Chapitre 12

FISH COMMUNITIES OF RIVERS

PEUPLEMENTS ICHTYOLOGIQUES DES RIVIERES

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Rivers are a most important feature of African hydrology whose combined lengths amount to some 13 million kilometres distributed mainly among many small lower order streams. The fish communities of the river systems are rich and diverse forming an important resource which serves as a basis for fisheries and for human food. Unfortunately, fish in rivers remain relatively poorly studied as compared with equivalent populations in lakes and reservoirs. Any understanding of the ecology of riverine fish must therefore depend much on extrapolations between systems which permit an overall view to emerge.

Because of the structure of this compendium, many of the concepts presented in this chapter have already been discussed exhaustively in preceeding chapters dealing with individual aspects of fisheries biology. Here, however, they are assembled in less detail, but with an emphasis on their adaptive significance to attempt to give a coherent picture of how they function together to enable fish and their communities to thrive in what at first sight appears a changeable and somewhat hostile set of environments.

1 — CHARACTERISTICS OF RIVER SYSTEMS

The behaviour and general biology of the species of fish inhabiting rivers are strongly adapted to the particular environmental characteristics of the river systems. It is, therefore, essential to preface any consideration of African river fish with some remarks on the nature of the rivers of the continent.

1.1 — Types of rivers. Several attempts have been made at classifying rivers which are based largely on the form and vegetation of the terrain through which the river flows. The first major distinction is between those rivers in which the volume of water passing through the river varies little with season (pooled rivers) and flood rivers which have pronounced seasonal variations in volume, giving a clear-cut flood regime having one or two flood peaks annually. This latter category of rivers has been separated by Jackson (1961) into reservoir and sandbank types. Flow in reservoir rivers is stabilized by some feature, such as lakes or swamps upstream and in sandbank rivers the flood, which is not stabilized, reaches an abrupt peak and diminishes rapidly often to a point where the river bed is left dry. The second fundamental distinction is that between forest rivers and savanna rivers. The rivers of the equatorial rain forests have the following characteristics which influence the nature and behaviour of their fish communities. Their floodplains tend to be restricted in area and sometimes internalized over the numerous islands which form between the braided channels. They are also heavily forested. Their flow regimes are usually relatively stable, of the reservoir type. The peaks of such floods as do occur are usually evened out by the long retention time of water in the flooded forests or because the water arrives at different times of the year from their various tributaries, or because there are two rainy seasons centred around the equinoxes, there tend to be two floods per year. The river water is frequently impoverished black water with low pH, low conductivity, negligible silt load and stained brown with humic acids. As a consequence of this and the heavy shading of the floodplain and river channels, primary production in such rivers is usually low and the main food source is allochthonous vegetable and animal matter falling into the water from the surrounding vegetation. Savanna rivers, on the other hand, have pronounced flood regimes, enriched less acid waters, high silt loads and are more open to insolation. Their floodplains are broad, open and colonized by grasses. Because of this they have a higher throughput of nutrients and a higher primary productivity which serves as the basis for numerous allochthonous food sources. Fig. 1, which shows the main river systems in Africa, together with the major floodplains and swamps also indicates the limits of the equatorial rain forests. From the map it is clear that many river basins may contain both forest and savanna rivers.

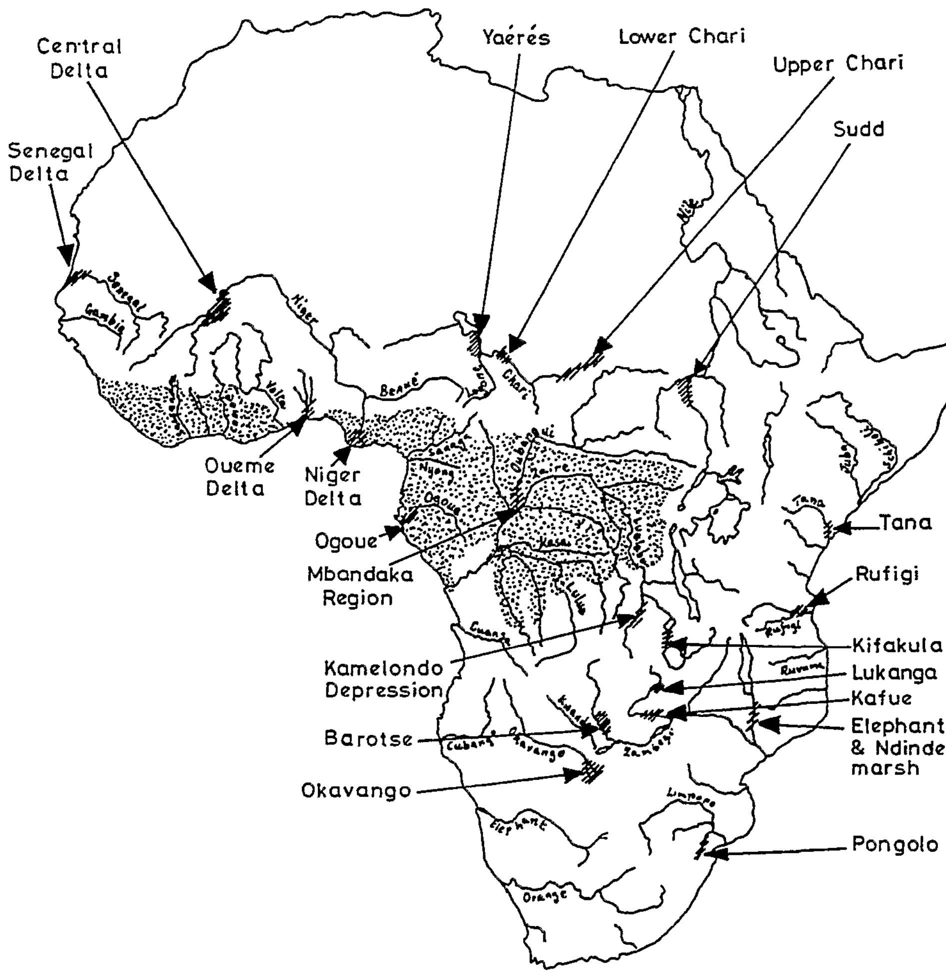

Fig. 1 : Map of principal rivers of Africa with major floodplains (hatched). The equatorial forest is stippled.

1.2 — Zonation of rivers. Recently, the view has emerged that the physical variables within a river system represent a constant gradient from source to mouth (Vannote et al., 1980). This concept is useful as a framework within which to consider nutrient and energy flows along the stream channel, but only contributes in a general way to any explanation of the nature and distribution of the fish fauna. This view is also coupled to the conventional idea of a river basin as having a concave longitudinal profile with steep reaches near the source and shallower slopes near the mouth. Such rivers proceed in a more or less orderly fashion from small, narrow and torrential low order headwater streams (rhithron), to broad, meandering and placid zones (potamon) near the mouth. In Africa such types of river are relatively rare and are probably more or less limited to southern Africa and to certain mountainous uplands such as the Fouta Djallon of Guinea or the Kenya Highlands. Furthermore, a true rhithron, as originally defined by Illies and Botosaneanu (1963) is most often absent because of the elevated temperatures of the waters of tropical African streams even at relatively high altitudes. The rhithron-like or rapids zones and potamon zones of tropical Africa tend to be distinct and the transition between the two is frequently quite sudden. In addition, because the African continent consists of a large central plateau the rivers descend in a series of steps to the sea with rhithron-like rapids reaches, which are termed rejuvenation zones alternating with potamon floodplain reaches.

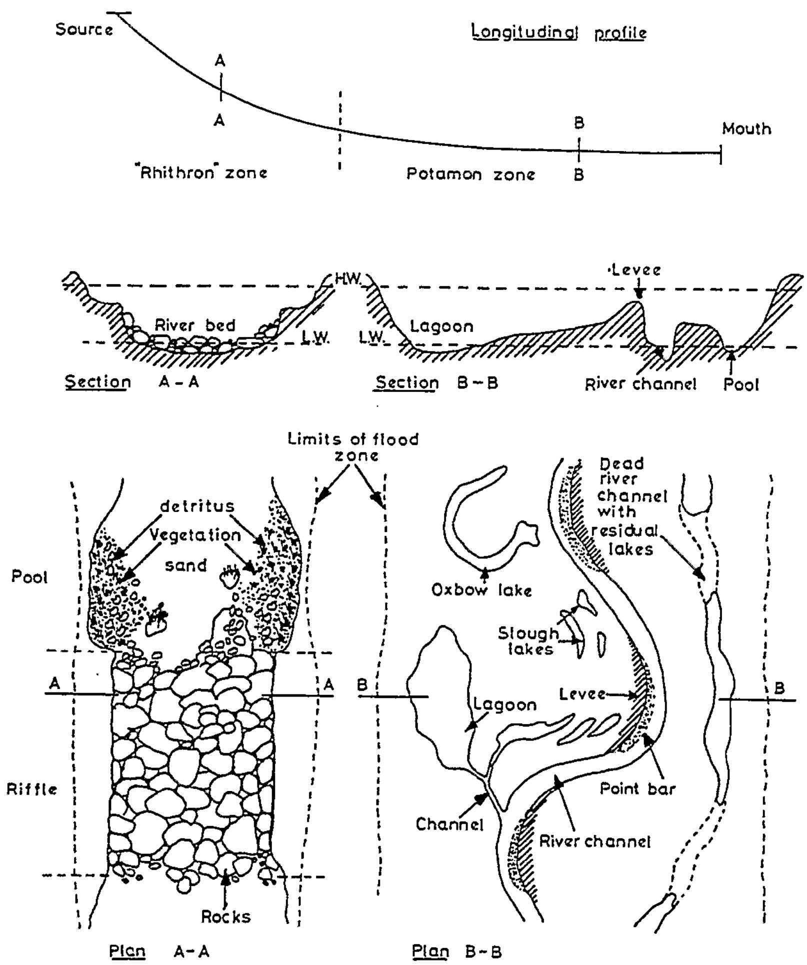

Fig. 2 : Main characteristics of a river showing morphology of rhithron (A-A) and potamon (B-B) zones.

The main features of the rhithron and the potamon, illustrated in Fig. 2, are as follows :

a) Rhithron-like or rapids zones generally show an alternation between
• steep, narrow and shallow riffles or rapids, and
• flatter, wider and deeper reaches termed pools. The riffles have high turbulent flow, coarse bottoms of boulders, rocks or pebbles and limited attached vegetation. The pools have lower flow, bottoms of somewhat finer material (sand or even mud and detritus) and some rooted vegetation.

b) Potamon reaches of flood rivers have wide, flat, meandering channels, mud bottom and considerable rooted and floating vegetation. They are divided into two main components — the main channel, which conforms to the definition « pools within perennial streams» of Gaigher (1973), and the floodplain. Zonation within the potamon is both longitudinal and lateral. Longitudinally, there is a repetition of differing habitats associated with the meanders of the channel. Laterally, there is the distinction between the main channel and its floodplain. The floodplain is normally an area of relatively flat land flanking the main channel. In exceptional cases larger floodplain areas arise by geographic accident and some of these, such as the Central Delta of the Niger or the Nile Sudd, are very extensive (see Fig. 1). The plain is usually higher near the river, where raised levees limit the main channel and slope downward toward the foot of the terrace confining the plain. Many bodies of water are found on the plain ranging from small temporary pools to larger permanent lagoons and swamps. The complexity of the potamon leads to a proliferation of habitats, which vary between the flood and dry season phases. Some of these have been listed by Welcomme (1979) (see Table 1).

