

Chapitre 15

FISH COMMUNITIES IN MAN-MADE LAKES

PEUPELEMENTS ICHTYOLOGIQUES DES LACS DE BARRAGE

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1 - INTRODUCTION

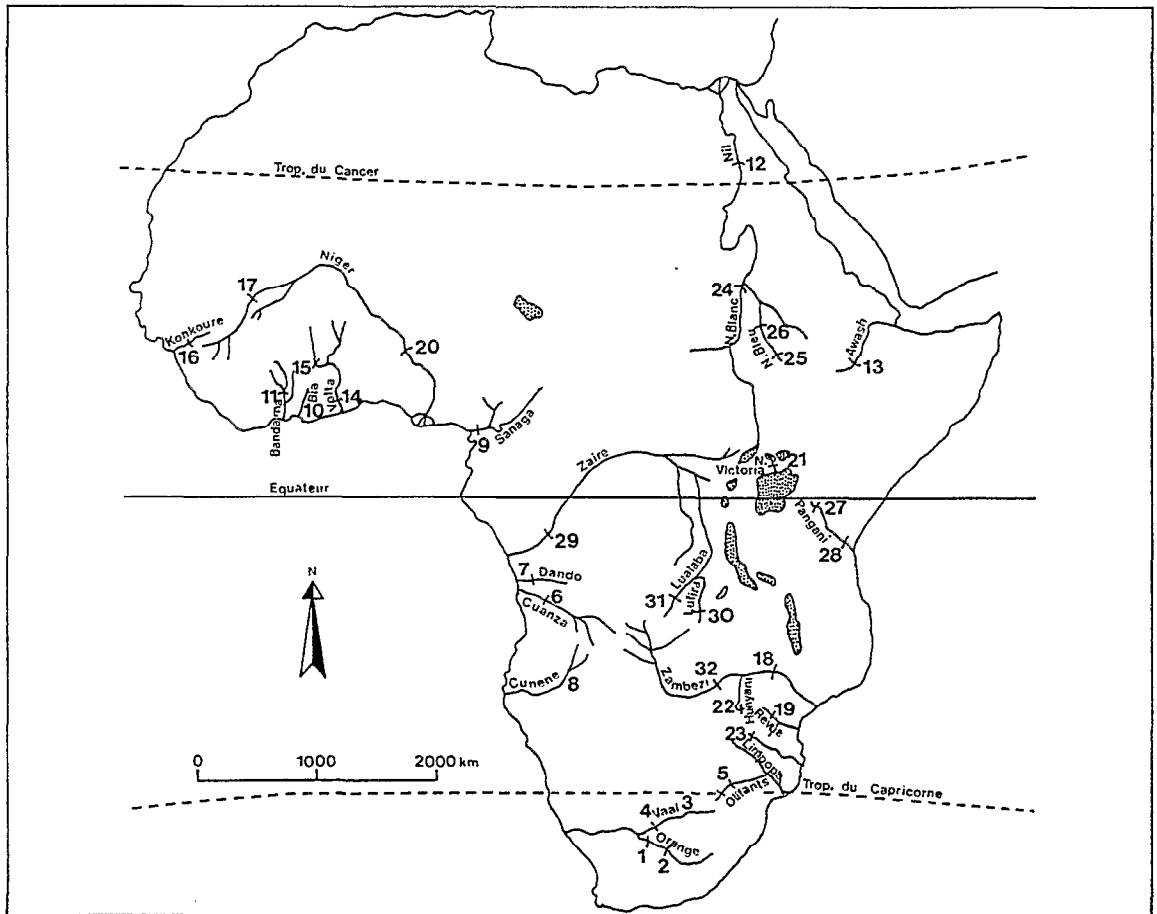
There are very few major rivers in Africa which have not had at least one barrier for the impoundment of water erected across them. This process, especially for the larger man-made lakes, has been comparatively recent, with many of the greater impoundments being filled in the decade or so prior to the mid 1970s. Several of the more immediate consequences of impoundment have therefore been examined, and there is a literature on these aspects largely pertaining to Africa (Ackerman *et al.*, 1973; Ward & Stanford, 1980).

Even so, it is not generally appreciated how great is the extent of reservoirs, large and small; more are built every year in order to meet the water demands of a rapidly multiplying human population. In Zimbabwe, for example, figures provided by the Ministry of Water Development show that there are over 100 large dams (more than 25m high) and about 8000 small ones. A similar situation probably applies over the whole of Africa, and while they must affect the fish fauna, few cases have been studied in any detail. It is a pity that very few data are available for Africa's smaller dams, and this is sure to be a rewarding field for the future.

Some of the larger African dams are listed in Table 1, while their locations and the river systems on which they are sited may be seen in Fig. 1.

The short-term sequence of events after an African river is dammed is becoming known. The fish community which becomes established tends to be distinctive for each impoundment, depending on many factors. Amongst these are the geography and climate of the lake basin and its catchment, physical and chemical characteristics of its water mass, the composition of the original fish fauna of the basin and the presence or absence of introduced species. But in spite of these attributes which are unique to each case, certain generalities are common to all. The communities of fish may be discussed in terms of these, with distinctive features of some individual lakes being quoted as examples of variation.

A useful bibliography on major African man-made lakes has been prepared by Ita and Petr (1983) to which reference for much of the detailed information which has been accumulated on African reservoirs during the past three decades may be made. Figure 2 (from Petr, 1978, after Freeman, 1974) summarises benefits and negative environmental consequences of dam construction, which is useful in placing the adaptation and development of fish communities in a proper relationship with other environmental consequences of impounding in the great rivers of Africa.

SOUTH AFRICA

1. Lake Le Roux
2. Lake Verwoerd
3. Vaaldam
4. Bloemhof
5. Loskop

ANGOLA

6. Casseque
7. Mamubas
8. Matala

CAMEROUN

9. Edéa

IVORY COAST

10. Ayamé
11. Kossou

EGYPT

12. Assouan

ETHIOPIA

13. Koka

GHANA

14. Akossombo (L. Volta)
15. Bui

GUINEE

16. Souapiti

MALI

17. Markala

MOZAMBIQUE

18. Cabora Bassa
19. Revue

NIGERIA

20. Kainji

UGANDA

21. Owen falls

ZIMBABWE

22. MacIlwaine
23. Kyle

SUDAN

24. Gebel Aulia
25. Roseires
26. Sennar

TANZANIA

27. Nyumba Ya Mungu
28. Pangani Falls

ZAIRE

29. Iroa
30. Mwadingusha
31. Nzilo

ZAMBIE/ZIMBABWE

- (Zambia/Zimbabwe)
32. Kariba

Fig. 1 : Geographical location and river system of some larger African man-made lakes.

