlings of *Oreochromis niloticus, Labeo coubie* and/or *Clarias gariepinus* produced through artificial reproduction of adults captured at harvest and held over the dry season (Baijot

EXTENSIVE FISH CULTURE IN THE GUINEA FOREST REGION: A MODEL OF INTEGRATED DEVELOPMENT AND OF RICE-FISH PRODUCTION

Highly developed in Asia, rice-fish production is almost inexistent in Africa.
It consists of farming rice and fish in the same rice fields.

While it often produces small fish, rizi-pisciculture nonetheless remains interesting because it can achieve adequate volumes (1000 kg/ha/y) at a low cost, even if they do not approach yields obtained from intensive production, which can be 10 to 20 times greater.

This practice still allows a farmer to diversify production without expanding the cultivated area while increasing protein production.

In the early 2000s, the IRD (French National Research Institute for Sustainable Development) and the MPA (Ministère des Pêches et de l'Aquaculture of Guinea) conducted an experiment with the SOGUIPAH (SOciété GUInéene de PAlmier à huile et d'Hévéa) in order to establish an extensive tilapia (mainly *Oreochromis niloticus*)/rice production system that could be easily adopted by farmers (Extensive pisciculture in Forested Guinea in the region of N'Zérékoré, south-eastern Guinea). The programme's ultimate goal was, obviously, to make the production system rapidly autonomous.

The fish stocking of rice fields requires the production of fry first of all. For an untrained farmer, mastering the simultaneous problems of fry production and fish fattening represented a difficulty that was compounded by the length of the full cycle from birth to harvest, 13 months on average, which is much too long.

The strategy adopted for the programme was thus to split the processes into two parts: the production of fry, a task entrusted to women, and the fattening of fish in the rice field, carried out by the farmers.

Fry production was carried out by plotting out non-cultivated sections in the rice fields, where breeding stock would be placed, in general 50 males and 100 females for 400 m^2. The fry produced naturally enter the areas planted with rice for food and shelter.
After four months, the fry are harvested and transferred to their fattening site.
This last stage takes 6 months, a period similar to other agricultural activities.

This activity creates a non-negligible additional income for farmers as it brings in 1000 euros/ha/year on average. This project led to an agricultural activity that is sustained in the N'Zérékoré region. It received support in 2008 from the French Embassy (amounting to 3 million euros) and continues to be supported by NGOs including APDRA (Association Pisciculture et Développement Rural en Afrique tropicale humide).

"ACADJAS"

The term "acadja" refers to a fishing technique practised in the lagoons of Benin and a few other West African lagoons (Pliya, 1980).
It is an artificial reef wherein arrangements of branches are placed in shallow waters, where they encourage the development of epiphytes and microorganisms and increase natural productivity.
The acadja also provides shelter to juveniles of several species, notably lagoonal cichlids.

An estimated 30 to 40 tonnes of branches are needed to construct a hectare of acadja (Welcomme, 1972b), and annual renewal is 50% as the wood is attacked by shipworms.
This has a non-negligible impact on surrounding terrestrial vegetation.

The "acadja-enclos" is a fish farming method derived from traditional acadja fisheries, in which the branches are replaced by bamboos planted vertically in lagoon sediment.
Fish stocking with *Sarotherodon melanotheron* tilapia may be natural or artificial, and production can reach 3 to 8 tonnes per hectare per year in the Ébrié lagoon, with no food supplements needed (Hem & Avit, 1994 ; Hem *et al.*, 1994).

et al., 1994), increasing productivity from 50-100 kg/ha/y up to over 600 kg/ha/y. In Niger, natural temporary waterbodies stocked with *C. gariepinus* can produce up to 200 kg/ha/y depending on rainfall, returning an average of $1,400 per person per year to the fish farmers/fishermen involved in their management (Doray *et al.*, 2002). In Southern and Eastern Africa, there were between 50,000 and 100,000 small dams producing between 1 and 3 million tonnes of fish per year, most of which is consumed by rural communities (Haight, 1994).

These types of decentralized fish production systems could have broad applicability across Africa's vast dry savannah area, including all or parts of virtually every African country. While such extensive aquaculture may not be the most productive in terms of fish output, the additional benefits of water table replenishment, flooding, and erosion control and possibilities for multiple uses such as livestock watering, irrigation, and capture fisheries could return substantial benefits to local communities and help in the fight against desertification (Roggeri, 1995), if ownership and management arrangements can be negotiated among the various and sometimes disparate user-groups.

Artisanal farming systems

Over 90% of African fish farmers operate one or a few earthen ponds of generally less than 500 m^2 in surface area, constructed and operated with family labour (King, 1993). These ponds typically produce between 300-1000 kg/ha (15-50 kg per crop), on an annual harvest cycle usually corresponding to fingerling availability, water supply or local demand. About half of the output from these systems is consumed by the family and half sold or bartered to neighbours. Little of the crop is sold for cash, either due to lack of access to wealthier markets or out of a need to meet more local food security priorities (Brummett, 2000). In these systems, the fishpond plays a role similar to that of the chicken coops, pigsties, fruit tree orchards, herb gardens and other micro-enterprises undertaken by smallholders to generate small amount of cash for emergencies, school fees, etc. (Satia *et al.*, 1992).

Few of the inputs for artisanal aquaculture are purchased, productivity being based almost entirely on composts, manures and other organic materials found on the farm and recycled through the pond. The best fish productivity in such systems in Malawi, where they have been intensively studied, is about 1,500 kg/ha/y, mostly of small tilapias (Brummett & Noble, 1995). These "farmponds" are generally integrated into other food production systems such as vegetable gardens where they serve as sources of emergency irrigation water and as bio-processors for by-products and wastes, turning low quality materials into valuable fish at minimal cost. In Malawi, farms with integrated fishponds produce almost six times the cash generated by the typical smallholder (Brummett & Noble, 1995). Similar systems exist throughout the continent, producing thousands of tonnes of fish annually for rural families.

Diversifying a smallholding by integrating aquaculture can also affect the ecological sustainability and economic durability of small farms. In Malawi, a serious drought from 1991 through 1995 had a major negative impact on smallholding agriculture. Yet in all cases studied, even though staple crops failed and farmers lost money, the integrated fishpond sustained the farm. By retaining water on the land, ponds enabled farmers to continue food production and balance economic losses on seasonal cropland. For example, in the 1993/94 season, when only 60% of normal rain fell, average net cash income to integrated farms was 18% higher than to non-integrated farms (Brummett & Chikafumbwa, 1995).

In areas with high population pressure, integrated aquaculture systems can help keep people alive and on the land producing food for themselves and their communities. However, as they generate minimal cash revenues and therefore no liquid capital for reinvestment and expansion, especially the purchase of inputs, they create little or no economic growth (Delgado *et al.*, 1998).

