The diversity of aquatic environments

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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.

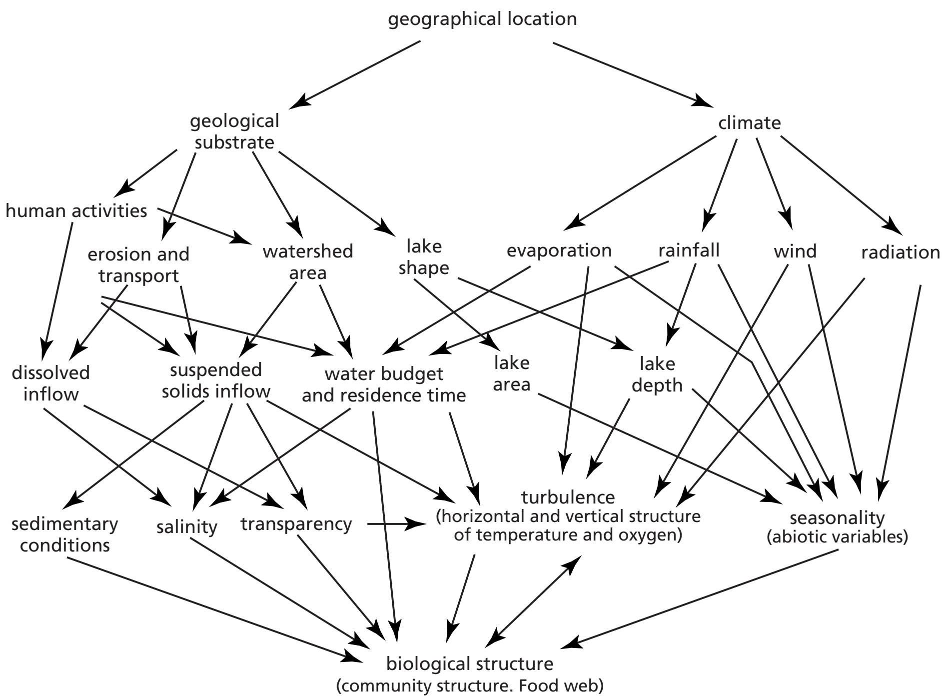


FIGURE 1.1
An example of a network of environmental abiotic characteristics that determine the quality of a lacustrine system. The proximal variables (bottom line of the figure) have a more direct action on the composition of communities.

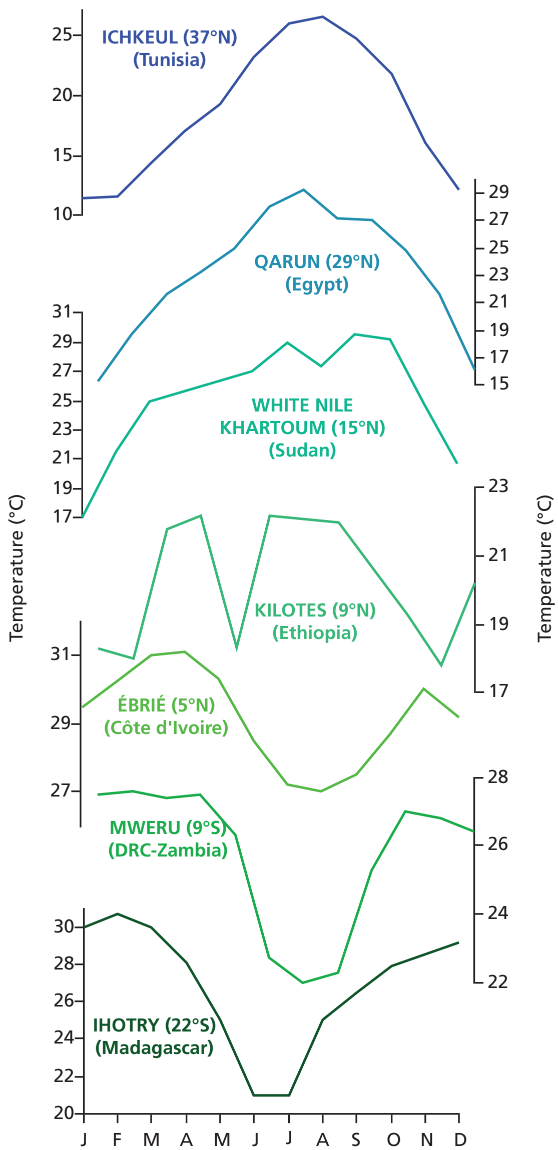
The role of physico-chemical variables: temperature and salinity