1.3 — Seasonality in flood rivers. The changes associated with the seasonal flooding are the major determining factors in the biology of the species inhabiting flood rivers.

In the rhithron and rapids zones, especially those of low order streams, the flood appears more as a series of erratic spates than as a smooth wave. As flow increases, the distinction between flood and riffle may disappear, turbulence and disolved oxygen tension become maximal and bottom material, vegetation and other objects such as tree debris which have fallen into the channel may be dislodged and swept downstream. In the dry season the system may become increasingly desiccated and flow slowed to a mere trickle. In most extreme conditions the riffles become completely dry, leaving the pools isolated one from the other. Under such circumstances dissolved oxygen concentrations in the remaining water fall until the pools become anoxic. Even these pools may eventually dry out too.

In the potamon seasonal changes are more complex. The flood curve appears as a much smoother wave as the spates from individual tributary streams are cumulated. The flood is initiated when rising water overflows the banks of the main channel to invade the floodplain. The advancing front, which is newly inundating dry ground, together with the terrestrial vegetation — dung and other organic substances — releases nutrients into solution, as indicated by rises in conductivity, and the decay of this material by micro-organisms causes a drastic lowering in dissolved oxygen. The water rises progressively to maximum flood, during which time there is a rapid proliferation of grasses and floating vegetation as well as zooplankton and benthos and epiphytic organisms. The level subsequently declines and water flows back through numerous channels of the plain, until eventually it is confined once again within the main river or within the various water bodies of the floodplain. Many of these are eventually lost through desiccation, although some floodplain lakes persist throughout the year. These permanent water bodies tend to become overgrown with vegetation and their water retains little oxygen, many become completely anoxic.

Table 1 : Major habitats of river-floodplain systems (from Welcomme, 1979)

<table>
<tr><th colspan="2">FLOOD</th><th colspan="2">DRY SEASON</th></tr>
<tr><th>River</th><th>Floodplain</th><th>River</th><th>Floodplain</th></tr>
<tr>
<td>1. Main channels : Rapid and turbulent flow; fairly uniform; floating sudd islands
2. Tributary streams :
(A) Small rocky torrential streams descending from unflooded terrace, or upstream of main floodplain area
(B) Small channels - linking floodplain to subsidiary marsh or lake areas above main floodplain level (type 1 lakes - Svensson, 1933)</td>
<td>1. Flooded grassland :
(A) Floating meadows : these are probably not uniform as there are slight differences in bottom substrate and relief, floral associations are variable
(B) Open water
(C) Littoral fringe areas at limit of advancing or retreating water, submerged grass; often low DO in turbulent wave-washed areas
2. Lagoons and depressions :
(A) Open water
• mud bottom
• sand bottom
(B) Standing vegetation
(C) Floating vegetation mats
(D) Floating leafed vegetation
(E) Submersed vegetation
3. Lakes (as above but with a greater proportion of open water and deeper)
4. Flooded forest :
(A) Dense rainforest
(B) Gallery or levée woodland
(C) Acacia and bush scrub
5. Flood areas outside main flood area (type 1 lakes - Svensson, 1933)</td>
<td>1. Semi-permanent channels : (Break up into an alternation of pools and rocky riffles)
(A) Pools (in extrem form pools become isolated and deoxygenated)
• mud bottom
• sand bottom
• leaf litter
a) forested
b) open
— floating vegetation fringe
— submersed vegetation
— emergent vegetation
(B) Rock riffles (a variety of habitats under rocks on surface of rocks)
(C) Tree trunks and other debris
2. Permanent channels : (Meanders produce a regular succession of habitats of varying depth and bottom type)
(A) Shallows
• mud bottom — with no current
• sand bottom — or with
• leaf litter — slight current
(B) Deeps with slow or faster current
a) shaded by forest
b) open
— floating vegetation
— emergent vegetation</td>
<td>1. Floodplain pools :
(A) Pools which dry out completely
(B) Marshy pools (heavily vegetated with little dissolved oxygen)
• surface film
• deeper water
(C) Shaded pools (in forested or wooded areas)
• clear
• with tree trunks and other debris
2. Lagoons :
(A) Deeper open waters
• mud bottom
• sand bottom
(B) Vegetated fringes
a) floating mats
b) submersed vegetation
c) emergent vegetation
3. Large lakes (subhabitats as for lagoons but more inclined to set up permanent stratification, greater depth, more open water relative to shoreline, often with sheltered and exposed shores)</td>
</tr>
<tr>
<td></td><td></td>
<td colspan="2">Backwaters connected to main channel : Lentic water regions, open to main channel with many of the characteristics of lagoons or lakes avobe, may be :
(A) Shaded
a) clear
b) with tree trunks and debris
(B) Open with
a) deep water
• mud bottom
• sand bottom
b) shallow water with
— floating vegetation mats
— submersed vegetation
— standing vegetation
— floating leafed vegetation
c) shallow littoral usually vegetated
Downstream larger water bodies : Lakes, sea or larger river system</td>
</tr>
</table>

2 — FISH COMMUNITIES OF RIVERS

2. 1 — Abundance of species in African river systems. African rivers, in common with those of other tropical areas, are inhabited by rich and varied fish faunas. The numbers of fish species present in any river is closely correlated with the size of that river as represented by its length or its basin area. Fig. 3, for instance, shows the numbers of species found in 25 African rivers, some of which are tributaries within the same major basin. Clearly, there is a close correlation between the number of species and the basin area, which is expressed by the relationship : $N = 0.499\,A^{0.434}$ where N = the number of species and A = the basin area in km^2. Similar relationships could doubtless be established for number of species as a function of river length or of stream order, which indicate that the number of species present in a river system increases steadily from source to mouth. This increase in specific diversity is most probably because of the greater number of ecological niches available in the larger systems as well as their somewhat greater degree of stabilty.

The diversity of African river faunas is also aided by the general tendency for the fish communities to contain a large number of small-sized species. Examination of faunal lists shows that within any one basin a large percentage of the species present have a very small adult length (equivalent to L_∞ in the Van Bertalanffy growth expression). Small size and rapid completion of life cycles are clearly advantageous in seasonal rivers, where such species can more readily adjust to the fluctuation in conditions. Pygmy species also have the advantage that they can benefit from many micro-habitats not available to larger species. They can seek refuge in the root masses of vegetation and other small crevices or they can colonize the surface area of the water to exploit the neuston or fine allochthonous food sources found there.

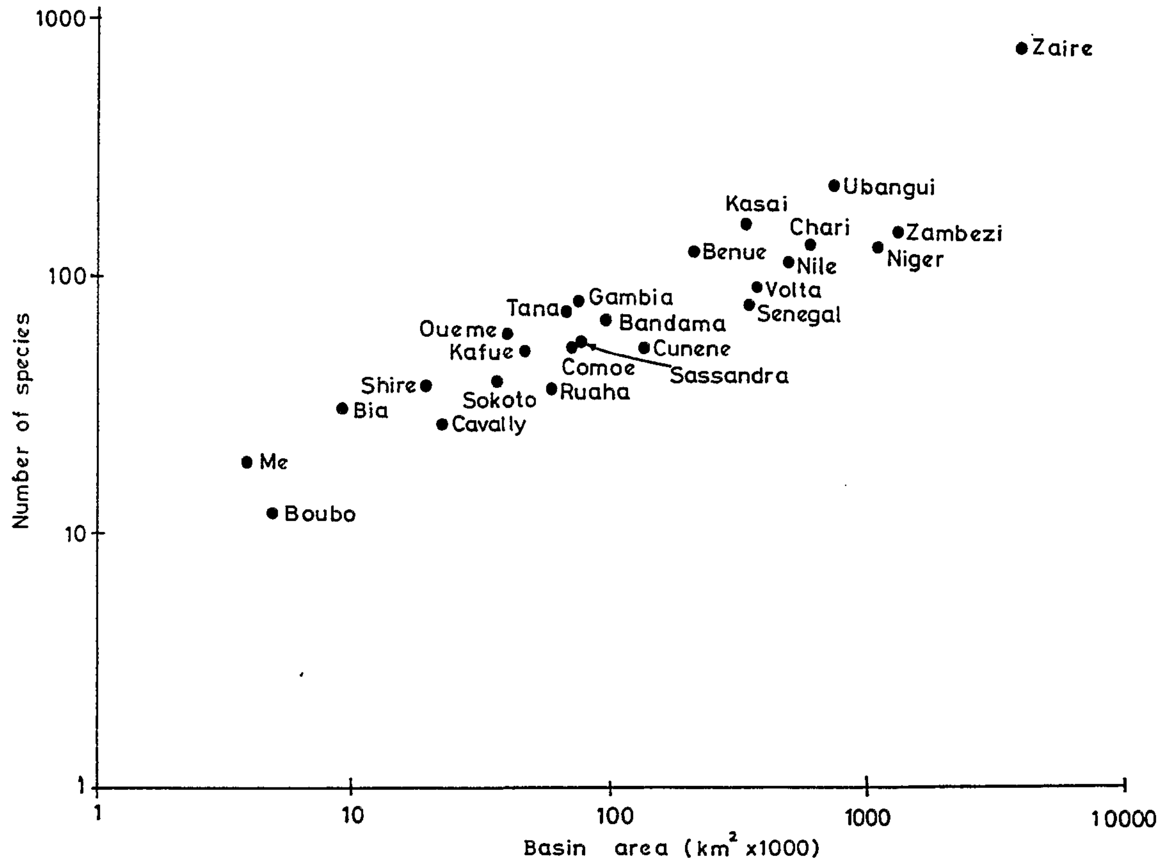

Fig. 3 : Number of fish species present in some African river systems as a correlate of basin area.

2. 2 — Zonation of fishes within river systems. Many attempts at establishing general principles for the biological zonation of rivers have been made over the years. Typical of such efforts are those of Huet (1949) who defined a rule of gradient, relating slope, river width and fish species present as a classification of north European streams, whereas Illies and Botosaneanu (1963) proposed a much wider separation into creon, rhithron and potamon zones, based on faunistic criteria. However, these attempts mostly originated in the North Temperate zone and are only with difficulty transferred to the Tropics. In Africa, for instance, the classification of Illies and Botosaneanu has only been applied successfully in some South African rivers (Harrison, 1965) or in the Luanza, a high altitude tributary of the Zaire River system (Malaisse, 1976), where a succession of rhithronic and potamonic characteristics similar to those found in Europe exist. In other parts of the continent, such as West Africa, where Sydenham (1977) has worked on the Ogun River, and Merona (1981) has worked on the Bandama River, or Central Africa, where Balon & Coche (1974) described the fauna of the Kalomo River, the zonation is much more obscure.