Small and medium-scale enterprises (SME)

Many of the more entrepreneurial farmers have seen the potential to diversify their traditional cash-crop investments (coffee, tea, cacao, bananas, etc.) by shifting some capital out of these traditional cash-crops to aquaculture. These farmers build more ponds, use higher technology, employ hired labour, purchase fingerlings and/or inputs (esp. feeds and/or fertilizers) and understand the concept of cash-flow. Rather than eat or give their fish away, they transport them to a town or city where wealthier consumers pay cash. The main difference, however, between SME and artisanal farmers is motivation; artisanal farmers primarily seek food security and farm diversification, while SME farmers seek cash, often at the expense of diversity and, sometimes, sustainability (Brummett *et al.*, 2005).

SME exploitations are subject to the plethora of social leveling mechanisms common in rural African communities and are usually obliged to sacrifice a percentage of their production (±30% in Cameroon according to Brummett *et al.* (2005)) to maintain their position in local society and minimize the threat of theft and/or sabotage (Harrison *et al.*, 1994). Other constraints include high transportation costs (for farmers distant from wealthier urban markets) and the lack of marketing infrastructure, especially ice plants and clean facilities, which limit the ability of producers to negotiate decent prices as fish start to decay towards the end of the day (Brummett, 2000).

In South Africa, the SME segment of aquaculture sector is relatively well-developed. The Aquaculture Association of Southern Africa (www.aasa-aqua.co.za) produces a newsletter and holds regular meetings funded by a growing number of secondary beneficiaries of aquaculture development, including banks, feed mills and processing plants.

Aquaculture SMEs are also expanding in Nigeria where over 2,000 farms with an estimated 60,000 ha under water produce 25-30,000 TPA (AIFP, 2004), mostly of sharptooth catfish, which are highly prized in the Nigerian market (Moehl, 2003). According to the farmers, this remarkable growth was achieved with virtually no support from the Nigerian national aquaculture research and extension services.

Even more recently, small and medium-scale aquaculture investments have been growing in Cameroon, Ghana, Uganda, Angola, DR Congo, Zambia and Kenya. Once a node of (mostly French) donor-assisted SME development, Côte d'Ivoire has, since the coup d'état in 2000, reverted to mostly artisanal production.

In general, however, SMEs have received little attention from African governments and even less from international donors, as they are not perceived to represent "the poor".

Large scale commercial

There are a few successful large-scale, commercial aquaculture investments in Africa, most notably in Tanzania (racks, seaweeds, export), Mozambique (ponds, shrimp, export), Zambia (ponds, tilapia, local markets), Zimbabwe (cages, tilapia, export), Ghana (cages, tilapia, local markets) with new investments coming on line in Uganda (cages, tilapia, export) and Kenya (cages, tilapia, local markets). Most of these have been built using foreign or foreign-earned capital and rely on foreign or foreign-trained technical expertise. Although all are not yet at full capacity, these farms each have planned production in excess of 1,000 TPA (Tonnes Production per Annum) and are targeting markets in larger African cities and/or the ever-growing international tilapia trade. All are vertically integrated to one extent or another, including feed manufacture, fingerling production, selective breeding programs, processing plants, retail sales outlets (local and overseas) in addition to production facilities.

Currently dominating this sector are cage-based tilapia systems using modified[1] Scandinavian salmon cage technology, most notably in Volta Lake and Lake Kariba. The largest of these is Lake Harvest, Ltd. based in Kariba, Zimbabwe where 3,000 TPA of 750 g tilapia are grown in 500 m^3 cages at a density of 50 kg/m^3. The company owns a state of the art processing plant which produces fresh fillets for air shipment to luxury markets in Europe.

Most African governments welcome large-scale aquaculture investments as employers, foreign exchange earners and, for those targeting local markets, fish suppliers. Access to land and water resources is generally good and most environmental regulatory bodies have been willing to negotiate permits. On the downside, aquaculture production systems are not highly labour-intensive, requiring between 0.05 and 0.1 person-year per tonne of fish produced. While this may be an important incentive for producers, maximizing the economic growth potential of aquaculture will require that governments interested in rural poverty alleviation encourage the development of an horizontally integrated aquaculture industry where technical assistance providers, feed growers and manufacturers, equipment and input suppliers and marketing chains create additional employment and business opportunities.

Ecological intensification and IMTA (Integrated Multi Trophic Aquaculture)

There are many definitions for the concept of ecological intensification (Dugué *et al.*, 2012) but it can be summarized as the use of natural mechanisms or ecological processes to increase production while using fewer inputs.

Sustainable intensification is also used sometimes (FAO, 2011), as compromises have to be made between increased short-term production while maintaining the productive capacities of socio-agro-ecosystems in the long term. These environmental and production goals are defined so that they can be managed sustainably over time.

NOTE 1

[1] For example, the use of special netting material that can resist the teeth of the predatory tiger fish, *Hydrocynus vittatus*.

Among ecological intensification systems, the one most heavily-researched and applied is undoubtedly IMTA (Integrated Multi Trophic Aquaculture).

In intensive aquaculture, large quantities of food are poured into the farms. This leads to the release of significant amounts of organic matter, either from the production of wastes by farmed animals or from the unconsumed food. The resulting pollution is harmful to the farmed animals themselves or to the environment (eutrophication).

With IMTA, wastes are recycled by one or several associated productions. For instance, intensive aquaculture produces nitrogen-containing waste that encourage the growth of aquatic plants. These plants are in turn consumed by herbivorous fishes.

Species used for intensive fish culture

Aquaculture production in sub-Saharan Africa essentially relies on two groups of native species – tilapias (187,625 tonnes in 2014, FAO statistics, 2015) and catfish (248,000 tonnes) – as well as introduced species, including carp (29,803 tonnes). Tilapias were used in the earliest aquaculture experiments in Africa, mainly in the Democratic Republic of the Congo and in Congo, primarily because they bred easily in captivity. Later, different species were tested to determine their aquaculture potential. In the Central African Republic in the early 1970s, the strong aquaculture potential of the catfish *Clarias gariepinus* was identified and extensive research was carried out on the species. In the 1980s, other species with good aquaculture potential were identified, notably in Côte d'Ivoire, based on their appeal to consumers and their zootechnical performance. The life cycle of some of these species has now been fully mastered, making it possible to start farming them.

Tilapia *s.l.*

Tilapia, which include the three genera *Oreochromis*, *Sarotherodon* and *Tilapia*, are without a doubt the most popular African species in terms of aquaculture. *Oreochromis niloticus* was one of the first to be cultured and remains the most common species (see box "Tilapia or 'aquatic chicken'"). Many other species have also been used: *O. andersonii*, *O. aureus, O. macrochir, O. mossambicus, Coptodon rendalli, T. guineensis, Sarotherodon melanotheron*. The latter, frequently found in West African estuarine and lagoonal systems, seems to be particularly suited to farming in brackish waters.