Table 1. Closure date, area, depth and estimated yield statistics and numbers of fishermen per km² of surface area at maximum retention level for some larger African man-made lakes.

| Lakes | Dam first closed | Area (km ²) | Max.depth (m) | Mean depth (m) | Cond. pS cm ⁻¹ | Yield kg ha ⁻¹ Yr ⁻¹ |
|-----------------|------------------|-------------------------|---------------|----------------|---------------------------|--|
| Ayamé | | 186 | 20 | 10.0 | 100 | 74 |
| Bloemhof | 1970 | 228 | | 5.6 | | Nil |
| Cahora Bassa | 1974 | 2660 | 151 | | | |
| Gebel Aulia | 1937 | 600 | 12 | 6.0 | | |
| H.F. Verwoerd | 1972 | 374 | 67 | 16.3 | 150 | Nil |
| Kafue Gorge | 1971 | 809 | 58 | | | 93 |
| Kainji | 1968 | 1290 | 55 | 11.0 | 73 | 57 |
| Kariba | 1958 | 5400 | 120 | 29.2 | 100 | 46 |
| Koka | | 250 | | 9.0 | | |
| Kossou | 1971 | 1710 | 57 | 14.3 | 100 | 80 |
| Loskop | 1939 | 168 | | 10.8 | | |
| McIlwaine | 1956 | 25 | 28 | 9.4 | 120 | 120 |
| Mwadingusha | | 393 | 14 | 2.6 | 217 | 127 |
| Nasser | 1964 | 3330 | 85 | 25.0 | 230 | 21 |
| Nyumba Ya Mungu | 1965 | 150 | 48 | 6.0 | 850 | 200 |
| Nzilo | | 280 | | 10.0 | 400 | 100 |
| P.K. Le Roux | 1976 | 138 | 90 | 13.8 | 150 | Nil |
| Roscires | 1966 | 290 | 68 | 10.0 | | |
| Sennar | 1935 | 140 | 26 | 16.0 | | |
| Vaal | 1938 | 293 | 52 | 8.1 | | |
| Volta | 1964 | 8727 | 70 | 19.0 | 118 | |

POTENTIAL ENVIRONMENTAL CONSEQUENCES OF A TROPICAL DAM

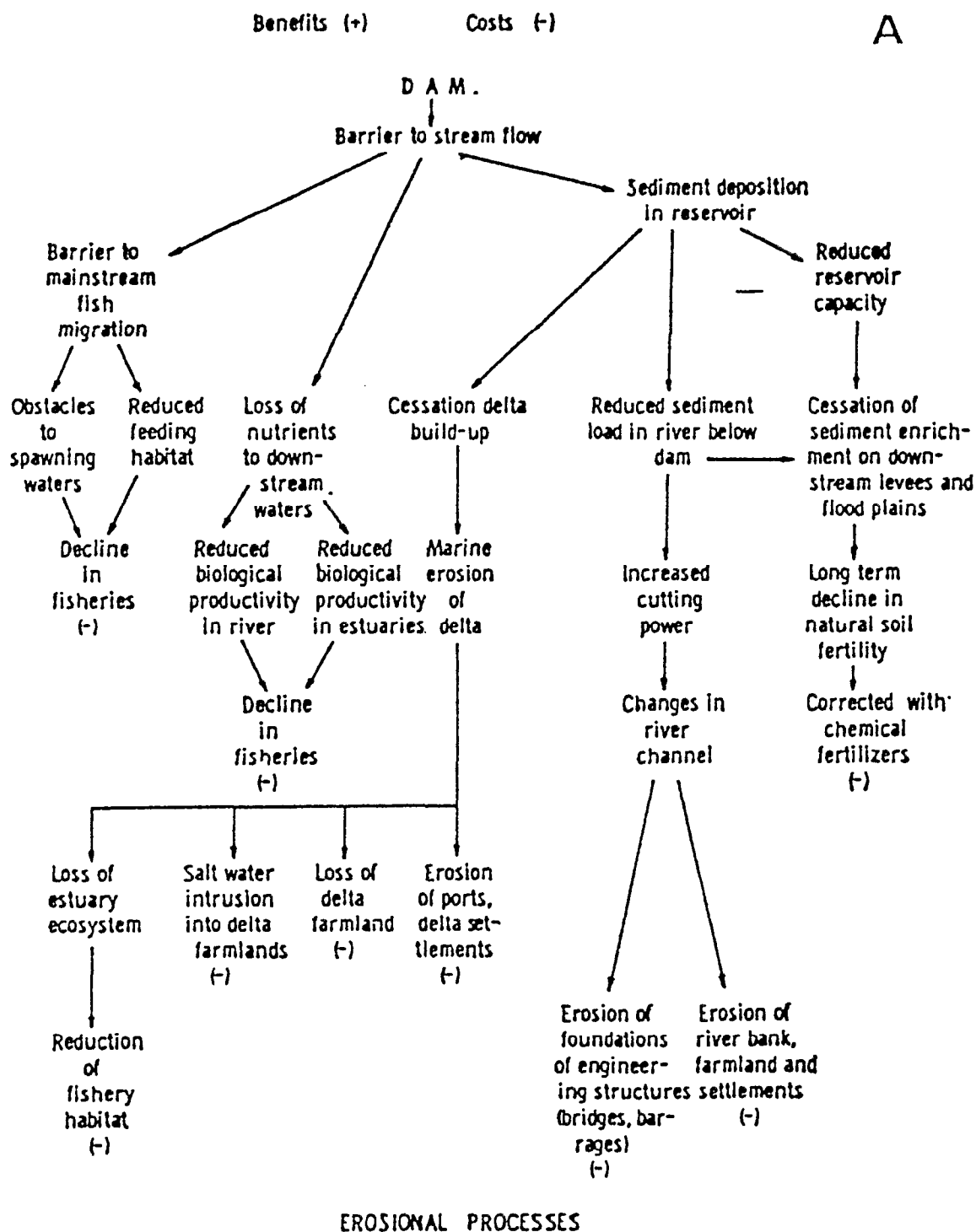


Fig. 2 : A simplified diagram of environmental consequences of a tropical river impoundment (redrawn and modified from Freeman, 1974 by Petr, 1978).