Provided there are no geographical discontinuities such as large waterfalls, the increase in the number of species along a tropical river tends to be by addition of species to those present rather than by the replacement of species characteristic of temperate systems in Europe (Huet, 1949) and North America (e.g., Minckley, 1963). In Africa, however, most large river systems have such discontinuities so there are sufficient important exceptions for this not to constitute a general principle; for example, the Zambezi River is divided into three faunistic zones, the middle of which between the Cabora Bassa rapids and the Victoria Falls. is the poorest, or in the Nile, the Kabalega Falls between Lake-Kyoga and Lake Mobutu marks a discontinuity between the generalized nilotic fishes downstream and a distinct riverine and lacustrine fauna upstream. Instead it is possible, from the work that has been done, to separate the causes of species distribution in water courses under two main headings geographical factors and geomorphological factors.

Geographical factors influence the taxonomic differences that may be encountered within a river basin. For instance, the isolation of subpopulations of species in small order streams can result in specific divergence over a long time period. In this way it is possible to observe two similar species occupying identical or similar niches in two separate streams of the same basin. This isolation is to a certain extent reinforced by the behaviour of the species themselves, which are often small, sedentary and have a short life cycle, which may contribute to a rapid rate of speciation. This tendency for species to diverge in the lower order streams of a river basin could account for much of the increasing diversity of species shown by larger river basins in Fig. 3 and for the relatively large proportion of species of small size in river fish communities. A second mechanism influencing distribution is river capture when species may be exchanged between systems. Such might explain the presence of soudanian species as defined by Daget (1965) such as *Mormyrus hasselquistii, Barbus stigmatopygus, B. leonensis, B. macrops* or *Kribia nana* in the north of the Bandama (Merona, 1981). The role of geographical accidents in determining fish distribution have also been emphasized by Crass (1962) and have been used to explain the peculiar distribution of certain cyprinids in the rivers of South and Central Africa. Here, for example, *Labeo forskahlii, Barbus mattozi, B. tangandensis, B. bernardcarpi, B. barotsensis, B. auriantacus, B. thamalakanensis* and *B. basilioides* in common with species of several other genera are found only in the Upper Zambesi above the Victoria Falls.

Whereas geographical considerations may influence the distribution of fish species between river systems, the distribution of the various types of species within any one system is more likely to be controlled by the geomorphology of any particular river reach. Thus, it is useful to distinguish two major fish communities, which are described in the following sections :

- communities of rhithron-like or rapids zones; and
- communities of the potamon,

although a certain amount of interchange may occur, particularly by certain elements of the potamon fauna which enter rapids to breed. Because many of the African rivers pass through several successive alternations between calm and rapids reaches, these two faunas likewise alternate along the length of the stream, which gives a type of zonation based purely on the flow or bottom characteristics peculiar to the river in which they are found. Species of several families have become adapted to life in rapids and as Poll (1959a, b) points out for the Zaire River. The inhabitants of downstream rapids are representatives of families which are normally found in the potamon, but which have occupied the rapids, rather than representatives of those families, such as the Kneriidae or Amphiliidae which are native to the rapids of the headwater streams of much of Africa.

Conditions become increasingly estuarine toward the mouth of the river where saline waters may penetrate many kilometres upstream in lowland rivers of slight slope. Here, a pronounced zonation of species occurs according to their salinity tolerance, although the zones move up and down-river as the interface between salt and fresh waters varies with state of tide or flood regime of river. Three groups of fish are to be found in the estuarine zone :

- a group of euryhaline freshwater species such as *Schilbe mystus, Synodontis schall* or *Chrysichthys auratus*;
- a group of estuarine species which may be of freshwater origin, for example *Chrysichthys nigrodigitatus, Sarotherodon melanotheron*, or marine origin *Liza falcipinnis, Ethmalosa fimbriata* or *Eleotris* spp., for instance, and
- a large number of truly marine species which penetrate the fresh waters for feeding.

2.3 — Communities of rapids and swift-flowing reaches. Species of fish inhabiting the rocky riffles of rapids reaches of rivers are highly adapted to the turbulent conditions there. There are three main groups of such fishes :

- those fishes which cling to the surface of the vegetation and rocks;
- those fishes which take refuge from the current in the crevices and holes between rocks; and
- those fish which can swim sufficiently fast as to resist the current. The first group is particularly well represented by members of the family Amphiliidae whose several genera are all adapted in various ways to life in strong currents. They are all elongated, streamlined and with the slightly humped form that results in the fish being forced onto the bottom by the flow. In addition, the various genera possess a variety of suckers or enlarged fin with which they can cling to the substrate. For example (Fig. 4a), *Amphilius* have sucker-like mouths and stiff pectoral spines, *Doumea* spp. have enlarged rigid pectoral spines, *Phractura clauseni* has been observed to cling to the edges of leaves with stiffened maxillary barbels. Similar structures are found in the Mochokidae, where *Chiloglanis* spp. have elaborate sucker-like mouths. Robustand serrated pectoral spines are found in some *Synodontis* and *Auchenoglanis* spp. and sucker-like mouths are also found among the Cyprinidae in both *Garra* and *Labeo* species. Two particular adaptations fit fish for life in the interstices of rocks and anchored vegetation, sinuous, serpentine form and small size. Both are found in African rapids fauna. Typical of the smallest element of the fauna is *Kribia nana*, which can squeeze into extremely small cracks but also has almost united pelvic fins which the fish can cling onto the substrate. Juveniles of several species which in their adult form are not normally found in rapids such as *Bagrus* or *Bryienomyrus brachyistus* may also be found in rock crevices. Elongated forms occur in several families (Fig. 4b), the Clariidae where *Gymnallabes* and *Clariallabes* are but two of a series of anguilliform fishes, the Polypteridae with *Calamoichthys calabaricus*, the Mormyridae with *Mormyrops*, the Mastacembelidae with *Mastacembelus* and *Caecomastacembelus* and the Cichlidae with *Gobiocichla* and *Leptotilapia irvinei*. Larger swift swimming streamlined species sometimes penetrate the rapids such as *Barbus altianalis* of the Nile or certain species of *Bagrus, Tilapia, Hydrocynus* and *Alestes*, but normally exposure to the fast current is limited and the fish soon drop back to shelter in the pools. Several of the adaptations to swift current also fit the fish to exploit the available food sources of the riffles. The swift swimming forms pick up allochthonous material falling onto the surface of the water whereas those fishes with sucker-like mouths usually feed on epilithic or epiphytic organisms and on small insects. The elongated fishes that can thread themselves among the rocks are particularly well situated to find the numerous insects that inhabit the bottom.

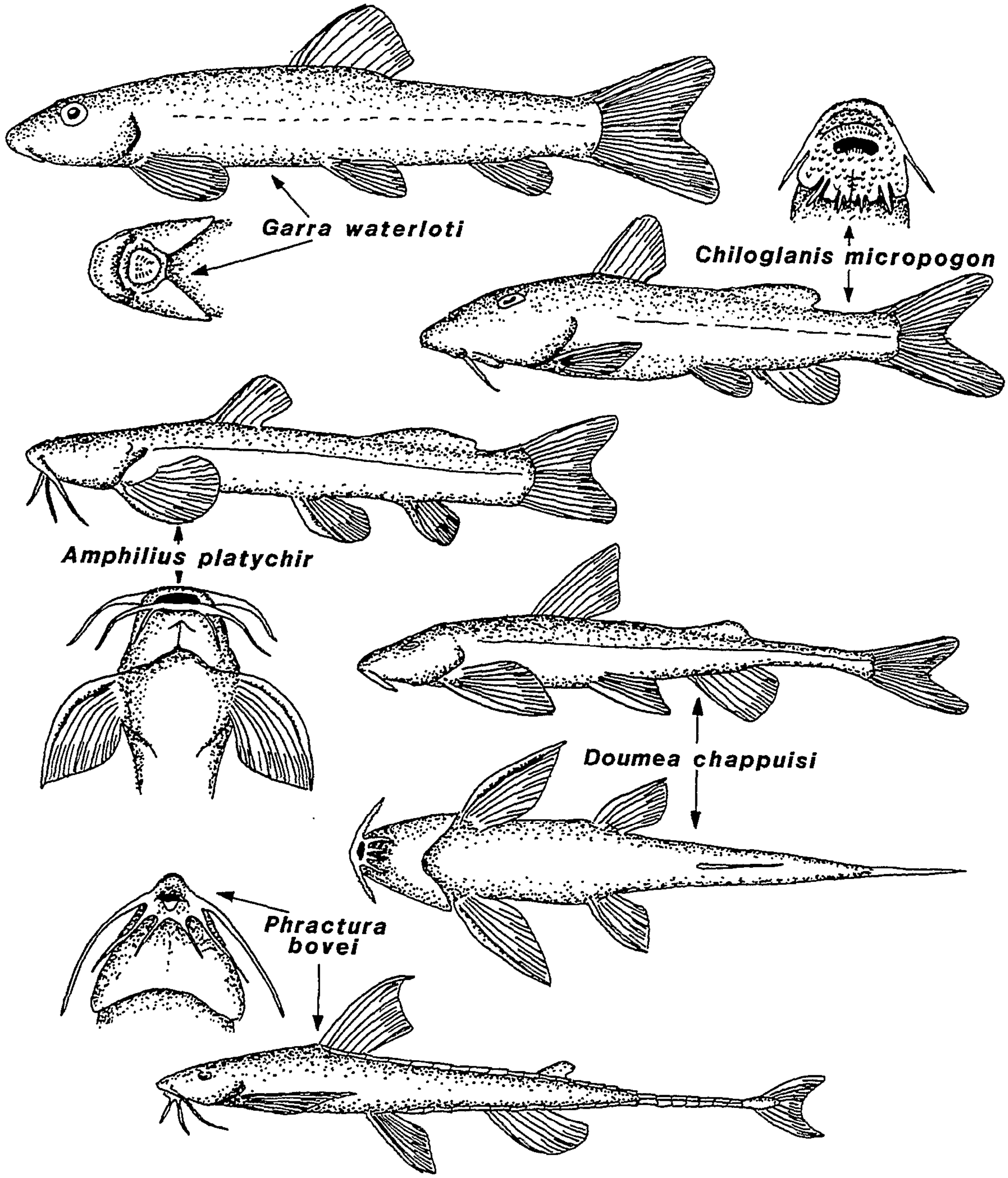

Fig. 4 A : Fish adapted to life in African rapids Species with spines or suckers.