Clarias

The main culture species at present are *C. gariepinus* (by far the most widely cultured) and to a lesser degree, *C. anguillaris* and *C. ngamensis* in Africa, with a few others bred for the aquarium trade, most notably the Namibian endemic blind cave catfish, *C. cavernicola*.

The only two members of the subgenus Clarias, *C. anguillaris* and *C. gariepinus* are very similar (Rognon *et al.*, 1998; Teugels, 1998; Teugels, 2003). Agnèse *et al.*

TILAPIA OR "AQUATIC CHICKEN"

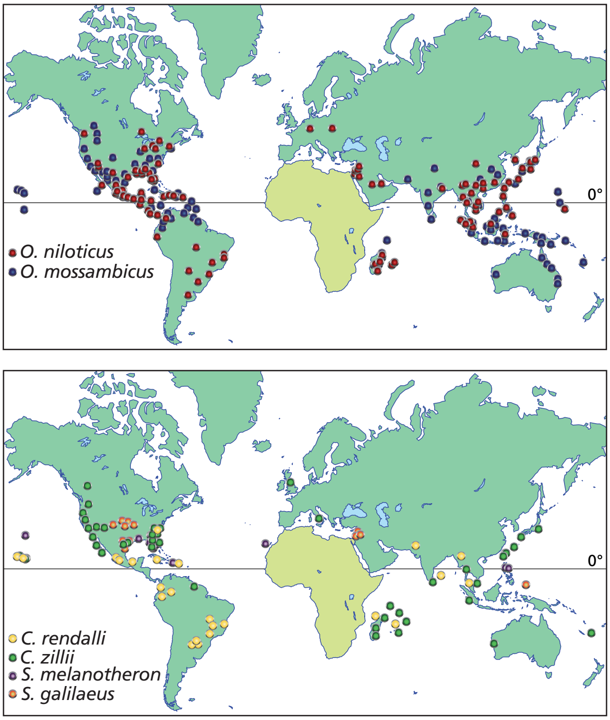
Many of these species are now found throughout the world, either because they were introduced into natural systems to improve fisheries or because they were used for aquaculture (figure 26.1). Global aquaculture production of tilapia has increased considerably over the past ten years and was estimated at nearly 4,466,000 tonnes in 2014, 95% of which was *Oreochromis* (FAO statistics, 2015).

Paradoxically, African fish farming only represents 5% (234,000 tonnes) of global tilapia production, even though these species are originally from Africa which hence represents the genetic reservoir for aquaculture carried out on other continents.

The bulk of global production is currently in Asia (3,813,000 tonnes, *i.e.*, 85% of the global tilapia production).

FIGURE 26.1.

Introduction of tilapias s.l. outside Africa (data from GBIF, 2015).



(1997) found some evidence that *C. anguillaris* and *C. gariepinus* in the Senegal River hybridize naturally under certain conditions. Possibly due to the relatively restricted natural distribution of *C. anguillaris* in the Nile and West Africa, *C. gariepinus* is the more widely studied and cultured of the two.

Other indigenous species

One of the merits of determining which native species may be of interest for aquaculture is that it highlights neglected and unfamiliar species that have good aquaculture potential (Legendre, 1992; Lazard & Legendre, 1994).

In addition to the genus *Clarias*, there are three other Clariidae genera that are of at least some potential interest and have been tested in aquaculture. The endemic *Bathyclarias* species flock in Lake Malawi (ten or so species) ranges in size from 60-135 cm and has been tried in ponds in Malawi (Msiska *et al.*, 1991). *Gymnallabes typus*, native to the lower course and delta of the Niger River and Cross River basin in Nigeria and Cameroon has been tested as an alternative to eels in trials in the Netherlands (Teugels & Gourène, 1998).

Reaching over 1 m in length and 55 kg in weight (Skelton, 1993), the non-*Clarias* Clariid that has received the most attention from fish farmers and is actually produced in a number of African countries is *Heterobranchus longifilis*. Otémé *et al.* (1996) report that, under optimum conditions, *H. longifilis* grows twice as fast as *C. gariepinus*. This species is found throughout Africa in the Nile, Niger, Senegal, Congo, Gambia, Benue, Volta and Zambezi River systems as well as all the coastal basins from Guinea to Nigeria, and in Lakes Tanganyika, Edward and Chad.

Chrysischthys nigrodigitatus was also a promising catfish species, reaching more than 60 cm and extremely appreciated in many countries. Even though the farming cycle of this species has been fully mastered since the 1980s (Otémé *et al.*, 1996), its culture has never become widespread owing probably to the combination of several factors, including sexual maturity achieved only after 3 years at least, a relatively short reproductive season (only 3 or 4 months a year), and slow growth rate. It takes a year on average to obtain fish weighing 350 g. Nigeria had an annual production of 600 tonnes in 1993 (Coche, 1994). More recent studies no longer mention it (Ozigbo *et al.*, 2014)

The African bonytongue (*Heterotis niloticus*) presents many favourable characteristics for aquaculture, a remarkably high growth rate, air-breathing characteristic, omnivorous diet and a very good market potential. Fish exceeds 500 g within four months and a mean body mass of 3 up to 4 kg can be reached within a twelve-month cycle (Monentcham *et al.*, 2009). Despite that, production remains relatively low. It stood at 5,000 tonnes in 2013 (FAO statistics) of which 3,900 were produced in Nigeria.

Alien species

From the history of introductions and the development of successful aquaculture elsewhere, it appears that the use of exotic species to speed up the rate of aquaculture development in Africa is unlikely to be an efficacious strategy. The major sustained aquaculture industries worldwide evolved from close working relationships between pioneering investors and local research-and-development institutions. The use of indigenous species avoids many environmental risks, facilitates broodstock and hatchery management at the farm level, and can increase the effectiveness of selective breeding programs. Public-sector involvement in the domestication and marketing of indigenous species can strengthen research, development, and education; broaden the range of investors; create more jobs; and increase the social benefits accruing as a result of aquaculture development.

Despite the abundance and diversity of Cyprinidae in African inland waters, no indigenous species has been truly domesticated to date. There were however several attempts to introduce Asian cyprinids such as the common carp (*Cyprinus carpio*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*), and grass carp (*Ctenopharyngodon idella*). The common carp was thus first introduced in Madagascar then disseminated to about ten other countries including Kenya, Ethiopia, Cameroon, Malawi, Côte d'Ivoire, and Nigeria.