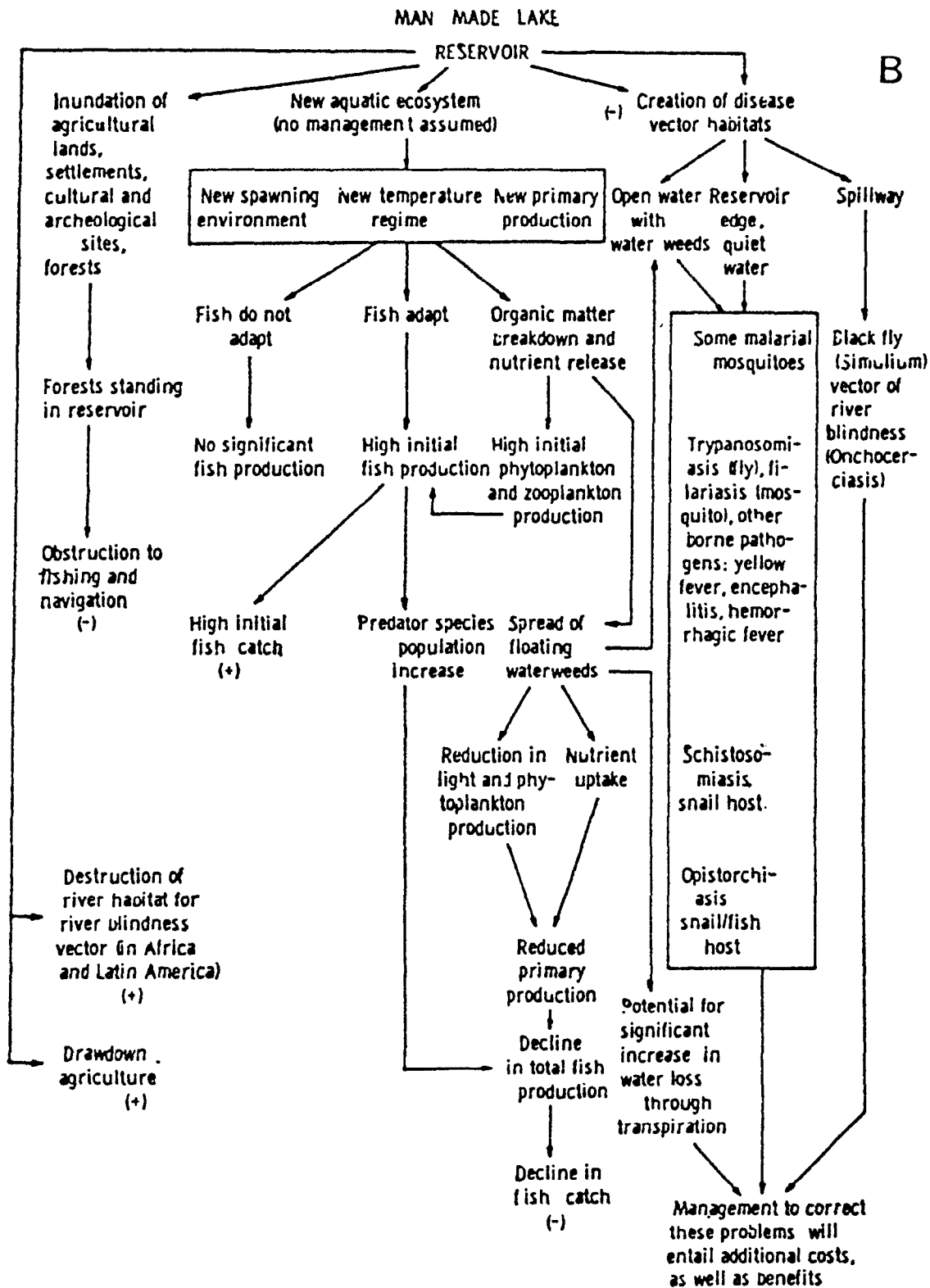


Fig. 2 : (continued)

DOWNSTREAM HYDROLOGY AND LAND USE

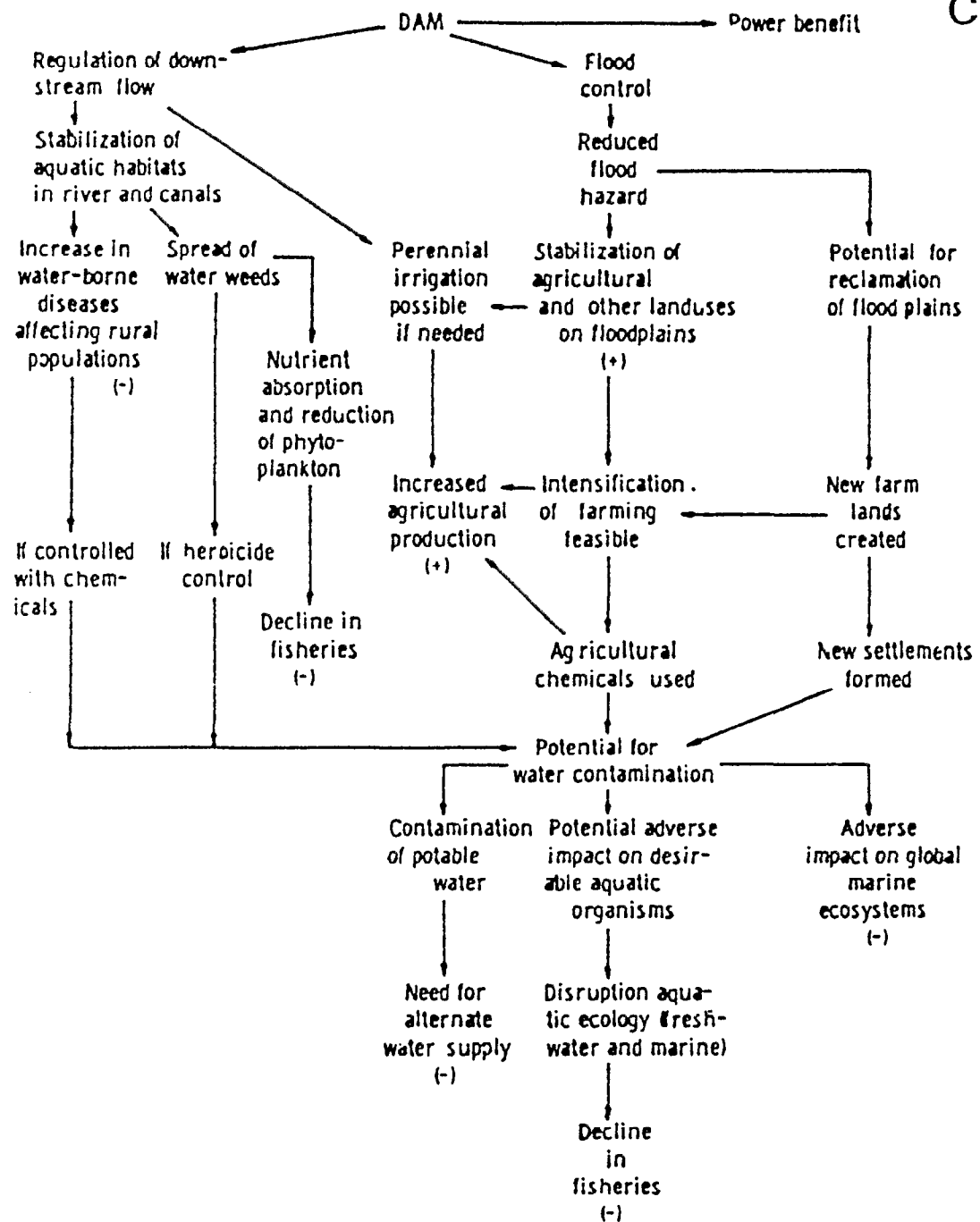


Fig. 2 : (continued)

2 - FAUNAL CHANGES IN THE COMMUNITY

2.1 - The influence of the river. The fish community in any man-made lake is primarily determined by the composition of the fish population in the river prior to impoundment. Immediately after impoundment deoxygenation caused by rotting vegetation may result in fish kills, as in the Volta Lake (Beauchamp quoted by Jackson, 1966; Denyoh, 1969). This may appear to be serious at the time but these effects are shortlived, with survival ensured even at the worst in the river waters flowing into the young impoundment. No records are known where a fish species which originally occurred has disappeared completely from a lake basin as a result of deoxygenation or other natural causes. But the construction of the dam wall may immediately prevent migrant fish from entering the new basin, unless especial provision such as fishways are made for them.