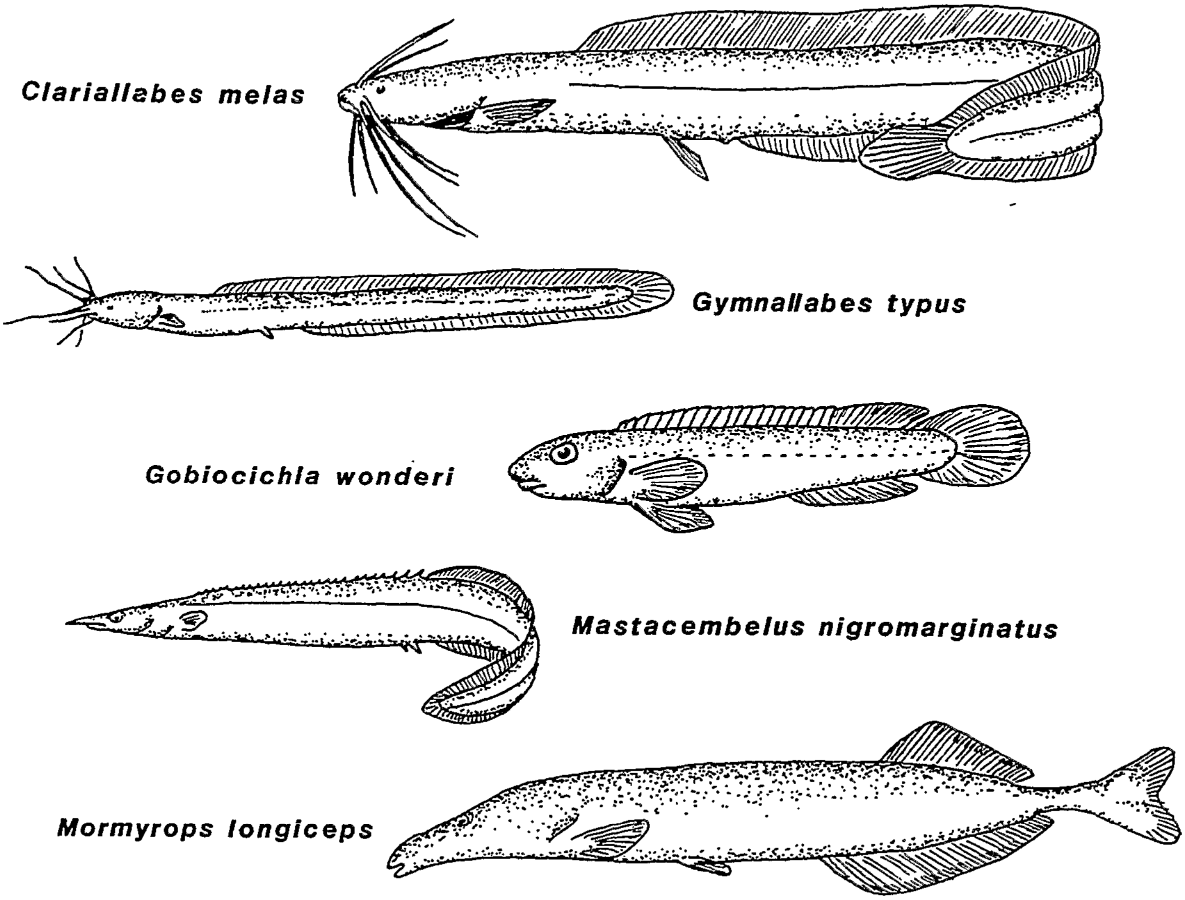

Fig. 4 B : Fish adapted to life in African rapids Species with elongated shapes.

The pool habitats are more varied and tend to have two main components; the central portion of the channel, which is relatively deep with clear sand or fine gravel bottoms, and the slack waters nearer the banks which are often heavily vegetated with floating and emergent aquatic and overhanging terrestrial plants. Here bottoms are usually composed of food-rich detritus from allochthonous leaf fall and from silt deposition in the quieter waters. The open waters of the pools are inhabited by a wide range of surface and mid-water living fishes such as species of *Raiamas, Barbus, Alestes, Micralestes* and *Petersius* which feed on allochthonous material and drift organisms. The bottom fauna of the pools is very rich especially in larger streams with some smaller Mormyrids, *Brienomyrus brachyistius, Pollimyrus lhuysii,* for example, or *Labeo* and *Synodontis* species. The shallower waters over sand bottoms are occupied by a variety of dwarf forms including *Kribia nana, Nannocharax* species and members of the family Knerrriidae.

The slack areas at the fringes of pools, the limited floodplains of the rapids reaches and perennial streams of the lowland zone have similar faunas, many of the elements of which recur within the floodplain of the potamon. Because there is a variety of microhabitats in the slacks small size is a great advantage. Niche selection seems very highly developed and all levels of the water column are occupied. Several genera of cyprinodonts occupy the water surface, particularly *Epiplatys,* although some *Alestes* such as *A. macrolepidotus* are also found there. The mid waters support clouds of dwarf *Barbus* and *Aphyosemion* species which are more often than not associated with the shade of floating lily leaves. The rich detritus of the bottom attracts several species of small *Mormyridae, Neolebias, Barbus* and *Labeo*, together with various small or dwarf chiclids such as *Pelvicachromis, Thysia ansorgii, Hemichromis bimaculatus*. Similar elongated fishs found in the rocks also occur in the floating vegetation at the fringes of the pools as the sinuous habit is equally adapted to such conditions. *Mastacembelus* and *Calamoichthys* particularly are conspicuous in such environments as they also frequent similar vegetation in the potamon.

An example of the variety of species found within the rapids of one river is the Bandama of the Ivory Coast, where a mosaic of habitats delimited mainly by velocity of current has been described by Merona & Albaret (1978). Here *Amphilius, Phractura, Labeo parvus, Synodontis bastiani* and *Mastacembelus* were found in rapids regions of turbulent waters; *Alestes imberi, Micralestes, Nannocharax* and certain species of *Barbus* preferred regions where the current was not so fast and in the slack water regions with vegetation *T. zillii, Alestes nurse, Raiamas,* some *Synodontis* species and *Chromidotilapia guntheri* were common.

While some rapid flowing rivers at low latitudes or rapids of larger rivers may be perennial, most of such streams tend to be seasonal and to show some degree of desiccation during the dry season. At these times of the year, flow may cease and the normally high degree of aeration of the water drops. Water in the pools particularly becomes low in dissolved oxygen. This means that the fish living in the rapids have to find refuge, presumably in the form of small residual waters among the rocks. In the pools themselves fish have to resist periods of relative anoxia, which they do by a range of adaptations similar to those described for potamonic species, many of which also occur in these waters.

2.4 — Communities of the potamon. The complexity of the habitats of the floodplain ecosystem is indicated in Table 1 and clearly any attempt to describe the communities of fish inhabiting them can only be superficial. This arises from the large numbers of species found in major floodplains and also from the lack of detailed knowledge of the behaviour of most of these species, particularly during the flood. Some indication of the distribution of fish in floodplains is given in Table 2 for a savanna river and Table 3 for a forested river. Distribution is also linked in these to major food type.

Because the fish fauna of the Zaire River is much more diverse than that of the Oueme, a simple listing tabulation can only be made at the generic level in Table 3.

Broadly speaking, it is possible to divide the fish species of the potamon into two main groups classified according to the strategies they adopt for copying with the adverse conditions of the dry season and the particular demands of the flood.

Firstly, there is that group of fishes which occupies the main channel during the dry season and moves out into the floodplain to breed and feed during the flood, although included in this group are some species, such as *Hydrocynus forskalii*, which apparently remain in the river channel at all times. Such species tend to be total spawners producing large numbers of eggs which are laid in one spawning just prior to or early in the flood season. Egg production can vary from about 127 000 eggs/kg of fish for *Hydrocynus forskalii* to 450 000 eggs/kg for *Barbus trispilos* (Albaret, 1979), and values for numerous species of *Alestes, Barbus, Labeo, Schilbe, Eutropius* and *Synodontis* range between these figures. Fish of this group rarely have any physical modification to resist low dissolved oxygen conditions, although it is fairly clear from work on similar species groupings in the Amazon River that the oxygen affinity of the blood can vary considerably, conferring some tolerance to low dissolved oxygen tensions in some species (Powers *et al.*, 1979). More normally, however, the fish avoid adverse conditions by migration, and movements for breeding and feeding tend to be coordinated with this requirement. Migrations have been classified by Daget (1960) into longitudinal, or those movements taken within the main river channel, and lateral, or those movements between the main channel to the floodplain. Lateral movements are undertaken by all species in this group and it is these movements which are aimed at avoiding adverse conditions on the floodplain during the dry season. Such movements appear to occur in a definite order which may be linked to the degree of tolerance of adverse conditions. Thus, resistant genera such as *Distichodus, Citharinus* or *Labeo* are apt to colonize the plain earlier and leave it later than more sensitive fishes such as *Alestes, Schilbe*

Table 2 : Main dry season habitats of fish species in the Ouémé River ordered by major trophic categories

TROPHIC CATEGORY	MAIN RIVER CHANNEL Bottom				FLOODPLAIN POOLS AND LAGOONS		
	Surface	Mud	Sand	Bank Vegetation	Surface	Bottom	Vegetated (Swampy) Areas
Mud and detritus feeders		*Heterotis niloticus* *Citharinus latus* *Labeo ogunensis* *Synodontis schall*	*Synodontis schall* *Labeo senegalensis*	*Clarias dahomeyensis* *Heterobranchus longifilis*		*Heterobranchus longifilis* *Heterotis niloticus* *Auchenoglanis occidentalis* *Phractolaemus ansorgii* *Citharinus latus* *Synodontis schall*	*Clarias dahomeyensis* *Neolebias unifasciatus*
Herbivores : micro			*Labeo senegalensis*	*Synodontis nigrita (Juv.)*	*Sarotherodon galilaeus*		
macro				*Distichodus rostratus* *Tilapia guineensis*			*Distichodus rostratus* *Tilapia guineensis*
Zooplankton	*Pellonula afzeliusi*						
Allochthonous and neuston feeders	*Alestes longipinnis*			*Alestes macrolepidotus*			*Epiplatys bifasciatus* *Epiplatys sexfasciatus*
Omnivores	*Alestes nurse*	*Marcusenius brucii* *Chrysichthys auratus* *Chrysichthys walkeri* *Synodontis melanopterus* *Synodontis nigrita*		*Clarias lazera*		*Synodontis nigrita*	*Clarias lazera* *Protopterus annectens*
Micropredators		*Synodontis sorex* *Physailia pellucida* *Hyperopisus occidentalis* *Mormyrus rume* *Brienomyrus niger* *Pollimyrus petricola* *Pollimyrus adspersus*	*Synodontis sorex* *Petrocephalus bane* *Petrocephalus bovei* *Cyphamyrus psittacus* *Eutropiellus buffei*	*Chromidotilapia guentheri* *Brienomyrus brachyistius* *Hemichromis bimaculatus*		*Chromidotilapia guentheri* *Thysia ansorgii* *Barbus callipterus* *Pollimyrus adspersus*	*Ctenopoma kingslayae*
Generalized predators	*Schilbe mystus*	*Chrysichthys nigrodigitatus* *Eutropius niloticus*		*Protopteurs annectens* *Calamoichthys calabaricus*		*Malapterurus electricus*	*Calamoichthys calabaricus*
Piscivores	*Hydrocynus forskalii* *Hydrocynus vittatus*	*Bagrus docmac* *Lates niloticus*		*Hemichromis fasciatus* *Polypterus senegalus* *Gymnarchus niloticus* *Hepsteus odoe* *Parachanna obscura*	*Hepsetus odoe*	*Parachanna africana*	*Hemichromis fasciatus* *Polypterus senegalus* *Gymnarchus niloticus* *Parachanna obscura*

Table 3 : The preferred biotopes of fish genera representing various trophic groups in equatorial forestwaters of Central Zaire (data abridged from Mattes, 1964 by Lowe-McConnell, 1975)