Control of reproduction

The supply of fry to fish farms still represents a bottleneck for many species of aquaculture interest that do not reproduce spontaneously in captivity. In the majority of cases, gonads develop normally in farmed fish, but final maturation of oocytes, ovulation, and spawning do not occur.

Collecting juveniles in the natural environment is an alternative that can help overcome this obstacle. However, this method has many disadvantages: inter-annual variability of catches, risk of mixing several species of unequal performance, and no possibility of genetic improvement. It is thus generally desirable, if not necessary, to do without natural resources and fully master the production of fry from captive breeders. This implies providing fish with the environmental stimuli needed for ovulation, or triggering the process using hormonal treatments.

Reproduction is controlled by the hypothalamic-pituitary-gonadal axis (Legendre & Jalabert, 1988; Goos & Richter, 1996). In species that achieve gonadal maturity but do not reproduce spontaneously in captivity, hormones needed for gametogenesis are produced in sufficient quantities. However, final maturation of oocytes, ovulation, and spawning do not take place because the peak in the release of gonadotropin (GTH) from the pituitary gland, needed to complete the process, does not occur. Downstream, at gonadal level, the release of gonadotropin that precedes ovulation triggers follicle cells to synthesize a steroid that induces oocyte maturation (17 α-hydroxy-20 β-dihydroprogesterone). Upstream, the release of gonadotropin by the pituitary is positively controlled by GnRH (Gonadotropin-Releasing Hormone) secreted by the hypothalamus and negatively controlled by dopamine. These hypothalamic controls are in turn dependent on environmental factors that are interpreted by the central nervous system.

In aquaculture, it is possible to trigger oocyte maturation and ovulation by intervening at different levels of this axis. This can be done by working on external factors and providing fishes with the stimuli needed for spawning (presence of specific spawning substrate, for instance) or by using various hormonal treatments. Depending on the species and methods used to trigger ovulation, eggs are obtained from either natural spawning or from gamete collection through abdominal massage of the breeders followed by artificial fertilization.

In *Clarias gariepinus*, which reproduces in the natural environment during the rainy season as waters rise, spawning in captivity can be triggered by simulating the flood. This is done by placing sexually mature breeders in a pool that is refilled after a drying-out period.

The use of hormonal induction techniques for oocyte maturation and ovulation, followed by artificial fertilization, are often preferred as they allow greater control of all the phases of reproduction and larval rearing (Legendre *et al.*, 1996). Moreover, they allow gamete conservation and various genetic manipulations, such as interspecies hybridization, gynogenesis, or polyploidy induction. These techniques nonetheless require the availability of qualified personnel and well-equipped hatcheries.

Sex control

Given that in Cichlidae, for example, males grow faster than females, it is advantageous to obtain monosex male populations that have better growth rates. This also offers the benefit of avoiding unwanted reproduction. Initially, selection was done manually after the appearance of the urogenital papilla, but this technique can only be used for fishes weighing around 20 to 50 grams. Moreover there is a non-negligible risk of error. A solution to limit the consequences of the latter is to associate a predator fish with the tilapia that will eat the fry that may be produced during the fattening phase. This combination of methods – manual sexing and predator-tilapia association – is deemed efficient and still remains in widest use in the context of artisanal African aquaculture, as it is the simplest to implement (Lazard, 1990b).

We can also consider hormonal sex inversion, and the masculinization of an alevin population by incorporating a synthetic steroid (17 a-methyltestosterone) in food (Baroiller & Jalabert, 1989). This method also offers the advantage of no longer requiring the elimination of the female half of juvenile stock, unlike manual sexing. The relatively empirical approach taken up to that point led rapidly to the adoption of masculinization treatments that are 100% effective, now used on a large scale in Asia. But questions have been raised regarding the fate of the breakdown products of the masculinizing hormone in animals intended for human consumption, as well as their potential ecological consequences. A possible solution lies in the use of natural hormones involved in the process of sexual differentiation, such as 11 b-hydroxy-androstenedione whose masculinizing efficiency has been demonstrated in *O. niloticus* (Baroiller & Toguyeni, 1996).

Genetic methods for sex control – gynogenesis, androgenesis, or interspecific hybridization – have also been used to produce monosex lines. Hybridization is presented later in this chapter. The principle of gynogenesis, in which only the female's genetic material participates in the development of the embryo, is as follows: oocytes are fertilized using irradiated spermatozoa. This does not prevent the spermatozoon from penetrating the egg cell and triggering its development, but destroys its DNA, thus eliminating any paternal genetic contribution. The normal diploid state of the embryo is then restored using chemical treatments or physical assaults (temperature, pressure) that block the first cell division. The principle of androgenesis is very similar, but in this case female genetic material is destroyed by irradiating oocytes. The two types of lines, gynogenetic and androgenetic, have been produced in *Clarias gariepinus* at the experimental scale (Volckaert *et al.*, 1994; Bongers *et al.*, 1995).

Food

In aquaculture systems, many investigations have studied the use of raw or compound feeds, formulated from agricultural and agro-industrial by-products available in tropical areas (Jauncey & Ross, 1982). Available data on the nutritional needs of African species remain limited and are especially focused on protein and energy requirements, and on the optimal protein/energy ratio in the rations. For tilapia juveniles, dietary protein requirements appear to be around 35% of raw protein regardless of species and dietary behaviour in the natural environment (Luquet, 1990). Among the Clariidae, optimal growth is obtained using feed containing 35 to 50% of raw protein. When taking into account the rations at which feed is distributed, this corresponds to an absolute requirement of 15 to 20 g of raw protein per kg of fish and per day, with a protein/energy ratio of 20 to 30 mg of protein per kJ of digestible energy (Wilson & Moreau, 1996).

In addition to the composition of dietary formulae, the different means of distribution of compound feeds (food ration, frequency, feeding period, food presentation) must also be taken into consideration as they can have a significant influence on nutritional efficiency and growth. For instance, in *H. longifilis*, the same dietary formula is used much more efficiently by the fish when it is distributed as pellets rather than in powder form (Kerdchuen, 1992). In this species, a very notable increase in growth is obtained when fishes are fed continuously rather than a series of meals. Feed distribution at night also yielded better results than when the fishes are fed by day (Kerdchuen & Legendre, 1991). Conversely, the tilapia *O. niloticus* is a diurnal species in which feeding essentially takes place during daytime (Toguyeni, 1996).