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

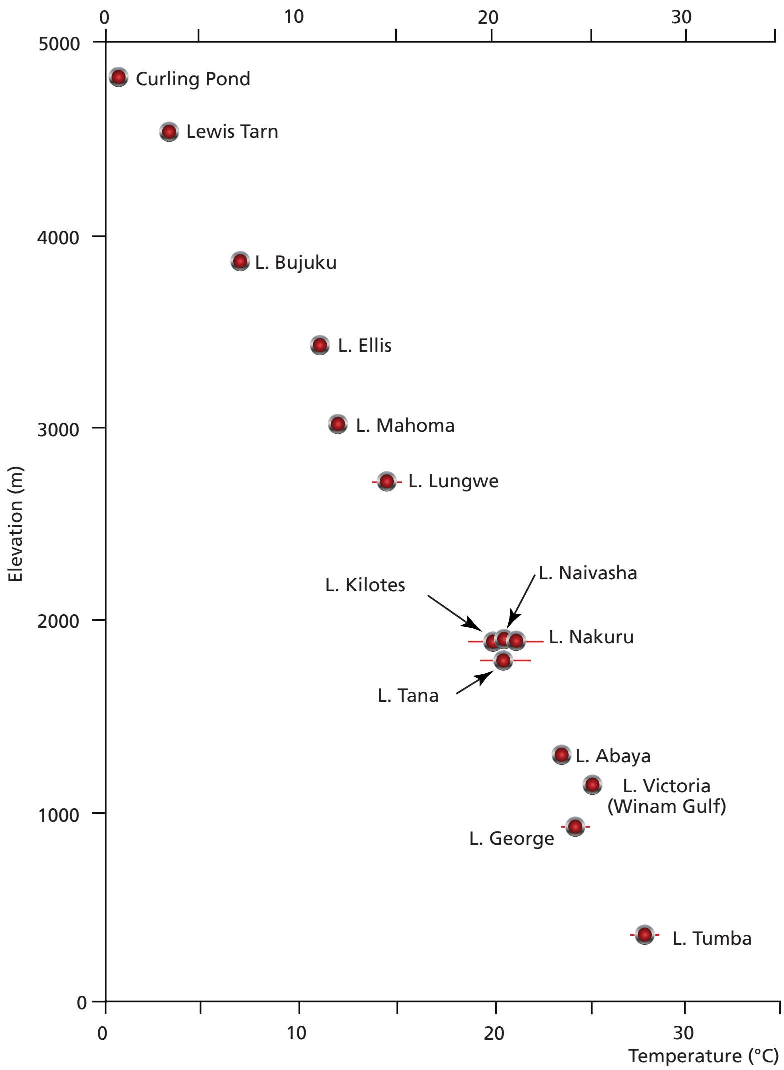


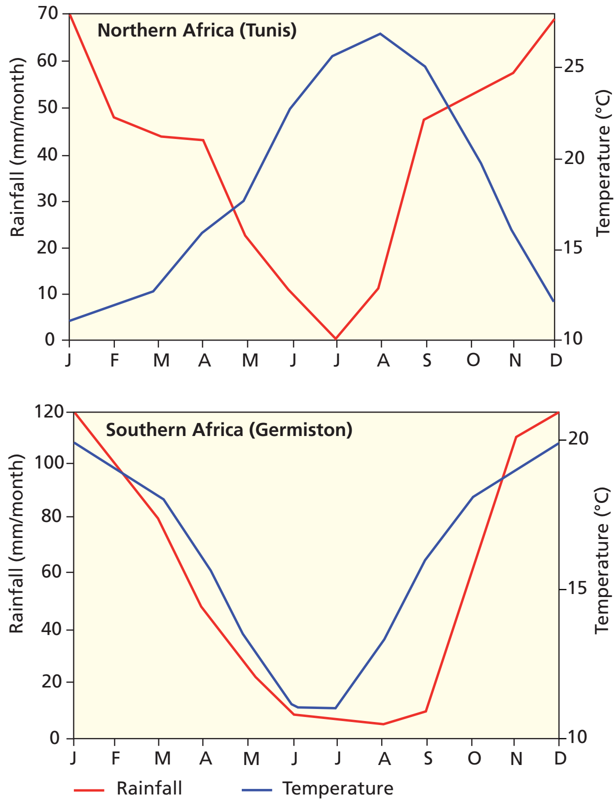
FIGURE 1.3.
Decrease of bottom water temperature according to altitude in some shallow African lakes (from Talling, 1992).