HABITATS / TROPHIC GROUPS	OPEN WATERS		MARGINAL WATERS			SWAMPS	FOREST STREAMS
	Pelagic zone	Benthic zone	Littoral	Bays, pools, creeks dead arms, channels	Floating prairies	Pools seasonal • permanent	
Mud-feeders		*Citharinus* *Labeo*	*Synodontis*			*Phractolaemus*	
Detritus-feeders	*Alestes*	*Gnathonemus* *Chrysichthys* *Auchenoglanis*	*Petrocephalus*	*Auchenoglanis* *Synodontis*		*Stomatorhinus* *Clarias* • *Clariallabes* *Channallabes*	*Clarias*
Omnivores	*Bryconaethiops* *Barbus*	*Gnathonemus* *Chrysichthys*	*Gnathonemus* *Petrocephalus* *Alestes* *Micralestes* *Petersius* *Bathyaethiops* *Distichodus* *Parauchenoglanis*	*Alestes* *Phenacogrammus* *Xenocharax* *Clarias*	*Distichodus* *Barbus*	*Stomatorhinus* • *Ctenopoma*	*Alestes* *Bryconaethiops* *Phenacogrammus* *Congocharax* *Neolebias* *Barbus* *Nannochromis* *Ctenopoma*
Herbivores algal-feeders				*Hemigrammo-petersius* *Pelmatochromis*	*Neolebias*		
macrophyte-feeders			*Eutropius*	*Distichodus* *Tilapia*	*Distochodus* *Synodontis*		
Plankton-feeders	*Microthrissa* *Clupeopetersius*		*Barbus*		*Aplocheilichthys*		
Carnivores using alloehthonous material (surface insects)	*Petersius* *Barilius*		*Micralestes* *Barilius*	*Phenacogrammus* *Bathyaethiops*		*Pantodon* • *Ctenopoma*	*Micralestes* *Phenacogrammus* *Epiplatys* *Aphyosemion* *Hypsopanchax*
Bottom † insect-feeders		*Gnathonemus* *Barbus* *Gephyroglanis* *Synodontis*	*Petrocephalus* *Marcusenius* *Gnathonemus* *Chrysichthys* *Tylochromis*	*Polypterus* *Petrocephalus* *Gnathonemus* *Microsynodontis*		*Polypterus* *Stomatorhinus* *Clarias* *Kribia* • *Ctenopoma*	*Barbus* *Auchenoglanis* *Clarias* *Eutropius* *Chiloglanis* *Amphilius* *Mastacembelus*

Table 3 : continued

HABITATS TROPHIC GROUPS	OPEN WATERS		MARGINAL WATERS			SWAMPS	FOREST STREAMS
	Pelagic zone	Benthic zone	Littoral	Bays, pools, creeks dead arms, channels	Floating prairies	Pools seasonal • permanent	
River margin carnivores			*Mormyrops* *Microstomatichthyoborus* *Eutropius*	*Polypterus*	*Xenomystus* *Nannocharax* *Hemistichodus* *Heterochromis* *Ctenopoma*		*Phractura* *Nannocharax* *Trachyglanis* *Hemichromis*
Mixed carnivores	*Mesoborus*	*Mormyrops* *Chrysichthys*	*Polypterus* *Mormyrops* *Schilbe* *Eutropius* *Malapterurus*	*Protopterus* *Clarias* *Pelmatochromis*	*Ctenopoma*	*Clarias*	*Hemichromis* *Ctenopoma*
Piscivores	*Odaxothrissa* *Hydrocynus* *Lates*		*Phagoborus*	*Parachanna*			*Hepsetus*
Fin-biters	*Eugnathichthys*		*Phago*	*Belonophago*			*Phago*

• Genera found in permanent swamps
† Over rocky bottoms or amongst tree debris genera include : *Gnathonemus, Chrysichthys, Dolichallabes, Synodontis, Nannochromis, Lamprologus, Mastacembelus.*

or *Synodontis*. Extensive longitudinal movements are perhaps limited to but a few species in Africa where migrations within the rivers rarely achieve the impressive proportions as the « Piracema » or « Subienda » of neotropical fishes. In fact, many of the better established migrations are potamodromous, associated with fish of riverine breeding habit moving from lakes to which they have become adapted. Nevertheless, Daget (1952) recorded *Brycinus leusiscus* as covering distances of up to 400 km upstream in its dry season migrations in the Niger river before the construction of the Markala Dam. Williams (1971) described movements in the Kafue River of up to 60 km upstream and 120 km downstream for several species including *Hepsetus odoe*. Potamodromous movements of up to 650 km upstream from Lake Chad were recorded for *Alestes baremoze* and *Alestes dentex* (Blache & Milton, 1962). Several species of *Labeo* undertake long migrations and *L. altivelis* particularly move up to 150 km up the Luapala River from Lake Mweru at the beginning of the floods. On the whole, however, the phenomenon of longitudinal migration remains poorly studied in Africa.

Secondly, there is a group of fishes which inhabit the floodplain or the floating vegetation mats fringing the main channel. Such species tend to be partial spawners exhibiting differing degrees of parental care, behaviour which secures the survival of the young under the difficult and often deoxygenated conditions of the early flood. Breeding seasons tend to be much more prolonged, starting earlier in the pre-flood period and persisting often up to peak flood, during which time several broods may be raised. Movements by these species are limited to a certain degree of lateral migration and during falling water are aimed at finding a permanent water body within the floodplain or a quiet backwater of the main river channel. Particularly striking among floodplain fishes are the various adaptations for resisting adverse or extreme environmental conditions. Several species have specific organs for airbreathing and these are sometimes so effective that fish such as *Clarias lazera* can migrate for considerable distances over moist land. Amongst African species only the lung fishes (*Protopterus*) and bichirs (*Polypterus*) have true lungs but several physostomous families have modified swim bladders which act in a similar manner. These include *Gymnarchus niloticus* and several species of Mormyridae and Notopteridae. Young forms of Lepidosirenidae, Polypteridae, Osteoglossidae and Gymarchidae also have external gills or filaments which are resorbed as the lungs or swim bladders take over the main respiratory function. Other families have developed other kinds of structure. Thus, the Channidae (*Parachanna* spp.) have suprabranchial chambers lined with a richly vascularized epithelium. The Anabantidae (*Ctenopoma* spp.) have labyrinth organs modified from the first gill arch and the Clariidae (*Clarias* and *Heterobranchus* spp.) have a similar arborescent organ developed from the second to fourth gill arches. Apart from these specific organs, several small fishes, particularly the Cyprinidontidae, for instance *Epiplatys* and *Aphyosemion*, have dorsally flattened heads and small mouths which serve to feed on surface-living insects. The same modifications, together with their characteristic posture, enables them to utilize the well oxygenated surface film of water almost indefinitely. Finally, as mentioned above, it is apparent that tropical riverine species have physiological adaptations which allow the blood to have very high oxygen affinities in those species living in regions of low dissolved oxygen tensions (Powers *et al.*, 1979). A second environmental hazard on floodplains is desiccation. Here the lung fishes particularly can survive long periods of dry weather by burrowing into the bed of a drying pool and secreting a cocoon of hardened slime in which they can survive until the next flood. Bruton (1979) in his review of the literature on survival of habitat desiccation by air breathing clariids supports the idea that *Clarias* species can also survive for some time in burrows in damp mud or wet sand. This ability, however, does not seem to extend to survival under completely dry substrates as in the case of *Protopterus*. Several cyprinodontus, notably species of *Nothobranchius*, can maintain recurrent populations in temporary pools through diapausing eggs. The fish complete their life cycle in a few weeks and lay their eggs in the bottom of a drying pool. These then remain in various stages of growth arrest until the next flood when a proportion of them are always ready to hatch (Wourms, 1972).

2.5 — Special considerations of small streams. Leopold, Wolman and Miller (1964) described the logarithmic relationship that exists between the number of streams in any river system, and their size as indicated by stream order. This relationship, which has been calculated at approximately :

$$\text{number of streams} = 1.97 \times 10^7 (0.21^{\text{stream order}})$$

by Welcomme (1976) indicates the very great number of small water courses on the African continent. In fact, order 1 streams alone probably number over 4 million and have a combined length of over half the total length of all water courses, making them the largest set of riverine ecosystems on the continent.

Low order streams may be either torrential (rhithronic) or potamonic in character, depending on the slope of the terrain and are particularly common in the headwaters of the major tributaries of the system, or draining the plateau toward the floodplain of the lower course of the river. Their channels are narrow and shallow, usually overhung with vegetation in their natural state and often blocked with fallen trees and other obstructions. Their waters are usually clear with little sediment load but because of their small size the channels tend to desiccate during the dry season, leaving the water confined in deoxygenated pools with high temperatures. The faunas of some very different streams have been described, such as the Kafunta in Uganda (Welcomme, 1969), the Ebo (Lelek, 1968), the forest brooks of Matthes (1964) or the headwater streams of the Bandama (Merona, 1981).

Despite their diversity of character, their ichthyofaunas have certain features in common.

- A very small number of species, consistent with the relationship between basin area and diversity;
- Faunas composed of species with very small adult lengths and consequently with short life spans and rapid biological cycles. Thus, dwarf species of cyprinid, characins and mormyrids, together with cyprinodonts are the most common fishes present. Other species may occur depending on the type of aquatic regime, torrential streams having rheophilic fishes and those areas which desiccate having species with modifications for auxiliary breathing such as *Ctenopoma*.

2.6 — Differences in communities between forest and savanna rivers. Although the same families and even genera are found in savanna and forest river systems, the species are usually quite distinct. Daget (1965), for instance, distinguishes between Sudanian and Guinean forms in the ichthyofauna of West Africa. The Sudanian forms are found in the savanna rivers and are extremely widely distributed in the Niger, Chad and Nile systems. The Guinean forms are much more restricted in range, are found in the south-flowing forested coastal rivers of West Africa and are related to the very distinctive ichthyofauna of the Congo-Zaire Basin.

As well as the obvious taxonomic differences between the faunas, there are also differences in the behaviour of the two types of communities arising from their response to their respective environments. Apart from the effects on the fish of the less intense seasonality of the equatorial forest rivers, there tends to be a difference in their degree of trophic specialization. The rather limited number of major studies on the fauna of the Zaire River (Poll, 1959; Gosse, 1963 and Matthes, 1964) have shown that the fishes are highly adapted to various feeding niches by specializations of the teeth, jaws, gill rakers and pharyngeal mechanisms. Specialists range from plankton-feeding small pelagic clupeids such as *Pellonula* to fin-nippers such as *Phago*. The species form separate associations linked with the several principal types of biotope as described by Matthes (1964) (see Table 3). This degree of specialization is probably favoured by the relatively stable hydrological regimes of these rivers and by the longer time thus available for feeding. Nevertheless, despite the degree of apparent specialization it would appear that à considerable proportion of the species present will take allochthonous material or detritus when it is available or when other sources of food are scarce during low waters. In fact, one may suspect together with Knöppel (1970) that the actual feeding behaviour of the fishes is less specialized than their anatomy would suggest. Knöppel, working in the Amazon — a similar river in many ways to the Zaire — found that despite a wide range of apparent specialization among 49 species, the gut contents indicated that there were no true specialists amongst them. In savanna rivers this is certainly true because such is the seasonal fluctuation in abundance of food that fish have to maintain maximum flexibility in food use. Here, the degree of physical specialization is already less than that shown by the Zaire River fauna and most species can be classified as either omnivores or generalized micro-predators, although same clear general categories do exist particularly fish-eating predators such as *Hydrocynus*, plankton feeders such as *Pellonula*, and bottom mud feeders including various species of *Labeo* and *Citharinus*. Dependence on allochthonous food sources is reduced on the savanna plains, but bottom deposits have replaced these as the most common alternative food source. Various species appear to shift their feeding preferences according to the seasonal availability of food. Typical of this are the *Brycinus* spp. studied by Daget (1952) that change from a diet of seeds and insects or even higher vegetation during rising water to feeding on plankton as the waters retreat. These findings would seem to go against the competitive exclusion principle, at least for certain types of river fish comunities, however, work by Zaret & Rand (1971) in a neotropical Panamanian stream seems to indicate that feeding specializations may be of value at times of food scarcity. At present this question remains very much open and can only be clarified after further studies become available.