In some species, larvae do not yet have fully developed digestive tracts at the time of the first feed, and have specific behavioural and dietary requirements that are different from those of juveniles and adults. This is the case of *Clarias gariepinus* or *Heterobranchus longifilis* in particular. For these fishes, good growth and survival results have been obtained in hatcheries by feeding larvae with *Artemia* (a small crustacean) nauplii as their first food. But more independent resources must be sought in the context of many African countries where such prey must be imported. In this sense, the use of locally available zooplanktonic prey may address this need, whether they are produced in associated farms or used *in situ* in fishponds. To be effective, the latter method would require the use of fine-meshed cages to protect larvae from predators, and extensive knowledge and good control of the pond ecosystem (Legendre, 1992). Recently, progress has been made in identifying artificial feeds adapted to the specific dietary needs of larvae. The use of a compound feed based on yeasts and beef liver thus made it possible to achieve a high survival rate in *H. longifilis* (Kerdchuen, 1992 ; Kerdchuen & Legendre, 1994). But growth is still inferior to that attained with *Artemia* or zooplankton, indicating that the dietary needs are still not fully covered.

Fish farming structures

Aquaculture is highly flexible and adaptable to a wide range of environments, markets and investment levels from small ponds that produce a few kg of fish for home consumption up to high density raceways or cages that can carry hundreds of kg per m^3.

Ponds are the cheapest and simplest systems to build and manage, the main problem being that they must be sited in areas where the soil is heavy enough to hold water and the topography has enough slope to permit complete draining without the use of expensive pumping.[2] Ponds also take up a lot of space as their carrying capacity seldom reaches 1 kg per m^2, being limited by the ability of the natural ecosystem to produce oxygen and absorb metabolic wastes. On the other hand, fish growing in the more or less natural environment of ponds are at relatively reduced risk of stress and disease and if properly fed can grow efficiently on a combination of low-value inputs and natural foods.

NOTE 2
Depending upon land value and/or water supply it can be cost-effective to use plastic liners in areas where pond construction would otherwise be impossible.

Raceways are round or elongate, usually built of cement with water flow-through or recirculation through a biofilter to add/replace oxygen and remove metabolic wastes. Raceways take up less space than ponds, are easy to harvest and can carry as much as 100 kg/m^3 of *O. niloticus* (Watanabe *et al.*, 2002; Ridha *et al.*, 2001) or 400 kg per m^3 of *C. gariepinus* (Hecht *et al.*, 1996). However, they are expensive to build and require electricity and/or a high volume of water, although most of the water is of good quality at the outfall and can be used for other purposes. Because there are no natural foods in raceways, the fish must be fed a complete diet. In addition, the artificial environment creates the potential for disease and mechanical damage to fish living in cramped quarters.

Recirculating systems are normally based on raceway technology with a filtration system installed to remove nitrogenous wastes, add oxygen and cycle the water back to the fish. These systems are very popular in areas close to big cities where land and water are scarce and expensive. They are, however, complicated and expensive to build and operate and even short electricity failures can result in disaster. Also, being unnatural environments, the fish face the same constraints as in raceways, including the need for a complete diet.

Most of these problems have been overcome in the SARI system (Système Aquacole à Recyclage Intégral: Fish Farming System with Complete Recycling). This recirculating system has been first dedicated to the black chinned tilapia *S. melanotheron* kept in brackish water. Fish excrements fertilize water and help the phytoplankton to grow (green algae). Zooplankton feed on this phytoplankton and is, in turn, eaten by juveniles of *S. melanotheron*. This system saves 2/3 of aliment incomes, 9/10 of usual water intake, and produces no waste water. A prototype build in 2013 was still functioning in 2015 (figure 26.2).

Cages come in many shapes and sizes depending upon the availability of materials, the type of water body into which they are installed, and the amount of money available to invest. The number of cages that can be installed in any given water body depends upon depth, water current, and wind velocity, all of which contribute to the circulation of water through the cage. Fish in cages lack access to most natural foods, so production depends upon the provision of a complete pelleted diet. Cages are easy to harvest and are modular so that the system can be scaled up as the farmer gains experience and the market grows.

In smaller water bodies, cages have a big advantage over capture fisheries in terms of resource utilization. Instead of having a mixed flock of different species and ages, caged fish are all in one place so they can be easily fed and

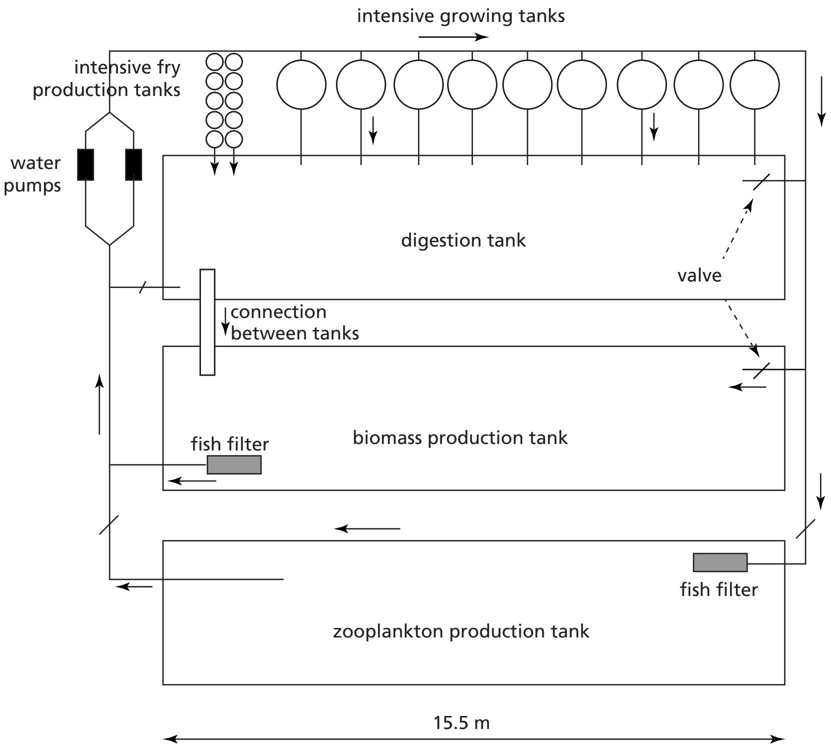


FIGURE 26.2.
The SARI prototype plan. The digestion tank ensures the complete degradation of organic effluent; the biomass production tank is dedicated for continuous supply of phytoplankton; the zooplankton production tank operates as regulator of phytoplankton biomass and for production of zooplankton biomass (from Gilles & Blancheton, 2010).

managed. The highest natural productivity of small water bodies is no more than 300 kg/ha. The same water body used for fed cages would be at least 3 tonnes per hectare.