The transformation of the ecosystem from the fluvial to the lacustrine is however a different matter. Species of the original fish population which are adapted to running water conditions may diminish or disappear in the waters of the new lake. Such species tend, when present in the dam, to orientate towards inflowing streams or areas influenced by such affluent rivers. A well documented example is that of *Labeo congoro* and *L. altivelis*, important commercial fish of the Middle and Lower Zambezi. In the Kariba area they were abundant in the main river before inundation, with a well-marked annual spawning migration up the tributary rivers (Jackson, 1961a). Kariba reached full retention level in 1963 and by 1971 the decline in the *Labeo* stocks was causing concern. Kenmuir (1971) noted that they were a fish strongly associated with flowing water, and attributed their decline in part to illegal fishing during spawning migrations. But there is little doubt that the inundation of the habitat is the main factor responsible. Begg (1974) has shown the progressive reduction in standing stock of *Labeo* as distance from the upper, more riverine end of the lake increases (Fig. 3).

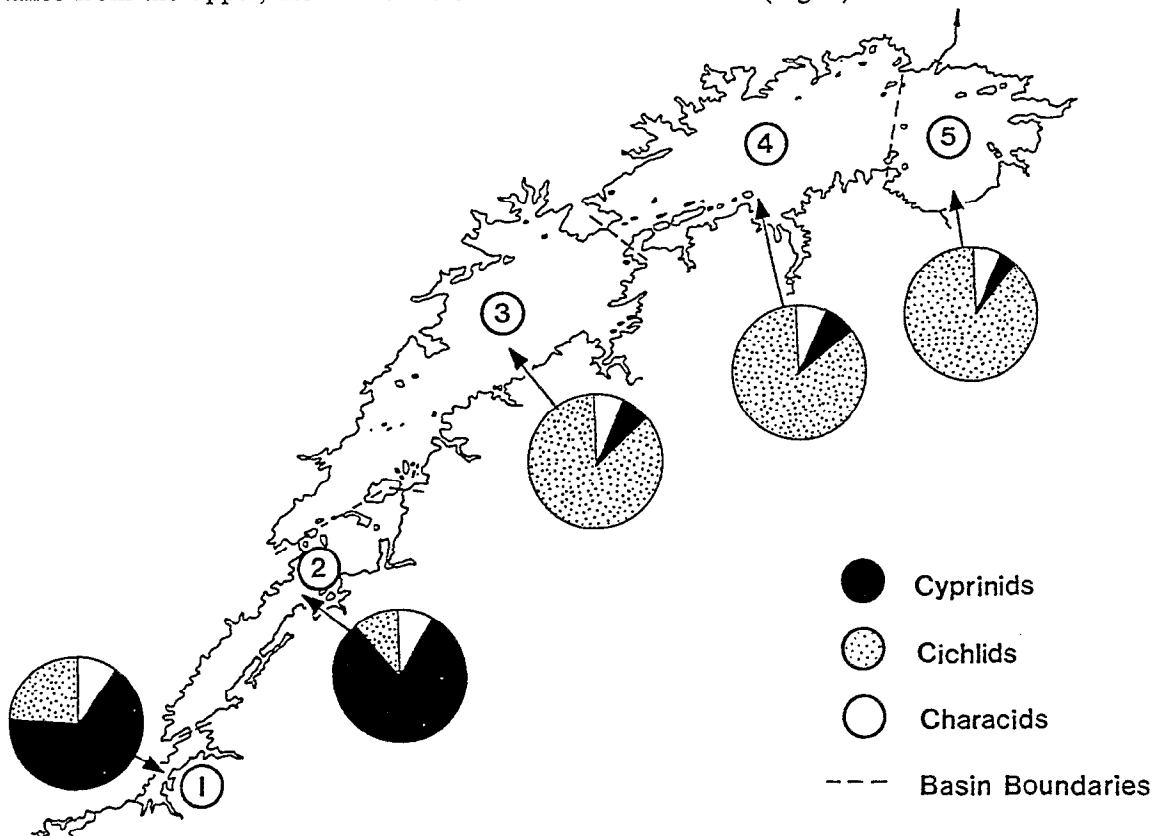


Fig. 3 : Changes in the relative abundance of three fish families in the different basins of Lake Kariba. Redrawn from Begg (1974).

Another fish which declined as a result of damming the Zambezi river is *Opsaridium zambezensense*, a small carnivorous cyprinid with, apparently, a definite preference for running water. Jackson (1961a) found it to be not uncommon in the Zambezi and Sanyati rivers in the Kariba basin before impoundment, and commented that the species was exceptional in preferring, during flood periods, to be in running water at the edges of the swollen river rather than in the still waters of backflooded areas. Begg (1974) records it as having virtually disappeared from the main body of Lake Kariba and intensive surveys since have confirmed its absence. *O. zambezensense* was also extremely abundant in the flowing water of the river before Cahora Bassa was closed; after closure the lake was formed very rapidly and *Opsaridium* disappeared immediately (Jackson & Rogers, 1976). A similar state of affairs applied for the small characid *Micrastes acutidens*. It was numerous in shallow flowing water of the Zambezi before the closed dam, but subsequently disappeared and is now only found in inflowing rivers (Bowmaker, 1973) and along the shoreline in some areas. These considerations indicate that a potential danger exists to the highly specialised rheophilic fish fauna of the Middle and Lower Zaire river (Roberts & Stewart, 1976) since the proposed hydroelectric schemes on this part of the river could be a serious threat to them.

Riverine fish may disappear from the impoundment for reasons other than the absence of a current. In West Africa there was a sharp decline in the number of Mormyridae in both Kainji (Turner, 1970) and Volta (Petr, 1969). Petr (op.cit.) suggested this was due to the preferred habitat being inundated to considerable depths without sufficient oxygen in the water there for these benthic-feeding fish. In Zimbabwean dams mormyrid distribution is governed largely by preferred substrate, *Marcusenius macrolepidotus* being abundant in Lake McIlwaine which is mainly sandy-or muddy-bottomed with *Mormyrus longirostris* favouring rocky areas (Marshall, 1982). When introduced to Lake Kyle, which is largely rocky, *M. longirostris* flourished and is the mainstay of a commercial fishery there. Dadzie (1980) recorded the rapid decline of *Mormyrus* species from the beginning of inundation of the Kamburu Dam, Tana River, probably because of the submerging of their riverine habitat to anoxic depths.

Clariid catfishes often become less abundant in man-made lakes than they were in the previous rivers or early stages of the dam. Marshall (1977) gives data on the proportions of *Clarias gariepinus* by mass in catches from Zimbabwean dams which in every case show a decline over a period of years. (Fig. 5 indicates the change in composition of the fish catch from Lake McIlwaine, Zimbabwe, over a period of years). Kenmuir (1977) and Jocque (1977) have noted similar declines in *C. gariepinus* and *C. lazera* in Lakes Kariba and Kossou respectively. The same authors (ibid.) also noted the virtual disappearance of the big clariid *Heterobranchus longifilis* from these two lakes. Mass mortalities of *Clarias gariepinus* have been reported from man-made lakes on the Orange River, South Africa (Tomasson *et al.*, 1983), caused by a lake-induced high population subsequently starving through lack of prey.