3 — ASPECTS OF THE DYNAMICS OF FISH COMMUNITIES IN RIVERS

Because most rivers in Africa have a pronounced seasonality caused by the annual or biannual floods, fish in river systems have patterns of breeding, growth and mortality which are quite different from those of lacustrine species [1]. In those rivers and perennial streams where fluctuations in flow are minimal, fish behaviour more nearly approximates to that in lakes with extended seasons of breeding, feeding and growth, whereas in most rivers more normal seasonal patterns for these functions have been described by many authors. These have been considered in detail in previous chapters of this work and by such authors as Lowe-McConnell (1975) or Welcomme (1979).

3.1 — Breeding. Certain aspects of the timing of breeding are characteristic of fish in river systems and influence the dynamics of their stocks. Reproduction of most fish in flood rivers is highly seasonal and coincides with the earlier phases of the flood. Work from as far apart as the Niger (see Daget, 1954 or FAO/UN, 1970) or the Kafue (Williams, 1971) illustrates how general this tendency is. Where there are two floods per year, for example in the Zaire River (Matthes, 1964) or in such small equatorial streams as the Kafunta (Welcomme, 1969) the species tend to have two breeding seasons, although it remains to be determined whether individual fish breed twice per year or only once. Generally speaking, total spawning species such as *Barbus, Alestes* or *Clarias* tend to have much more discreet breeding seasons, whereas multiple spawners often have more extended seasons from just prior to the onset of the floods until peak floods. Indeed, some species such as the *Oreochromis* of the Shire River in Malawi, have been recorded as breeding outside the flood season entirely. This concentration of breeding activity at the beginning of the floods by most species in the system means that the juvenile fish are released into the river or onto the floodplain as the area of water is increasing.

3.2 - Feeding. Feeding by fishes in rivers is clearly linked to two main factors, food supply and population density. Because the amount of food available in the system is maximal and the density of populations is minimal during the flood, the peak of feeding activity occurs during this time in most species. Conversely, in the residual water bodies and main channels of such seasonal systems as the savanna rivers, many fish stop feeding altogether during low water. Even in species which have a perennial food source, such as allochthonous feeders, piscivorous predators or mud eaters, such as *Heterotis niloticus* (Daget, 1957) the rate of feeding is slowed considerably throughout the dry season possibly because the energy to be obtained from the diminishing food resource is more than counteracted for by the increasing energy required to forage and ingest it. Some species, however, may continue to feed unchecked throughout the

1/ With the exception of lakes such as Chilwa or Mweru Wa Ntipa, which because of their great fluctuations in level more closely resemble floodplains year, for instance the *Clarias ngamensis* studied by Willoughby & Tweddle (1978). There is less evidence for similar seasonality of feeding among the fishes of African equatorial rain-forest rivers, although information from the Zaire (Matthes, 1964) would seem to indicate reduction in feeding intensity with a falling back on alternative food source at low water.

3.3 — **Growth.** The intensified feeding during the flood period allows fish to build up substantial stores of fat to carry them through the lean months of the dry season and to provide for the build up of gonadial products for the next breeding season. This also means that many species accomplish the major part of their growth during the flood season. Dudley (1972), for instance, recorded that 75 percent of the expected first year's growth in length of *Oreochromis andersoni* and *O. macrochir* took place within six weeks of the flood peak in the Kafue River. When growth in weight is considered, even more extreme results have been obtained whereby the weight has actually fallen throughout the dry season (see, for example, *Alestes baremoze* : Durand & Loubens, 1970). The patterns of growth with rapid increases in length during the flood and nearly zero growth in the dry season produces the sort of growth curve modelled by Daget & Ecoutin (1976) for *Polypterus senegalus* (Fig. 5) and many other workers have used similar models for other species.

3.4 — **Mortality.** Of the several possible causes of natural mortality in rivers, three appear to be of major importance. Stranding or isolation of fish in temporary pools left by the retreating flood is probably the greatest single cause of death in flood rivers, although obviously this type of mortality dwindles in importance in those systems with less severe regimes. Also linked to the severity of the flood regime are those deaths which arise from adverse conditions, deoxygenation, high temperature, overcrowding, etc., during the dry season. The greater the duration of low water, the greater the mortality from these causes. The third source of mortality is predation. There is little information on predation rates during the flood, a period when the fish are very dispersed, but there is no doubt that the loss of fish to predators increases considerably as the community is concentrated at the end of the floods. At this time, predation by other fish, birds and a variety of reptiles and mammals is maximal although continuing losses of fish undoubtedly occur throughout the dry season. This adds up to a pattern of low mortality at the community level during the flood, increasing mortality rate during falling water possibly with a maximum at about bankfull and continuing high mortality during low water.

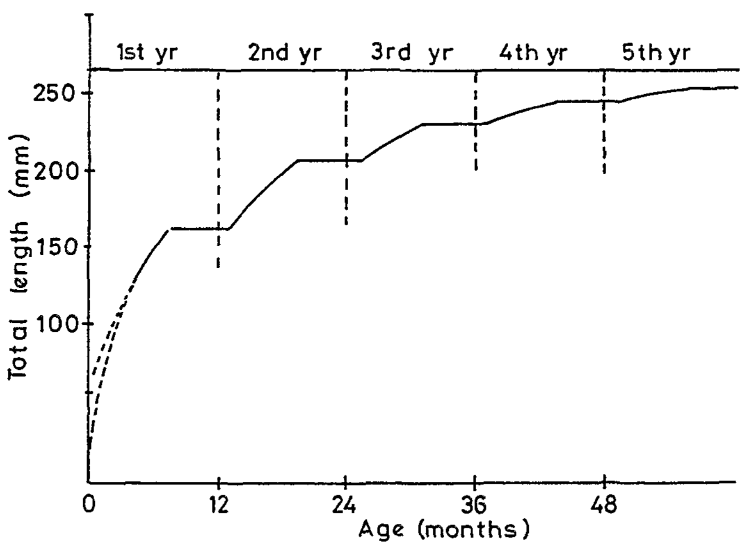

Fig. 5 : Mean linear growth of *Polypterus senegalus* for the first five years of life (after Daget and Ecoutin, 1976).

3.5 — Dynamics. The patterns for growth and mortality in flood rivers have been combined by Welcomme & Hagborg (1977) to give a simulation of the dynamics of a fish community in a flood river. The resulting curves (Fig. 6) indicate that biomass (and numbers) increase rapidly to a maximum at bankfull on the falling flood. Biomass thereafter declines to a minimum just prior to the following flood. The degree to which the increase occurs may be linked to both the extent of flooding and the amount of water remaining in the system at low water. This prediction is to a certain extent confirmed by the behaviour of fish catches in response to the flood regimes of preceding years. Thus catches are generally better in years following good floods than in years following poor ones, a principle described by regressions for a series of data from three African rivers by Welcomme (1975). The simulation for flood rivers cannot be extended validly to those rivers having only small annual variations in flow. Here, the dynamics may be very different due to the more lacustrine patterns of growth and mortality.

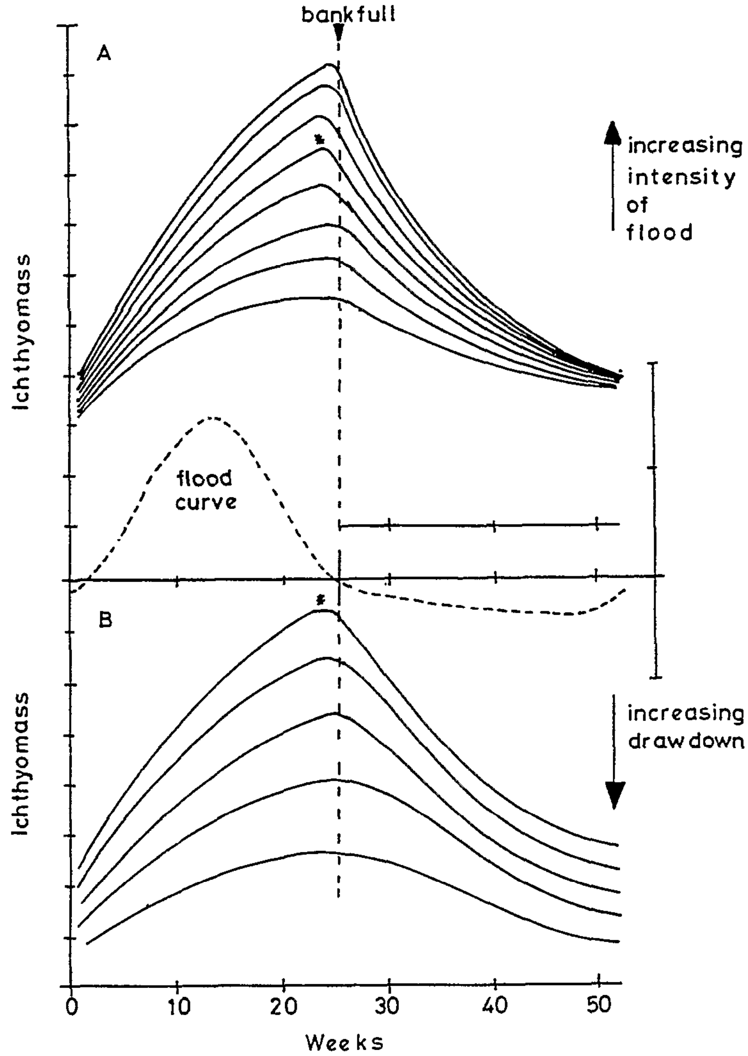

Fig. 6 : Computer-generated curves showing changes in total ichthyomass with time for different flood regimes where (A) the low-water regime is constant and the high-water regime varies; and (B) where the igh-water regime is constant but the low-water regime varies. Curve* in A and B correspond.

3.6 — Adaptive significance of the dynamics and population structure of rivers fish communities. From the above, it is apparent that the species of fish inhabiting the potamon of rivers are adapted in all aspects of their biological functions to a single event and the seasonal flood. A great range of adaptations is present and the various breeding and feeding strategies obviously result in variations in breeding success and growth between years in response to differences in the flood regimes. Because of this, fluctuations in the relative abundance of individual species between years can be expected to occur and, indeed, have been recorded from many river systems. The best example of this kind of variation is perhaps the history of change in relative abundance of *Hydrocynus brevis* and *Hydrocynus forskalii* during the Sahelian drought of the Niger (Dansoko, Breman & Daget, 1976). Although very similar in form and function, *H. brevis* breeds on the floodplain during the floods, whereas *H. forskalii* passes the whole of its life in the river and breeds in the main channel at low water. Consequently, *H. brevis* predominates in years of good flood and *H. forskalii* is the more abundant in years of drought.