All food production systems require water and conflicts over access to increasingly scarce resources are creating conflict in almost all African countries. Although plants provide more food per litre of water than animals, animals provide higher quality protein. Among animals, fish are by far the most efficient energy users. Channel catfish (*Ictalurus punctatus*), for example, gain 0.85 g of weight for every gram of feed consumed, compared to 0.48 g in chickens, the most efficient warm-blooded animal, and 0.13 in beef cattle (Lovell, 1989). Fish production, being conducted entirely underwater, would seem to be potentially one of the greater water consumers. However, consumptive use of water by aquaculture is, in theory, negligible. Also, aquaculture has the advantage over rain-fed plant crops by being somewhat disconnected from rainfall periodicity. Through the use of recirculation technology and/or integration of cage aquaculture into other water use schemes, consumptive use of water can be reduced even further to the amount lost to evaporation and leakage, which in water-stressed areas are often controlled with the use of plastic liners and/or greenhouse-like covers.

Tilapia culture in ponds is growing rapidly and typically produces standing crops of 5-6 tonnes per hectare with a consumptive water use of about 2,800 l/kg of fish produced, including the amount needed for feed production[3] (Brummett, 1997), less than the 3,500 l/kg required for broiler chickens (Piemental *et al.*, 1997). Lazard (2002) reported production of up to 15 tonnes/ha/y of tilapia in static water ponds in Côte d'Ivoire. In South Africa, pond-based flow-through systems can produce *C. gariepinus* standing stocks of up to 40 tonnes/ha/8 months with a water exchange rate of 2-6 l/sec/ha, equivalent to 3,600 l/kg. Overall, commercial freshwater aquaculture probably uses something on the order of 5,000 l of water per kg of fish produced, although most of this use is non-consumptive, being either directly usable for other purposes or indirectly usable following settling or biofiltration to remove excessive nutrients and/or suspended solids.

NOTE 3
Producing the feed used by commercial fish growers requires approximately 1.54 million liters of water to produce 1 tonne of fish food, containing 48% soybean meal and 41% corn meal (Lovell, 1989).

Genetic manipulations and fish culture

Selecting high-performance genotypes

In aquaculture, the goal is to produce fish of a tradable size as quickly as possible. To do so, there has been an attempt to select the most efficient strains, and one of the possible ways is through genetic improvement which consists of replacing a population composed of certain genotypes by other genotypes that perform better in an aquaculture setting. Such selection programmes have been carried out successfully for temperate species such as trout, but are still in preliminary stages for African species. That said, a number of tilapia farms are beginning to apply the principles of quantitative genetics. The GIFT (Genetic Improvement of Farmed Tilapia) programme conducted by ICLARM, for instance, consists of collecting different tilapia strains and evaluating their growth characteristics in different environments (see box "The GIFT Tilapia").

There have also been attempts to modify species performance artificially by trying to obtain advantageous characteristics through the production of hybrids or other genetic manipulations such as polyploidy induction.

Polyploidy is a condition in which individuals have extra sets of chromosomes. An individual normally possesses two sets of chromosomes in its cells and is referred to as diploid. Triploidy affects individuals with 3 sets of chromosomes; those with 4 sets are called tetraploid. These two situations can be obtained in fish by subjecting fertilized eggs to thermal shock or high pressure, or by chemical treatment. Triploid individuals are sterile and, in theory, the energy absorbed through food, which would not be used for gonadal development or reproduction, would instead be available for greater somatic growth. Moreover, the nuclei of polyploid cells are bigger than those of diploid cells and, in some species, the cell's cytoplasmic volume increases proportionally. In some cases this therefore results in larger cells and an overall increase in body size. In *Clarias gariepinus*, triploids have been obtained by subjecting eggs to cold shocks (Henken *et al.*, 1987). No difference in growth or efficiency in nutrient use was observed between diploid and triploid *Clarias,* but the amount of flesh remaining after evisceration was noticeably greater.

THE GIFT TILAPIA

The GIFT Tilapia was selected in the Philippines in 1988 by ICLARM (the International Center for Living Aquatic Resources Management), now the WorldFish Center, the BFAR (Philippines Bureau of Fisheries and Aquatic Resources, the FAC-CLSU (Freshwater Aquaculture Center of the Central Luzon State University, the UPMSI (Marine Science Institute of the University of the Philippines), and the Institute of Aquaculture Research, Ltd., in Norway (Ansah *et al.*, 2014).

Wild Nile tilapia germplasm from Egypt, (Nile Delta), Ghana (Volta), Senegal (Senegal) and Kenya (Lake Turkana) were collected together with four commercial Nile tilapia strains from the Philippines (three strains originated from Ghana, and one stock originated from Egypt).

The best-performing purebred and crossbred groups were selected, based on their growth performance, in order to build a stock with a broad genetic base. This constituted the original GIFT strain on which selective programs have been applied.

Rapidly the GIFT strain resulted in body weight up to 58% higher than "non-GIFT" strains on "average" farms in Asia where it has been disseminated (Bangladesh, People's Republic of China, Philippines, Thailand, and Vietnam).

In 1999, a Norwegian company got an exclusive agreement for the long-term continuation of the GIFT breeding programme. DNA marker-assisted selection has been applied in order to increase the selection differential that resulted in gains of 10%-15% per generation over more than six generations.

The outcome of the GIFT project generated interest from developing countries not only in Asia but also in Africa.

An expert consultation in 2002 in Nairobi confirmed the policy of the WorldFish Center not to introduce the GIFT strain into countries where *O. niloticus* is indigenous, mainly because interbreeding of the GIFT strain with locally-adapted native populations might compromise wild aquatic genetic diversity.

Instead, the WorldFish Center decided to help African countries to apply the GIFT methodology to the genetic improvement of indigenous tilapias in Cote d'Ivoire, Egypt, Ghana and Malawi.

But it is quite a paradox that the African continent whence originated tilapia benefits the least from the GIFT strain, even though much of the continent has a high potential for tilapia farming.

Finally, after growing pressure for the dissemination of the actual GIFT germplasm to Africa, the WorldFish Center approved the Policy on the Transfer of GIFT from Asia to Africa in 2007.

GenoMar also supplied the genetically improved strain to hatcheries in Zambia, Angola, and Uganda. The Ghana Aquaculture Research and Development Center (ARDEC) received the GIFT strain in 2012, with the expressed objective of comparing its growth performance.

It is now clear the GIFT tilapia will expand its range all over Africa, even if some countries like Ghana prohibited the culture of this strain because the environmental risk assessment has not been completed yet.

The crossing of neighbouring species can produce hybrid individuals possessing characteristics that are sought after in farmed animals: sterility, monosex lines, improved disease resistance or growth compared with parents, combinations of biological traits that were present separately in the parents, among others. The performances of hybrids are nonetheless hard to predict from the outset and must be tested experimentally.