2.2 - Potamodromesis. The fact that some fishes moved about and ascended rivers was known to some earlier workers, and sometimes ascribed to the spawning impulse, but this phenomenon was not adequately understood until the upsurge of research following World War II. Thus Ricardo Bertram *et al.* (1942) were aware of the spawning migrations of *Barilius* and *Labeo* out of Lake Malawi, but war cut short their work, leaving the first detailed observations to be made by Lowe (1952). Daget was the first to study floodplain migrations (1949) and migrations at a river barrier (1950). Greenwood (1955) first verified the eggs and alevins of a fish which migrated from a lake to spawn in an affluent stream, and Whitehead (1959) and Jackson (1959) first defined and classified fish genera and species which habitually undertook seasonal spawning migrations at times of flood out of lake and river respectively. Myers (1949) coined the term «potamodromous» for fish having such behaviour. Mortimer & Bell-Cross (1960) and Bell-Cross (1960) made quantitative records of fish moving out of a stream into a dam in the Kafue system, showing that of 23 fish species known to occur in the stream 15 attempted an upstream migration into the dam during its rainy season.

An impoundment can therefore, in addition to affecting the rheophilic members of the fish community, create serious adversity for species which undertake seasonal potamodromesis up rivers. Such migrations may be inhibited either because the dam wall creates a physical barrier

to upstream movement or by the resulting impoundment being so large that the fish become «lost» in it and no longer able to find the tributary river in which they spawn. The fish locate these rivers by detecting changes in water quality. It has been shown in man-made lakes such as Kariba that river water can move or «flow» along its own bed even when this is beneath the lakes; thus inflowing floodwater from the Sanyati River entering Lake Kariba can preserve its distinctive character and is perceptible to potamodromous fish for many miles along the lake, even to the wall where it enters the turbines to excite the fish in the river below (Bowmaker, 1973; Kenmuir, 1978). Such river persistence in lakes may be of considerable antiquity, as shown by Greenwood's (1957) mention of fishermen believing that *Barbus altianalis* entered Lake Victoria from the Nile by ascending the Ripon Falls and then proceeded along the sunken bed of the Kagera river to spawn in this river above lake level hundreds of kilometres away. This postulated an upstream migration along the Nile millennia after the formation of a lake which isolated the upper Nile into a component now called the Kagera. That the fisherman's idea is plausible, and the river «scent» may be followed in spite of having been overlaid by a lake is supported by the recent Kariba work. Admittedly we are here dealing with a warping, not a dam, so the old bed rises towards the Falls, but the rise is gradual and the old valley still distinct. Regrettably this immemorial migration has since 1956 been stopped by the Owen Falls Dam which prevents the fish from ascending though they attempted to do so, congregating below the dam after closure (Greenwood, 1957).

By the advent of the huge man-made lakes in the 1960s the general nature of migrations from a larger water body onto a floodplain or up a tributary was sufficiently well known for its effect upon man-made lakes' fish communities to begin to be assessed. Harding (1962) found by echosounding in 1960 in the forming Lake Kariba that several species of potamodromous fish congregated near the mouths of rivers just prior to the breeding season whose start coincides with the first rains, and that a breeding migration up these rivers occurred with the first flooding. Harding (1962 :32) stated «that of the several species which run to the rivers to breed *Clarias mossambicus*, *Labeo congoro* and *L. altivelis*, *Hydrocynus vittatus* and *Alestes imberi* are perhaps the most important». By 1962 the two *Labeo* species comprised 75% of the commercial catch at Simamba close to the dam wall (Harding, 1966). But a few years later *Labeo* stocks had seriously declined in the same area, i.e. the most lacustrine basin of the dam (Kenmuir 1971). Begg (1974) attributes this to the inundation of the lower reaches of tributary rivers here such as the Sanyati, pointing out that the remaining unflooded part of the river offers less suitable habitat.

The fact that extremely high populations of potamodromous fish can build up in the first few years of an impoundment's life is due to the high survival rate of those juveniles spawned at the time of closure, as has been shown for Kariba (Jackson, 1960) and Cahora Bassa (Jackson & Rogers, 1976). The rising waters ensure a low natural mortality by providing vastly increased habitat, food and cover from predators, compared with the old river where post-spawning dry-season conditions were often highly adverse for the survival of young-of-the-year fish (Jackson, 1961a). This effect is enhanced by the greatly increased fertility of the brand-new lake, due to nutrients being leached from newly inundated soil or released from decaying terrestrial vegetation, resulting in the exponential increase of all kinds of organisms (Balinsky & James, 1960).

These conditions are short-lived and the influence of the huge mass of static water soon becomes all-important. As Paugy (1979) has remarked, the riverine fish community is faced with two choices in a lentic environment : to disappear or to adapt to the new conditions. Many species are highly successful in adopting the latter course.

Before discussing such adaptations we may summarise the three main effects of the man-made lakes' fish communities on the old river : firstly the dam wall may be a barrier to the longitudinal movement of fish. This applies particularly to fish which migrate to and from the sea, the best African examples being that of eels (*Anguilla* spp) (Jubb, 1964; Jackson, 1966) and mullet of the family Mugilidae (Jackson, 1979). In such cases there tends to be a disruption of the life cycle which leads to extinction of the species above the barrier. Longitudinal withinriver migrations may also take place to seek warmer temperatures, as with the tigerfish *Hydrocynus vittatus* (in southern latitudes) which tend to move downstream towards a lower altitude and

thus a warmer temperature for breeding purposes, with non-breeding and younger fish recolonising the upstream areas (van Loggerenberg, 1980). The construction of a dam prevents these movements so that fish disappear above the dam wall (Pott, 1969). Secondly, breeding movements, are inhibited because the floodplain or tributary river previously used by the species as spawning and nursery areas are drowned by the rising water of the man-made lake. There are many cases of this happening in most Africa man-made lakes but the examples from Kariba mentioned above are the best documented (Bowmaker, 1973; Begg, 1974). Thirdly, the old river possessed species which were so rheophilic that they could not survive in non-flowing waters. These tend either to be adapted to living in torrents and rapids such as *Chiloglanis*, or to feeding upon insects and organisms carried down by the current, of which *Opsaridium zambesense* is a good example. Fish such as the Mormyridae of the Tana and Volta Rivers declined because they feed and breed among rocks which are no longer scoured and oxygenated by the river but lie covered in silt and often in deoxygenated water after the lake is formed. Large *Barbus* species do not move on to floodplains to breed, but spawn in the mainstream river (Tomasson *et al.*, 1984) and will diminish if such breeding sites are flooded. Some are rheophilic and tend to disappear from man-made lakes, however *B. aeneus* is more adaptable and colonizes impoundments though it still must spawn in rivers (Allanson & Jackson 1983).

2.3 - The influence of the reservoir. Many riverine members of the fish community, and tilapias in particular, prefer the still-water pools and marshes of the old river (Jackson, 1966). These benefit considerably when the creation of the reservoir vastly increases such stable, stagnant conditions. In addition, a new pelagic niche is created in which openwater, shoaling, planktonivorous species can thrive to a far greater extent than was previously possible. Adaptations to seasons of alternate flood and drought are no longer necessary, and the stable well-vegetated conditions may create desirable habitat for species from elsewhere, so that additions to the fish community may be expected.