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	

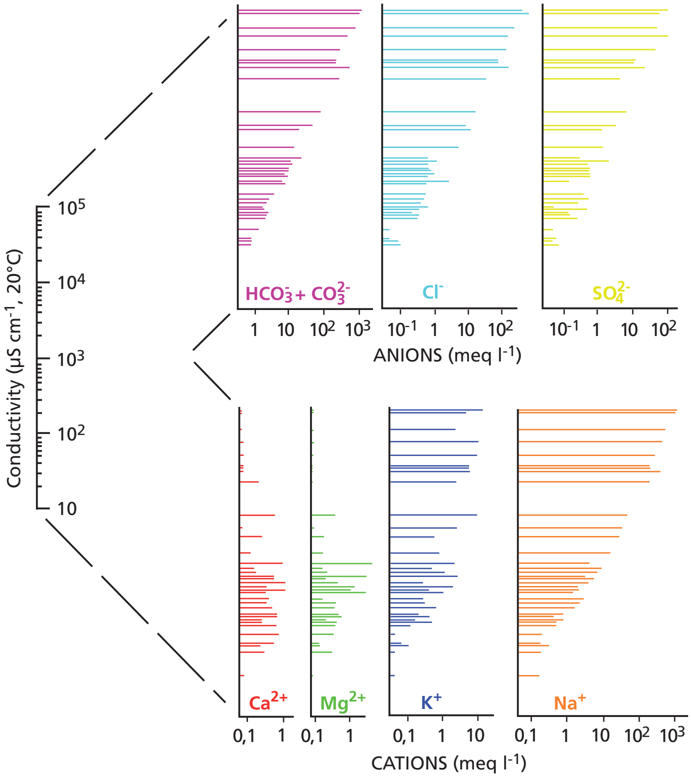


FIGURE 1.5.
Concentrations of major anions and cations as a function of conductivity for a series of African lakes in East and Central Africa (from Talling & Talling, 1965)

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.

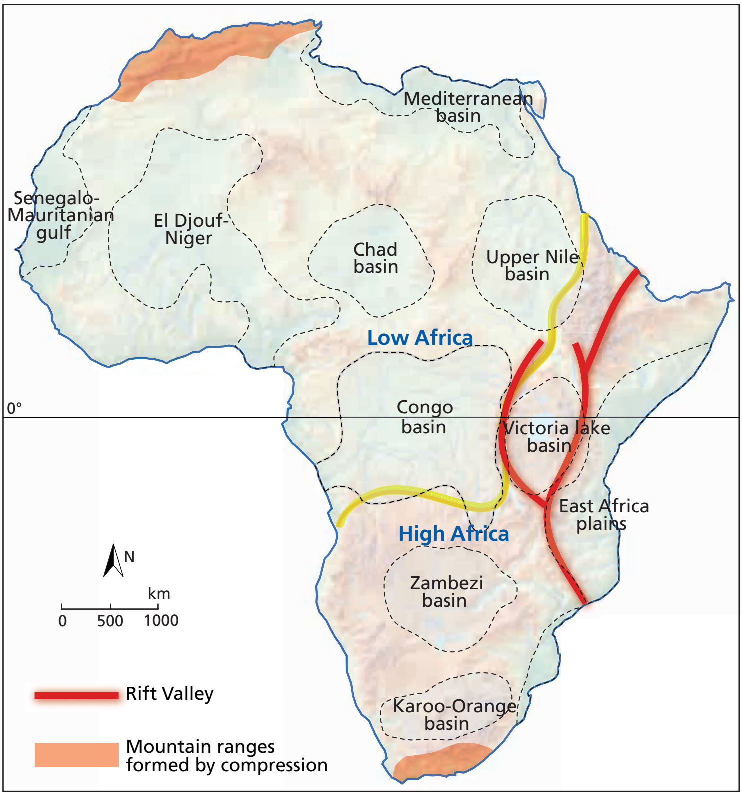


FIGURE 1.6.
General topography of Africa showing the principal hydrographic basins, the altitude zones above 1,000 m, and the approximate division between lower and higher Africa (redrawn from Beadle, 1981).