It has thus been noted in tilapia that the crossing of certain *Oreochromis* species led to the production of hybrids that were all male (Wolfarth & Hulata, 1981). These hybrids were interesting as they provided male tilapia, which grew faster than female tilapia, and also prevented unwanted reproduction in fish farms. In practice, however, it turned out to be very difficult to maintain this production of very high percentages of males through hybridization, in particular due to contamination of parental strains of progenitors by hybrid descendants (phenomenon of introgression). At present, the use of these hybrids has yielded to other methods of sex control that are more efficient and easier to implement, such as hormonal inversion.

Genetic diversity in cultured stocks

Romana-Eguia *et al.* (2005) observed a strong loss of genetic variation in selected lines for size specific mass selection in the tilapia *O. niloticus*. The degree of inbreeding within the selected lines was higher (107.9%) than the control line (64.2%) after four generations. While changes in genetic diversity arose as expected in the selected lines because of artificial selection, genetic variabilities in the control lines was unexpectedely lowered by genetic drift and by unconscious selection. Looking specifically at the GIFT strain of Nile tilapia (*Oreochromis niloticus*), Ponzoni *et al.* (2010) observed that the rate of inbreeding was 0.0037 per generation and the effective population size was 88. They concluded that the mate allocation strategy has been successful in containing inbreeding and that the effective population size is satisfactory for the sustainability of the selection program. Fry production in *Oreochromis niloticus* is often achieved by mass spawning of males and females stocked in ponds. Fessehaye *et al.* (2006a) demonstrated that territorial behavior and reproductive competition among males may lead to a large variance in reproductive success among individual males, leading to one-third of males siring more than 70% of the offspring. The rate of inbreeding could be about twice the inbreeding expected in an idealized population of the same census size. While Fessehaye *et al.* (2006b) observed that the level of inbreeding did not affect survival and body weight at harvest in *O. niloticus*, Vitalaru *et al.* (2014) concluded that inbreeding can lead to morphological abnormalities. Substantial declines in performance are associated with usual hatchery management practices (Brummett, 2013). Genetic variability of fish held in African hatcheries is 40-70% less and growth rates 12-40% less than wild stocks (Eknath *et al.,* 1993; Morissens *et al.,* 1996; Pouyaud & Agnèse, 1996; Brummett *et al.,* 2004).

As with Tilapia species, domestication or captive *Clarias* breeding has resulted in a certain amount of genetic change, usually deterioration. Da Costa (1998) found a 20% difference between cultured and wild stocks of *C. anguillaris*, with the cultured stock performing significantly worse. Otémé (1998) and Agnèse *et al.* (1995) found that a population of *H. longifilis* held for four generations on a government research station had reduced genetic variability, lower fry growth rate and survival, higher levels of fry deformity and greater variability in larval growth rate. Van der Bank (1998) found that mean heterozygosity in a captive population (0.3%) of *C. gariepinus* was an order of magnitude less than in a wild population (5%). Hoffman *et al.* (1995) found that wild *C. gariepinus* grew 15-43% better under culture conditions than populations that had been held on-farm. Van der Walt *et al.* (1993a) reviewed genetic variability in *C. gariepinus* and found strong evidence of inbreeding, founder effects and genetic drift in most captive populations.

Good genetic management can reverse many of these negative consequences of domestication and even improve performance. Van der Bank *et al.* (1992) and Grobler *et al.* (1992) showed that out-crossing to other captive stocks and with wild fish raised mean heterozygosity of a farmed population to 7.6% compared to 5% in a wild stock. Similarly, Teugels *et al.* (1992) found that populations of *C. gariepinus* that were purposefully out-crossed among research stations were significantly more heterozygous than fish held in isolation on a single station. Among *C. gariepinus* stocks, significant variation in growth indicates that selection for better performance in aquaculture is possible (Van der Bank 1998). Van der Walt *et al.* (1993b) showed that a well-maintained experimental line of *C. gariepinus* outperformed wild strains and a population held on a local hatchery. Martins *et al.* (2005) documented significant variation in growth among juvenile *C. gariepinus*, implying that selection is possible.

Conservation status

Most members of the genus *Clarias* are under no particular danger of extinction at the present time. Four species, all African, appear on the IUCN Red List of Threatened Species (2007): *C. alluaudi, C. cavernicola, C. maclerni* and *C. werneri*. The closely related, and easily confused, *C. alluaudi* and *C. werneri* (Seegers, 1996) are considered as of Least Concern, with widespread distributions and no particular threats. *C. cavernicola* and *C. maclerni*, on the other hand are considered as Critically Endangered. *C. cavernicola* is endangered due to the fact that its entire range is a single 45 m^2 pool in the Aigamas cave, Namibia and the water level is going down due to groundwater extraction in the area. *C. maclareni*, while under no specific threat, occupies one small lake, Barombi Mbo (diameter of 2 km).

Although *Clarias* species are generally quite hardy, Mohamed *et al.* (1999) found that a section of the Nile River which received heavy levels of industrial pollution contained significantly fewer *C. gariepinus* than other sections and attributed this to poor water quality. As they are originally best adapted to swampforest habitats, *Clarias* species worldwide have come under increasing pressure as forests become increasingly fragmented (Sudarto, 2007).

Interactions between farmed lines of *Clarias* and wild populations may represent a significant threat to the genetic integrity of the latter. There appears to be a significant amount of genetic differentiation across the distribution of *C. gariepinus*, with populations in West/Central Africa differing morphometrically (width of pre-maxillary toothplate, length of occipital process, and dorsal fin length) from those in Eastern and Southern Africa (Teugels, 1998), possibly reflected in earlier taxonomic recognition of three species, two of which – *C. mossambicus* and *C. gariepinus* – have since been incorporated into *C. gariepinus*. Transcontinental movement of populations used for aquaculture may pose a threat to this differentiation.

In Africa, the *H. longifilis* x *C. gariepinus* hybrid, once thought to be sterile, has been recently shown to have the capacity to interbreed with wild *C. gariepinus*, creating what is effectively a transgenic Clariid, with unpredictable consequences for the wild populations, but quite possibly including a reduction in overall fecundity and therefore fitness leading to reductions in the wild stock

(T. Hecht, personal communication, 2005). Euzet & Pariselle (1996) found that "heteroclarias" juveniles were susceptible to *Henneguya* infections to which both pure *Heterobranchus* and *Clarias* were immune, raising further questions about the wisdom of creating this hybrid.

In addition to the dangers posed to indigenous biodiversity by these inter-specific and inter-generic hybrids, concerns have been expressed about the possible negative consequences of escapees from monogenetic but domesticated culture populations reducing the fitness of conspecific wild populations. The magnitude of this threat is proportional to the genetic distance between wild and captive populations. If the difference is extreme, introgression of domesticated genomes into what is theoretically defined as a perfectly fit wild population unavoidably reduces the purity of the wild genome. Whether such a change in gene frequencies represents a real threat to survival is unknown. Both in the wild and in captivity, shifting gene frequencies are a natural consequence of any significant change in the environment. In cases where important or rare *Clarias* biodiversity may come under such a threat, every effort should be made to assess the actual risks prior to introducing cultured populations to a new area.