In general, therefore, the previous river had seasonally alternating favourable and unfavourable periods. The new man-made lake, for all except a few torrenticolous and current-loving species, tends to approximate the previous favourable conditions and to maintain them. The result is that not only does the relative abundance of individuals of the various species change but the species composition of the community changes as well, and the tendency is for the new man-made lake to harbour after a few years more species than were present in the previous river.

A good review of the general development of man-made lake ecosystems is given by McLachlan (1974). The process can be summarized as follows: initially there is high fertility with a great increase in plankton (Stephens, 1949; Brook & Rzoska, 1954) and, as a consequence, an increase in other aquatic organisms including fish (Balinsky & James 1960; Jackson, 1961b). However, in the fish communities, the initial increase is mainly of potamodromous fishes whose juveniles show a high survival rate after the first post-closure spawning. This year-class is strongly represented but later year-classes diminish steadily in the more lacustrine basins of the dam. The various tilapias do not usually have extensive migrations or spawn large numbers of eggs at one time, but have several spawnings of smaller broods per annum in suitable shallow water, and for this reason their numbers do not increase with such explosive rapidity in the new reservoir. In Kariba Jackson (1959) found that shortly after closure only 0.75% of the fish caught were *Oreochromis mortimeri*, while eighteen months later Harding (1962) reported that 24% was of this species. Similar tendencies seem apparent in Lake Nasser, closed in 1964. Here the mean of *Labeo niloticus* landings for the three years 1966-68 was 22.6% of the total catches but the mean of 1970-72 declined to only 12.7% of the catches. For the same two sets of years the tilapia (*Oreochromis niloticus* and *Sarotherodon galilaeus*) percentage of the landings rose from 33.2% to 46% (Latif, 1976). By 1981, tilapias made up 90% of the catch (Latif, 1984). Similarly in Volta lake, the genera *Labeo* and *Chrysichthys*, as well as *Alestes nurse* which is migratory (Daget, 1949), were originally quite abundant in the southern (lower) part of the lake but soon become greatly reduced in this area, their place being largely taken by *Sarotherodon galileus* (Evans & Vanderpuye, 1973).

The initial effects of the reservoir on the fish community then are the phasing out of riverine species, usually after a rapid build-up of their population during the first year of impound-

ment, though this may be more marked in some reservoirs, e.g. Kariba and Cahora Bassa, than in others. Shortly afterwards the more lacustrine-orientated species increase rapidly in response to the general outburst of productivity caused by the initial abundance of nutrients, both in numbers and in proportion to the riverine forms, which are greatly reduced except where conditions in the lake are more riverine. Later a period of lower production sets in, caused partly by a decline in the supply of nutrients leached from the new-covered soil or from rotting terrestrial vegetation, and partly through such nutrients being taken up by growth of the aquatic vegetation, both rooted and free-floating. This new flora is of great importance to the fish community.

2.4 - The role of aquatic vegetation in the reservoir. The first aquatic vegetation to appear are phytoplanktonic algae with the pioneering blue-green *Anabaena* and *Microcystis* often dominant, forming massive blooms in the nutrient-rich water. An epiphytic and epilithic algal flora soon forms on substrates such as drowned trees and rocks, its quantity and density depending on the degree of light penetration allowed by the turbidity of that particular impoundment's water. As in natural lakes, invertebrates colonise this mat of algae, the whole being collectively known as *aufwuchs*, and is a valuable fish food (McLachlan, 1970; Petr, 1970).

In the first very large African man-made lakes tree-clearing was recommended to facilitate the use of nets (Jackson, 1961a) and this was carried out in selected areas in Lakes Kariba and Kainji, where it did indeed facilitate the setting of fishing gear such as gillnets and seine-nets without entanglement. In the uncleared lake Volta fishermen were using water less than 5m deep for this reason, and underfishing occurred because a «refuge» for fish was created (Evans, 1969; Vanderpuye 1973). Tree removal may result in productivity loss; the first to appreciate the importance of submerged trees in a man-made lake as forming a substrate for *aufwuchs* and thus a food source for fish was Dr Barbara Douglas (1966). McLachlan (1969, 1970) showed clearly the importance of macrophytes and submerged trees as a substrate for fish food organisms in Lake Kariba. Petr (1970) discussed the role of trees in Lake Volta. Bowmaker (1970) found that in Kariba more *Oreochromis mortimeri* were caught among the drowned tree-trunks than in the cleared areas. However, over the passage of years the trees themselves disappear, alternately being attacked by woodboring beetles when dry and the ephemeropteran *Povilla adusta* when submerged, as well as being weakened by fungal rot so that they finally snap off at the waterline (Bowmaker, 1975). Clearing costs must therefore be weighed mainly against short-term benefits, since natural clearing in the littoral will be largely complete within two decades. For these reasons extensive clearing, except for shipping lanes and harbour areas, is no longer recommended (Jackson, 1974), although it would still be necessary if bottom-trawling was envisaged. Such natural disappearance of the previous flora is part of the general pattern of decline of fertility in the early to median years of man-made lakes, but before this happens they have, to a very considerable degree, influenced the changed fish community pattern by initially providing protection for small or young fish from roving predators, particularly *Hydrocynus*, and by providing a substrate on which additional algal and associated invertebrate food can grow.

The next plant invasion is usually by floating aquatics, which benefit greatly by the stagnant water conditions and greater water fertility caused by the initially increased supplies of dissolved nutrients. An extreme example is Lake Cahora Bassa, which from its inception was colonized by no less than four major floating aquatic plants. One of these was the endemic *Pistia stratiotes*, another was *Azolla nilotica*, non-endemic but of African origin, and the third and fourth the notorious *Salvinia molesta* and *Eichhornia crassipes*, both exotics from South America. After one year the water hyacinth *E. crassipes*, taller and more robust than the others, completely dominated the floating mat composition (Bond & Roberts, 1978). Later the mats were largely destroyed by lake level fluctuations (Bernascek & Lopes, 1984). The hyacinth has also colonised several other man-made lakes, such as Gebel Auliya on the White Nile in the Sudan (Rzoska, 1976).

From the point of view of the fish community (though perhaps not of the fisherman), the advent of floating aquatics in a man-made lake is probably beneficial. Perhaps the most important is the fact that, in a large impoundment, the mat of plants takes up a large quantity of nutrients from the water in which it floats, so that these are locked up within the dam basin

rather than being lost by downstream discharge (Mitchell, 1973; Bowmaker *et al.*, 1978). The plants have great significance in providing food and shelter for other organisms eaten by fish and, probably most importantly, by releasing these trapped nutrients once again to the food cycle when these plants themselves die and decay. In some cases, as in natural wetlands, anoxic water through plant decay may cause fish kills, but this is rare in impoundments.

In Kariba, the floating mat of *Salvinia* has had an important effect on the fish community by promoting the growth of rooted shoreline vegetation (Bowmaker, 1973b). This was because plants killed by draw-down formed a mulch on otherwise bare shorelines to enable the growth especially of the creeping plants *Panicum repens* and *Ludwigia stolonifera* to establish themselves. These and other rooted species were of great benefit to the fish community. *O. mortimeri* spawning was, for example, after being most successful in the first few years in Kariba, greatly reduced when the terrestrial vegetation disappeared through decay, leaving bare shores not immediately colonised by rooted aquatics (Van der Lingen, 1973). As soon as these became established the survival of juvenile tilapia increased greatly (Donnelly 1969).