Another type of adjustment to varying flood conditions is suggested by Dudley (1979) who found both *Oreochromis macrochir* and *O. andersoni* to be stunted but more abundant during years of poor flood when lessened amounts of water were left in the Kafue system during the dry season, than during years of good flood when the fish grew and matured at greater size-behaviour thought by him to enable the species to respond more quickly to good flood conditions when they occurred. As little data of this type exists for other species it is interesting to speculate whether similar adaptations are, in fact, widespread and that with changing flood conditions the total of the individual variations among species or even within a species permits, the community as a whole to adjust to the new conditions as they occur in such a way as to maximize production or biomass. Hints from other parts of the world would suggest that these mechanisms are indeed widespread. For instance, Stott (1967) found that the cyprinids *Rutilus rutilus* and *Gobio gobio,* exist in two phases within a North Temperate river, one phase being static and territorial, the other being migratory. By extension to other European waters such as the Danube where the migrating phases are dominant one might assume that intra-specific adjustments can also be made. Whatever the mechanism it would appear that floodplain fish communities are very resilient to short-term changes in flood regime, and recover rapidly when more normal conditions are established. They will not, however, resist long-term alterations in the nature of the flood and changes in species composition and overall abundance, both upstream and downstream of dams, rapidly follow upon impoundment of the river. Stabilization of the flow regime in this way probably favours those elements of the community which are behaviourally adapted to the more static habit, and migratory species tend to disappear.

4 — ESTIMATES OF STANDING STOCK

Only very few estimates of standing stock exist for African rivers and these are quoted here to give some indication of the size of the fish communities inhabiting such waters. Clearly in view of the fluctuating nature of the ichthyomass as shown in the preceding section it is difficult to establish a mean value which would be comparable with other types of water. Furthermore, such estimates should be interpreted only in relation to a particular phase in the flooding of the system for reasons of accessibility. Samples are taken most often at low water when the fish are concentrated in the main river channel and in the residual waters of the floodplain. Because of this the biomass per unit area figures obtained are usually at the high end of the annual range.

4.1 — Estimates from main river channels. Some estimates have been made on ichthyomass in small tropical streams which give more or less comparable results. Malaisse (1976) for example found values of 1.3, 26.1 and 31.7 kg km^{-1} in successive downstream reaches of the Luanza River and Balon & Coche (1974) quote similar figures of 7, 21 and 91 kg km^{-1} for the Kalomo tributary of Lake Kariba. Estimates from the main channel of the potamon are much higher and Kapetsky (1974) found standing stocks of five main commercial species of 106.5 ± 29.2; 576.7 ± 129.2 and 396.6 ± 63.9 kg km^{-1} in three reaches of the Kafue River. In the Chari River, Loubens (1969 and 1970) obtained estimates of 15 138 fish ha^{-1} weighing 861 kg ha^{-1} by poisoning a pool in the Chari River. Daget, Planquette & Planquette (1973) also using poisons, obtained estimates from two sites on the Bandama River. In both of these there was a loss of biomass during the dry season, from 3417 fish ha^{-1} (125 kg ha^{-1} to 1411 fish ha^{-1} (50 kg ha^{-1}) in five months at one site and from 2271 fish ha^{-1} (257 kg ha^{-1} to 996 fish ha^{-1} (113 kg ha^{-1}) in six months at the others.

Quiet back waters of the main channel may harbour higher standing stocks. For example, Loubens (1969) found 2 150 kg ha^{-1} in a side arm of the Chari consisting of over 22 000 fish ha^{-1}. The same side arm gave subsequent estimates of 5 616 kg ha^{-1}, 1 600 kg ha^{-1} and 369 kg ha^{-1} showing something of the variability that may be expected from the same water body. These figures, however, may be relatively high as Daget, Planquette & Planquette (1973) found only 149 kg ha^{-1} and 350 kg ha^{-1}in a Bandama River back water.

4.2 — Estimates from floodplain pools. Fish populations in floodplain pools during the dry season may be influenced by a number of factors. For instance, Fox (1976) estimates 100-200 kg ha^{-1} to be usual in unenriched pools of the Okavango Delta, whereas pools enriched by cattle dug around the edge of the swamp had the much higher ichthyomass of 700 kg ha^{-1}. The form of the water body and the nature of its bottom may also play a part in determining both the types of species present and the ichthyomass. Reizer (1974) found that long narrow pools in the Senegal had higher standing stocks (205 ± 155 kg ha^{-1}) than round pools (13 ± 6 kg ha^{-1}), and Holden (1963) showed that a greater proportion of fish in the Sokoto River preferred intermediate sand/mud bottoms (1 012 kg ha^{-1}) as opposed to sand (785 kg ha^{-1}) or mud (233 kg ha^{-1}). The presence or absence of vegetation can also influence the standing stock as University of Michigan *et al.* (1971) found population densities in the Kafue Flats to be higher in vegetated areas than open water areas during floods (2 682 kg ha^{-1} as against 337 kg ha^{-1}). In the dry season this may be reversed, with very low populations under vegetation and ichthyomasses of up to 426 kg ha^{-1} in open waters. Nevertheless, very high standing stocks have been recorded from vegetated pools from the Ouémé, where the natural water bodies of the floodplain have been enlarged and extended as a form of fish culture. Here, values of between 2 100 kg ha^{-1} and 1 500 kg ha^{-1} were obtained from 34 and 26 ponds, respectively, the catch consisting uniquely of airbreathing fishes.

4.3 — Estimates from whole systems. Only one attempt has been made at a comprehensive estimate for fish from a whole section of a river-floodplain system. This was carried out by University of Michigan *et al.* (1971) by extrapolating from a limited number of samples in four habitats of the Kafue Flats (Table 4).

Table 4 : Summary of high water and low water estimated of ichthyomass from the Kafue River and floodplain system (from University of Michigan *et al.*, 1971)

	Area (ha)	Ichthyomass (kg/ha)	Total ichthyomass (t)
High water			
Open water lagoon	126 000	337	42 462
Vegetated lagoon	16 000	2 682	42 912
Grass marsh	136 000	64	8 704
River channel	5 300	337	1 786
Total	283 300		95 864
Low water			
River channel	4 800	204	959
Open water lagoon	113 000	426	48 138
Vegetated lagoon	14 000	592	8 288
Total	131 800		57 400

CONCLUSION

Know edge of the ecology of fish communities in African river systems is still somewhat limited, although sufficient work has been carried out to theorize on some of the general principles regulating the communities in some types of rivers. In general, fish in the large savanna rivers such as the Niger, Senegal or Kafue have been best studied, although there is a need for more work to clarify certain issues. Of the purely biological questions that need resolutions. For example, those relating to responses to year-to-year differences in water regimes, the significance and extent of migration, estimates of standing stocks, seasonality of feeding and reproduction, and detailed analysis of niche selection during both dry and wet seasons. Also necessary is an improved understanding of the energy flow through the river system and the species of animals and plants living in it. At present the information needed for such understanding is lacking, particularly concerning the complex nutrient and energy interrelationships between the dry and wet phases of the floodplains. Perhaps of more immediate importance, however, is information on how such fish communities behave both under heavy exploitation by a fishery and to environmental modifications such as dams or other forms of flow control.

Less attention has been paid to the fisheries of equatorial forested rivers and much more work needs to be carried out on all aspects of the biology and ecology of the species inhabiting such waters in order to elucidate their productivity patterns.

RÉSUMÉ

En dépit de la grande extension du réseau lotique africain, son ichtyofaune est moins intensivement étudiée que celle des lacs et des réservoirs.

Les rivières peuvent être classées en fonction de leur régime hydrologique (amplitude des crues) ou en fonction de la zone de végétation qu'elles traversent. Les cours d'eau de la forêt équatoriale ont, en général, des crues peu marquées, leur eau est acide, pauvre en ions et en matière en suspension et la production primaire y est faible. A l'inverse, les rivières de savanne ont des crues prononcées, une eau chargée en minéraux et limon, elles bénéficient d'un ensoleillement important et leur production primaire est élevée. La zonation physique des rivières africaines ne ressemble pas en général à celle des rivières des régions tempérées car la succession des différentes zones est souvent perturbée. Néanmoins, on peut distinguer des zones de rhithron qui comprennent des rapides sur rochers et des vasques d'eau plus calme et des zones de potamon dans lesquelles le lit est large, plat et méandreux et qui sont des plaines d'inondation. La caractéristique essentielle des rivières africaines est le rythme saisonnier des crues qui exerce une forte influence sur la biologie des poissons.

Du point de vue des communautés ichtyologiques on note une grande richesse spécifique corrélée à la taille du bassin et une abondance de petites espèces au cycle court. Mis à part les zones estuariennes, originales par la présence d'espèces marines et estuariennes dans les peuplements, on distingue schématiquement des communautés de rhithron et des communautés de potamon. Dans les premières, les espèces de rapides présentent des adaptations leur permettant de résister au courant (ancrage, refuge ou nage puissante), alors que les espèces des vasques sont en général de petite taille et occupent, par une sélection très poussée des niches, tous les microhabitats disponibles. Les communautés du potamon sont schématiquement composées de deux groupes d'espèces à stratégie différente. Les unes migrent dans la plaine d'iondation pour se reproduire et s'alimenter. Elles ont une reproduction à ponte unique et présentent peu d'adaptations à l'anoxie. Les autres, généralement sédentaires, habitent la plaine d'inondation et les bords du lit principal. Leur reproduction est à pontes partielles et il existe des adaptations à l'anoxie. Les cours d'eau de premier ordre présentent un certain nombre de caractéristiques physiques originales (caractère temporaire, eau pauvre en ions et sédiments, lit étroit et peu profond, etc.). Leur ichtyofaune, relativement pauvre, est composée de petites espèces à cycle court. Une comparaison entre rivière de savanne et de forêt fait ressortir des différences, aussi bien d'ordre taxonomique que comportemental. Une tendance à une spécialisation alimentaire plus marquée dans les rivières de forêt est notée, bien qu'il existe de nombreux contre-exemples.

Le caractère saisonnier des crues provoque chez les communautés de poissons une dynamique particulière. Pour un grand nombre d'espèces du potamon, la reproduction intervient au début de la crue. Suit une phase d'alimentation intense qui provoque une croissance accélérée. A la fin de la décrue et pendant l'étiage l'alimentation est limitée par la disponibilité d'aliments, la croissance ralentie ou totalement stoppée, et la mortalité est maximale. La combinaison des courbes de croissance et de mortalité indique que la biomasse augmente rapidement jusqu'au retrait des eaux, puis diminue jusqu'à un minimum situé juste avant la crue. L'importance de la biomasse serait liée à la durée de l'inondation d'une part et au niveau d'eau minimum de l'étiage d'autre part. De ces observations il ressort clairement que les poissons développent des adaptations à la crue saisonnière. Des ajustements existent également vis à vis des variations interannuelles de la crue, aussi bien au niveau de l'espèce (vitesse de croissance ou taille de maturation modifiées) qu'au niveau de la communauté (changement de l'importance relative des espèces). Il apparaît que les communautés résistent bien aux changements à court terme, mais sont irréversiblement modifiées par des altérations définitives (cas des barrages).