Most of the Tilapia species like *Clarias* cannot be considered as ciritically endangered but some of them are threatened like *O. esculentus* and *O. variabilis* in the Lake Victoria basin, *O. karongae* and *O. idole* in the Lake Malawi drainage (IUCN Red List of Threatened Species (2007)). If there is no critically endangered species, some populations can be considered as seriously threatened, especially in species important for aquaculture like *O. niloticus* and *O. mossambicus*. For example, the newly discovered natural population from the Loboi swamp (Nyingi *et al.*, 2008) seems to be restricted to a few-hundred-metre-small hot stream ending into a swamp connected with the Lake Baringo drainage. The swamp, mainly composed of papyrus, is acting as a biological barrier that keeps fish from moving from the lake to the stream or vice versa.

Today, these populations are threatened due to environmental instability and anthropogenic activities within the region. The macrophytes within the swamp have been receding significantly due to encroachment of the swamp for agriculture and harvest of papyrus for roofing and other uses. The swamp itself has been reduced by at least 60% in the last 30 years due to irrigation activities (Harper, 2003). Finally, one other great danger to this unique genetic resource of the Nile tilapia is the recent growth of aquaculture development in the region. Fish from other basins are currently being introduced for culture in ponds closely associated to streams of the region. Escapees from these ponds would certainly pollute the genetic integrity of the natural populations of the Nile tilapia

This is exactly what happened in Lake Baringo that hosts one of the *O. niloticus* subspecies, *O. n. baringoensis*. Haplotypes of this subspecies were found to be introgressed with those of *O. leucostictus*, a species endemic to Lake Albert in Uganda but introduced into Lake Naivasha, which neighbours Lake Baringo (Nyingi *et al.*, 2007). This introgression was initially thought to be unaccompanied by any detectable transfer of nuclear DNA. Specimens of *O. leucostictus* were suspected of having been introduced into Lake Baringo for the purpose of improvement of tilapia stocks. They may however have escaped from aquaculture activities in the region. In a second study, Ndiwa *et al.* (2014) demonstrated that not only was there a notable amount of nuclear gene transfer, but that this introgression also occurred in adjacent natural population of *O. niloticus* from Lake Bogoria hotsprings in the Loboi River drainage. It is very likely that the recent intensification of aquaculture activities in this drainage may be responsible for these introgressions.

This tilapia is not the only one to be introgressed. D'Amato *et al.* (2006) observed many introgression cases in the Mozambique tilapia (*Oreochromis mossambicus*) in its native range, southern Africa. Hybridization of *O. mossambicus* was indicated by the presence of *O. niloticus* and *O. mortimeri–andersonii* mtDNA specimens in the Limpopo basin and of *O. karongae* mtDNA in specimens from Malawi.

So far it is clear that tilapia are prone to hybridizing quite easily with closely related species occurring naturally or introduced due to human interventions. In Africa, the most important culture species are still mainly taken from the wild and populations are often taken to a different basin far beyond their natural range, thus interrupting the natural allopatry with related species and populations. The complex nature of hybridization and introgression between cichlid species raises major concerns for the long-term integrity of tilapia species. Paradoxically, fish culture activities could represent a major threat for aquaculture natural resources, resulting in the rapid decline or total disappearance of the native populations.

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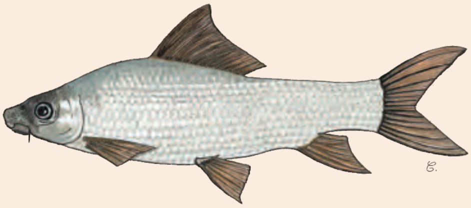

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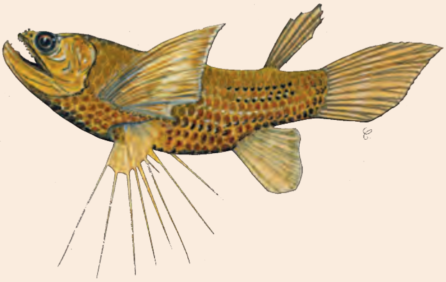

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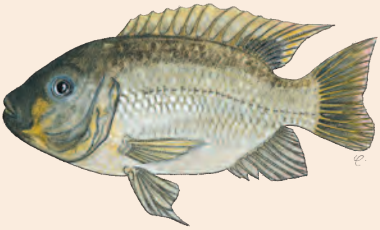

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The equilibrium of inland hydrosystems is presently a cause for concern, with species extinction rates there estimated to be 5 times higher than for terrestrial fauna in the 21st century. Urgent measures must be taken to conserve these ecosystems particularly with regard to fishes, which represent an especially rich and diverse evolutionary heritage.

Fishes were long unaffected by human activity on the African continent, but anthropogenic pressure has increased in recent decades. Good management of African continental waters is thus of paramount importance in terms of heritage and economics, as fishes are a vital natural resource for the people in sub-Saharan Africa.

In view of biodiversity conservation, African fishes are investigated here as a biological model owing to their enormous ecological and genetic diversity. It is essential to know the ecology and structure of various communities, and to understand the impact of human activity. This book discusses the diversity of environments, the origin and evolution of species, survival and adaptive strategies, the structure of fish communities, and the impact of human activity. It also devotes a section to fisheries and fish culture.

This ambitious project summarizes the current state of knowledge on African fishes and their populations, highlighting the mechanisms regulating their equilibrium and the causes contributing to their erosion. It is a reference not just for readers involved in African aquatic environments, but for anyone interested in biodiversity conservation in general.

Didier Paugy and ***Christian Lévêque*** are research directors at IRD. They have published numerous works on the systematics, distribution, and ecology of West African fresh water fishes, and expanded the collections of the MNHN in Paris.

Olga Otero is a professorial lecturer at the University of Poitiers (Institute of Paleoprimatology, Human Paleontology: Evolution and Paleoenvironments). She studies the evolution and diversification of African fishes to reconstruct the relationships between their spread, diversification, and the paleoenvironment.

With contributions from:
Jean-François Agnèse, Jean-Jacques Albaret, Rémy Bigorne, Randall Brummett, Lionel Cavin, Gaël Clément, Fabrice Duponchelle, Yves Fermon, Bernard Hugueny, Raymond Laë, Marc Legendre, Jacques Lemoalle, Alison Murray, Aurélie Pinton, Jos Snoeks, Kathlyn Stewart.

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