The establishment of vegetation thus plays an important role in the formation of fish communities in man-made lakes. It enables the fish which are small when adult, such as small minnows and cichlids to survive in greater numbers than previously in the river. This is because vegetation improved the habitat by increasing food availability, spawning facilities, shelter from predators etc. This has been reported for Kariba where the 28 species recorded from the pre-impoundment river have been augmented to over 40 (Bowmaker *et al.*, 1978). Visser (1973) lists the average composition of the 150 species of the fish community of the Niger river near Kainji, before impoundment, per 10 000 specimens. Of these only 35 species or 23% of the total, all over 18cm TL when adult, comprised 7093 or 71% of the number. Today, in the established man-made lake of Kainji, the numerous small clupeids, barbs, cyprinodonts, etc. are relatively far more numerous in the fish population.

The role of aquatic vegetation in man-made lakes is one that is continuously changing, varying from planktonic to benthic algae, then macrophytes, initially floating but later with rooted plants establishing, with their success depending upon factors such as turbidity and degree of draw-down. A very valuable contribution to the fish community is made by plants taking up nutrients which would otherwise be lost to the dam through the outflow. Later, however, this role as a nutrient store might be taken over by another community; this probably contributed to the decline of *Salvinia* in Kariba after its initial proliferation (Marshall & Junor, 1981). The nutrients might be taken up by large populations of small microphagous planktonic filter-feeders such as the copepod *Metadiaptomus meridianus* and various water fleas of the genus *Daphnia* (Hart *et al.*, 1983). Where a large population of truly pelagic zooplanktonivorous fish build up, such as the clupeid *Limnothrissa miodon* feeding on planktonic grazers (the water flea *Bosmina longirostris*; Junor & Begg 1971), the nutrient store may in part be transferred to them. Rooted macrophytes may be eliminated by injudicious introductions of a higher plant feeder such as *Tilapia rendalli*, which has destroyed the rooted vegetation in several Zimbabwean impoundments resulting in the stunting and decline of *Oreochromis mossambicus* populations in Lakes Sebakwe and Ngesi, and of the largemouth bass *Micropterus salmoides* in Lake Kyle (Junor, 1969). Recovery would only be possible by intensive fishing of *T. rendalli*. Therefore amongst the important effects of man-made lakes on their fish communities is the dynamic and everchanging nature of the plant biomass within the ecosystem as affected by various biotic and abiotic factors.

2.5 - The Pelagic zone. The pelagic zone is of especial significance in man-made lakes, because only in rare instances were any of the fishes of the river before impoundment capable of adapting to life in the pelagic open water, well away from shore, which was immediately created by the river's impoundment. Apart of course from predators which would follow their prey wherever they went, the riverine fish with pelagic potential needed to be small, shoaling in habit and mainly planktonivorous.

Such were *Pellonula afzeliusi* and *Sierrathrissa leonensis* which in Lake Kainji had an estimated 3140 ton average biomass (Otobo, 1978), and *P. afzeliusi* and *Cynothrissa mento* in Lake Volta (Reynolds, 1970, 1971), none of which were numerous enough in the old river to war-

rant commercial exploitation but after impoundment became sufficiently abundant to form the basis of potentially important fisheries (Otobo, 1974, 1978). The important criterion of success as an offshore species is the ability to feed on zooplankton, and it is probably this which accounts for the success of the clupeid fishes of the genera *Limnothrissa*, *Pellonula*, *Sierrathrissa* and *Cynnothrissa* in the large impoundments. Characid fishes such as *Alestes*, *Micralestes* and related genera are on the other hand primarily insect feeders (Lek & Lek, 1977; Marshall & Van der Heiden, 1978; Paugy, 1978, 1979-80a, 1979-80b) and so limited to areas where insects are abundant, i.e. inshore. For this reason, *Alestes lateralis*, erroneously supposed by Balon (1971) to be a pelagic species though in fact confined to water less than 20m deep, was soon supplanted in Kariba by *Limnothrissa* which efficiently utilised pelagic zooplankton though capable of survival in shallow water, and rapidly became outstandingly successful in this impoundment (Bowmaker *et al.*, 1978; Cochrane, 1978). It is also established in Lake Cahora Bassa and though a fishery for it has been much delayed this is now contemplated and should also be very successful (Bernacsek & Lopes, 1984). In Lake Le Roux the minnow *Barbus anoplus*, previously known only from shallow sheltered waters, penetrates in small numbers into the most off-shore waters (Allanson & Jackson, 1983) and utilizes zooplankton there (Cambray, 1983).

Open waters of man-made lakes may also be temporarily occupied by other fish, some of which, such as *Alestes lateralis* mentioned above, must spawn on submerged vegetation, even though a seasonal spawning migration is not necessary (Balon, 1971). Other species use the open-water habitat for only part of their life-history, such as *Barbus aeneus* in Lake le Roux which range out to over 1 km from shore at an intermediate life-history stage when up to 30 cm in fork length (Tomasson *et al.*, 1984), feeding at this time upon zooplankton and returning later to resume a benthic/predatory feeding mode (Eccles, 1984).

Finally an important group of fishes which adapt to the pelagic zone created in a man-made lake are the predators which move out to feed on the shoaling pelagic species (Jackson & Bruton, Chapter 21). They are not totally pelagic in that they must return to shore periodically to spawn and, unlike the clupeids which are their main prey, the juveniles spend some time, usually up to a length of about 18 cm, on floodplains or among vegetation (Coulter, 1976). The most important of these are the Nile perch (*Lates niloticus*) which, having a *tapetum lucidum* behind the retina which increases feeding efficiency under dim-light conditions, are efficient in turbid impoundments (Ryder & Henderson, 1974) and the tigerfishes of the genus *Hydrocynus*.

In Kariba, the importance of the introduced sardine to the tigerfish is illustrated by the fact that it now constitutes 70% of their prey (Kenmuir 1971). Some modified their habits from a species which patrolled the shoreline in search of prey to penetrating from the lake edge into the most open water many kilometres from the coast, so enabling the population to increase (Junor & Marshall, 1979). Tigerfish appeared in the pelagic catches from the beginning of the sardine fishing programme (Cochrane, 1976) but since they are not as fecund as their prey (Jackson & Bruton, Chapter 21), and because they were a bycatch and not a target species in the fishery, they were rapidly fished out and from being over 10% of the pelagic catch in 1977 they fell to less than 1% in 1980 (Marshall *et al.*, 1982).

3 - ADAPTATIONS IN THE FISH COMMUNITY

Adaptations of species within the community are of interest, firstly those which take place in existing populations and secondly in the potential which these new lakes may have in indicating processes whereby the evolution of species in the longer-lived natural African lakes may have come about.