Il existe peu d'estimations de stock dans les rivières africaines et les données disponibles sont extrêmement variables. La zone de la rivière, les caractéristiques physiques, l'environnement végétal, l'époque, sont autant de facteurs de variation de la biomasse de poisson dans un milieu donné. Il est nécessaire, pour donner une estimation globale d'un système, d'échantillonner à différentes saisons tous les habitats constitutifs.

REFERENCES

ALBARET J.J., 1979 - Revue des recherches entreprises sur la fécondité des poissons d'eau africains. *ORSTOM, Réunion de travail sur la limnologie africaine*, Nairobi, 16-23 décembre. 67 p.
BALON E.K. & COCHE A.G., 1974 - *Lake Kariba : A man-made tropical ecosystem in Central Africa.* Monographica Biologicae : The Hague, Junk. 767 p.
BLACHE J. & MILTON F., 1962 - Première contribution à la connaissance de la pêche dans le bassin hydrographique Logone-Chari Lac Tchad. *Mém. ORSTOM*, 4 (1). 142 p.
BRUTON M.N., 1979 - The survival of habitat desiccation by air-breathing clariid catfishes. *Env. Biol. Fish.*, 3 (3/) : 273-280.
CRASS R.S., 1962 - Physical barriers and the dispersion of freshwater fish with particular reference to Natal. *Ann Cape Prov. Mus.*, II : 229-232.
DAGET J., 1952 - Mémoires sur la biologie des poissons du Niger, 1. Biologie et croissance des espèces du genre *Alestes. Bull. Inst. Fr. Afr. noire*, 14 (1) : 191-225.
DAGET J., 1954 - Les poissons du Niger supérieur. *Mém. Inst. Fr. Afr. noire*, 36. 391 p.
DAGET J., 1957 - Mémoires sur la biologie des poissons du Niger moyen, 3. Reproduction et croissance d'*Heterotis niloticus.* Ehrenberg, *Bull. Inst. Fr. Afr. noire*, 19 : 295-323.
DAGET J., 1960 - Les migrations de poissons dans les eaux douces tropicales africaines. *Proc. IPFC*, 8 (3) : 79-82.
DAGET J., 1965 - Poissons de Côte d'Ivoire (Eaux douces et saumatres). *Mém. Inst. Fr. Afr. noire*, 74. 385 p.
DAGET J. & ECOUTIN J.M., 1976 - Modèles mathématiques de production applicables aux poissons subissant un arrêt annuel prolongé de croissance. *Cah. ORSTOM (Hydrobiol.)*, 10 (2) : 59-70.
DAGET J., PLANQUETTE N. & PLANQUETTE P., 1973 - Premières données sur la dynamique des peuplements de poissons du Bandama (Côte d'Ivoire). *Bull. Mus. natn. Hist. nat.*, (Paris 3^{m} Ser.) 151 : 129-43.
DANSOKO F.D., BREMAN H & DAGET J., 1976 - Influence de la sécheresse sur les populations d'*Hydrocynus* dans le delta central du Niger. *Cah. ORSTOM (Hydrobiol.)*, 10 (2) : 71-66.
DUDLEY R.G., 1972 - Biology of *Tilapia* of the kafue floodplain, Zambia : predicted effects of the Kafue Gorge Dam. Ph. D. Dissertation, University of Idaho, Moscow, U.S.A. 50 p.
DUDLEY R.G., 1979 - Changes in growth and size distribution of *Sarotherodon macrochir* and *Sarotherodon andersoni* from the Kafue floodplain, Zambia, since construction of the Kafue Gorge Dam. *J. Fish. Biol.*, 1205-223.
DURAND J.R. & LOUBENS G., 1970 - Variations du coefficient de condition chez les *Alestes baremoze* (Pisc. Charac.) du bas Chari et du Lac Tchad. *Cah. ORSTOM (Hydrobiol.)*, 4 (1) : 27-41.
FAO/UNDP, 1970 - Report of the Government of Nigeria on fishery investigations on the Niger and Benue Rivers in the northern region and development of a programme of riverine fishery management and training. Based on the work of M.P. Motwani. *Rep. FAO/UNDP (TA)*, 2771. 196 p.
FARQUHARSON F.L., 1962 - The distribution of Cyprinides in South Africa. *Ann. Cape Prov. Mus.*, II : 233-251.
FOX P.J., 1976 - Preliminary observations on fish communities of the Okavango Delta. In : *Proceedings of the Symposium on the Okavango Delta and its future utilization.* National Museum, Gabarone, Botswana, 30 August-2 September 1976. Gabarone, Botswana Society : 125-130.
GAIGHER I.G., 1973 - The habitat preferences of fishes from the Limpopo River system, Transvaal and Mozambique. *Koedoe*, 16 : 103-116.
GOSSE J.-P., 1963 - Le milieu aquatique et l'écologie des poissons dans la région de Yangambi. *Ann. Mus. R. Afr. Centr. Zool.*, ser. 8v, *Sci. Zool.*, No 116 : 113-270.
HARRISON A.D., 1965 - River zonation in Southern Africa. *Arch. f. Hydrobiol.*, 61 (3) : 380-386.
HOLDEN M.J., 1963 - The populations of fish in dry season pools of the River Sokoto. *Fish. Publ. Colon. Off.*, 19. 58 p.
HUET M., 1949 - Aperçu des relations entre la pente et les populations des eaux courantes. *Schwiez. Z. Hydrol.*, 11 : 333-351.

ILLIES J. & BOTOSANEANU L., 1963 - Problèmes et méthodes de la classification de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. *Mitt. int. Verein theor. angew Limnol.*, 12 : 1-57.

JACKSON P.B.N., 1961 - *The fishes of Northern Rhodesia.* Lusaka, Zambia, Government Printer. 140 p.

KAPETSKY J.M., 1974 - Growth, mortality and production of five fish species of the Kafue River floodplain, Zambia. Ph. D. Dissertation, University of Michigan. 194 p.

KNÖPPEL H.A., 1970 - Food of Central Amazonian fishes. Contribution to the nutrient ecology of Amazonian rain forest streams. *Amazoniana*, 2 (3) : 257-352.

LELEK A., 1968 - The vertical distribution of fishes in the Ebo Stream and notes to the fish occurence in the Lake Bosumtwi, Ashanti, Ghana. *Zool. Listy*, 17 (3) : 245-251.

LEOPOLD L.B., WOLMAN M.C. & MILLER J.-P., 1964 - *Fluvial processes in geomorphology.* San Francisco, W.H. Freeman and Co. 522 p.

LOUBENS G., 1969 - Etude de certains peuplements ichtyologiques par des pêches au poison (1re note). *Cah. ORSTOM (Hydrobiol.)*, 3 (2) : 45-73.

LOUBENS G., 1970 - Etude de certains peuplements ichtyologiques par des pêches au poison (1re note). *Cah. ORSTOM (Hydrobiol.)*, 4 (1) : 45-61.

LOWE-McCONNEL R.H., 1975 - *Fish communities of tropical freshwaters.* London, Longman. 337 p.

MALAISSE F., 1976 - Ecologie de la rivière Luanga. J.J. Symoens ed. *Cercle hydrobiol. de Bruxelles.* 151 p.

MATTHES H., 1964 - Les poissons du lac Tumba et de la région d'Ikela. Etude systématique et écologique. *Ann. Mus. R. Afr. Centr. Zool.*, ser. 8v, *Sci. Zool.*, 126 : 204.

MERONA B. de, 1981 - Zonation ichtyologique du bassin du Bandama (Côte d'Ivoire). *Rev. Hydrobiol. Trop.*, 14 (1) : 63-75.

MERONA B. de & ALBARET J.-J., 1978 - Répartition spatiale des poissons dans les radiers des rivières de Côte d'Ivoire. ORSTOM, Bouaké, No 17. 78 p. multigr.

MINCKLEY W.L., 1963 - The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildl. Monogr. Chestertown*, 11. 124 p.

POLL M., 1959a - Recherches sur la faune ichtyologique de la région du Stanley Pool. *Ann. Mus. R. Congo belge, Sci. Zool.*, 71 : 75-174.

POLL M., 1959b - Aspects nouveaux de la faune ichtyologique du Congo belge. *Bull. Soc. Zool. France*, 84 : 259-271.

POWERS D.A. *et al.*, 1979 - A comparative study of the oxygen equilibrium of blood from 40 genera of amazonian fishes. *Comp. Biochem. Physiol.*, 62A : 67-85.

REIZER C., 1974 - Définition d'une politique d'aménagement des ressources halieutiques d'un écosystème aquatique complexe par l'étude de son environnement abiotique et anthropique. Le fleuve Sénégal moyen et inférieur. Docteur en Sciences de l'envirionnement. Dissertation Arlon. Fondation Universitaire Luxembourgeoise, 4 vol. 525 p.

STOTT B., 1967 - The Movements and population densities of roach *Rutilus rutilus* (L.) and gudgeon [*Gobio gobio* (L.)] in the River Mole. *J. Anim. Ecol.*, 36 : 407-423.

SVENSSON G.S.O., 1933 - Freshwaters fishes from the Gambia river (British West Africa). Results of the Swedish expedition, 1931. *K. Svensk. Vetenskskopsabad. Handl.*, 12. 13 p.

SYDENHAM D.H.J., 1977 - The qualitative composition and longitudinal zonation of the fish fauna of the River Ogun. *Rev. Zool. Afr.*, 91 (4) : 974-996.

University of Michigan *et al.*, 1971 - The fisheries of the Kafue River Flats, Zambia, in relation to the Kafue Gorge Dam. Report prepared for FAO/UN acting as executing agency for UNDP. Ann Arbor, Michigan, University of Michigan, FI : SF/Z-M 11 : *Tech. Rep.*, 1. 161 p.

VANNOTE R.L., 1980 - The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37 : 130-137.

WELCOMME R.L., 1969 - The biology and ecology of the fishes of a small tropical stream. *J. Zool. Lond.*, 158 : 485-529.

WELCOMME R.L., 1975 - The fisheries ecology of African floodplains. *CIFA Tech. Pap.*, 3. 51 p.

WELCOMME R.L., 1976 - Some general and theoretical considerations on the fish yield of African rivers. *J. Fish Biol.*, 8 : 351-364.

WELCOMME R.L., 1979 - *Fisheries ecology of floodplain rivers.* London, Longmans. 317 p.

WELCOMME R.L. & HAGBORG D., 1977 - Towards a model of a floodplain fish population and its fishery. *Environ. Biol. Fish.*, 2(1) : 8-24.
WILLIAMS R., 1971 - Fish ecology of the Kafue River and floodplain environment. *Fish. Res. Bull. Zambia*, 5 : 305-330.
WILLOUGHBY N.G. & TWEDDLE D., 1978 - The ecology of the commercially important species in the Shire Valley fishery, southern Malawi. In : *Symposium on river and floodplain fisheries in Africa.* Bujumbura, Burundi, 21-23 November 1977. *CIFA Tech. Pap.*, 5 : 137-152.
WOURMS J.P., 1972 - The developmental biology of annual fishes. 3. Pre-embryonic and embryonic diapause of variable duration in the eggs of annual fishes. *J. Exp. Zool.* : 182, 389, 414.
ZARET T.M. & RAND A.S., 1971 - Competition in tropical stream fishes : support for the competitive exclusion principle. *Ecology*, 52 (2) : 336-342.