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 km^2, 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 $\mu S.cm^{-1}$ being its highest limit in Lake Chad), while *Phragmites*, *Typha* and *Cyperus laevigatus* are tolerant to higher salinities (up to 20,000 $\mu S.cm^{-1}$ 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

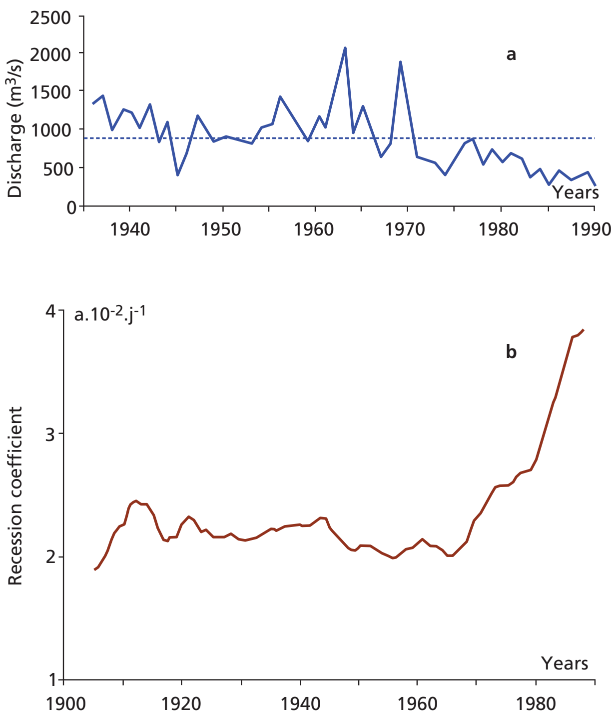


FIGURE 1.9.
a: monthly discharge at low flows (Ubangi); b: evolution of the recession coefficient of rivers in the Sahelo-Sudanian part of Africa) (from Olivry *et al.*, 1993).

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 (km²)	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 km²; Tanganyika, 32,900 km²; Malawi, 30,800 km²) 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.

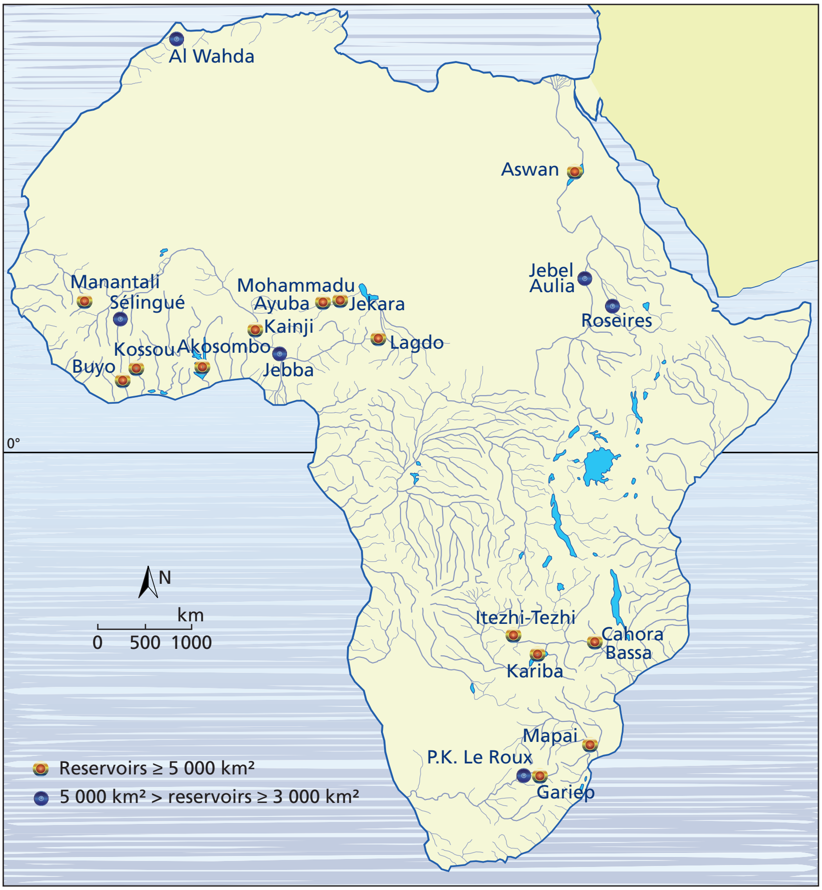
Dams	Basins	Countries	Closing date	Area (km^2)	Maximum depth (m)
Akosombo	Volta	Ghana	1964	8 270	74
Nasser/Nubia	Nile	Egypt, Sudan	05/1964	6 850	110-130
Kariba	Zambezi	Zambia, Zimbabwe	1958	5 364	120
Kafue Gorge	Kafue	Zambia	1972	1 600-4 340	2 *
Cahora Bassa	Zambezi	Mozambique	1975	2 665	156
Kossou	Bandama	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 $\mu S.cm^{-1}$ 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.

Scientific editors

Didier Paugy Christian Lévêque Olga Otero

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