3.1 - Immediate adaptations to the new regime. Many instances of adaptations in feeding habit or mode of existence during non-reproductive life history phases have been recorded for African man-made lakes. The most dramatic is probably that of the spread of the tigerfish *Hydrocynus vittatus* over Lake Kariba in search of the introduced sardine *Limnothrissa miodon*, while this adaptation to a new diet has been recorded for *Lates* as well as *Hydrocynus* in Lake Kainji

(Lelek & El Zarka, 1973). In Lake Volta the mid-water dwelling catfishes *Schilbe mystus* and *Eutropius niloticus*, previously generalized feeders, adapted to feeding largely on the burrowing nymphs of the ephemeropteran *Povilla adusta* which proliferated greatly in the many drowned trees of the new lake (Petr, 1970). As pointed out by Lowe-McConnell (1975), this provides a good example of a generalised feeder in the river changing to a more specialised source of food in a new environment. In Lake Cahora Bassa juveniles of both *Eutropius depressirostris* and the cyprinid *Labeo congoro* were very abundant in the population explosion of certain species which took place in the first year after closure. Presumably because insufficient other food was available for the very numerous *Eutropius*, at 11-14cm fork length they swallowed *Labeo* of up to 65 % of their own length, resulting in gross bodily distortion (Jackson & Rogers, 1976). Similarly in Lake Kossou, the characin *Alestes baremoze* changed its diet largely from insects to zooplankton (Paugy, 1978; Kouassi, 1979), and some morphological adaptations were also noted (Paugy, 1979). Eccles (1984) records similar zooplanktonivory in *Barbus aeneus* in Lake Le Roux in the earlier life-history stages of this large cyprinid which then ranges widely several kilometres from shore.

However, while variations in diet occur widely in adult fluvial fish which have successfully adapted themselves to a man-made lake environment, in one important aspect there seems great rigidity and no change. This is in reproduction, where there is no case on record of any fish, in colonising a new lake, adapting or changing its reproductive habits. If it was previously potamodromous, then this behaviour remains. If the circumstances of the new environment prevent the old behaviour, then the species becomes greatly reduced in number or even dies out in consequence.

3.2 - Problems of speciation. Adaptations of fluvial communities to lacustrine conditions are of relevance when considering the evolution of the endemic fish species in African lakes, especially the Great Lakes of Victoria, Tanganyika and Malawi. Here the species-flocks of highly adapted assemblages of related species, each endemic to a particular lake, have long excited the attention of students of evolutionary processes. Much discussion has taken place (for recent reviews see Greenwood, 1974; Fryer, 1977; Ribbink *et al.*, 1983). The invasive behaviour of riverine fish into large, newly formed and unpopulated man-made lakes may contribute some useful information, especially regarding the role of the specific mate recognition system in speciation (Ribbink, this volume). This has relevance to a primary aspect of the problem of intralacustrine evolution: how, in large continuous water bodies with no physical barriers, did speciation proceed to the extent known today? How, in fact, did the process start in the first place?

Four theories have been proposed to account for this: the earliest of «explosive» sympatric speciation including Regan's (1922: 159) idea of «evolution by habitual segregation»; the second, multiple colonizations from affluent rivers, suggested at that time by Mayr (1947); the third of microgeographical isolation by ecological barriers, i.e. habitat preferences, first stated by Lowe (1954: 85) and later gaining a wide vogue; the last, on which Greenwood (1974) lays emphasis, envisages evolution and speciation taking place when the lake was broken up into a number of smaller ones. Later work has modified these four theories in detail. Thus, in the first, Regan (1922) was influenced by Gulick's (1905) ideas derived from observing snails in Hawaiian valleys, taken further by Kosswig's (1947) recognition of selective mating as an isolating factor, followed by Greenwood's (1954: 85) supposition of «cross-incompatibility» of intralacustrine populations, and recently the recognition concept of Paterson (1980) has been examined in the field by Ribbink *et al.* (1983). These are all elaborations of the first of the above theories.

No single theory is likely to account for all the facts. Evolution and speciation took place, almost certainly, as a result of a complex sequence involving all of the mooted theories, to a greater or lesser extent at different periods in the lakes' history. Each possibility is untenable only if its implications are carried to extremes. If a moderate view of the interactions of each with another is taken, a plausible picture emerges. Thus, in the second theory, we cannot accept its ultimate implication, that a highly specialised cichlid species-flock member sprang, complete with its greatly modified dentition, from some adjacent river straight into a Great Lake community. Yet some riverine haplochromines in various stages of specialization must have inva-

Table 1 : Distinctive features of 'r'- and 'K'- selected fish communities of tropical Africa (based on concepts given by Lowe-McConnell, 1977).

| Ecological attributes | Type of selection | |
|------------------------------------|---|---|
| | 'r'- selection | 'K'- selection |
| Habitat | Upwelling areas, estuaries, continental shelves off large deltas, flood plains, marshes, swamps, etc. | Coral reefs, rock reefs, littoral and benthic areas of the great lakes of East Africa |
| Species group | Mostly pelagic marine fishes (sardines, anchovy, Carangidae, etc.), but also <i>Engraulicypris</i> , <i>Stolothrissa</i> , <i>Limnothrissa</i> , etc. | Mostly demersal fishes (eels, Sciaenidae, catfishes, Cichlidae, Serranidae, <i>Synodontis</i> , etc. |
| Diversity index | Less diverse with dominant species. Example : <i>Oreochromis alcalicus grahami</i> in Lake Magadi | Very diverse and species with more or less equitable distribution |
| Environmental stability | Fluctuates seasonally, with variable influx of nutrients | Negligible fluctuations in environment |
| Survivorship curve of fish species | Sharply falling and concave | Distinctly rectangular |
| von Bertalanffy growth coefficient | Relatively high | Relatively low |
| Predation effects | Predation results in homogeneity which may restrict speciation, e.g., Lake Baringo | Predation results in heterogeneity which may promote speciation, e.g., Lakes Tanganyika and Malawi |
| Protection cover | Schooling behaviour | Formation and defence of territories |
| Movements by species | Schooling prey species with diurnal migrations | Schooling by day, dispersing and feeding by night |
| Energy flow per unit biomass | high : (a) with few trophic levels, energy flow per unit biomass is high ; (b) in fluctuating and less efficiently organized systems, the cost of maintenance is high | low : (a) with many trophic levels, energy flow per unit biomass is low ; (b) in stable efficiently organized systems, the cost of maintenance is low |
| Natural mortality | Usually high, sometimes catastrophic, indiscriminate and more or less density-independent with occasional mass mortalities | Relatively low and mostly due to predation also fairly density-dependant |
| Longevity | Prey fish with short life-span | Longer life-span |

Table 1 : continued

| Ecological attributes | Type of selection | |
|-----------------------------------|--|---|
| | 'r'- selection | 'K'- selection |
| Reproduction mode | Numerous pelagic eggs, some prolific substrate-spawners (e.g., the 'tilapias'), no parental care, protandry (change of sex from male to female) in Polynemidae | Spawning displays, pairing and highly developed parental care, protogyny (change from female to male), e.g., in Serranidae, Labridae and 'swamp-eels' |
| Competitive ability of individual | Competitive ability low; competition low and variable, absence of territorial behaviour | Competitive ability high, competition high and variable; presence of territorial behaviour |
| Status of trophic levels | Few trophic levels | More trophic levels |
| Feeding adaptation | Specialists at low trophic levels | Adaptative feeding types but with some specialists which may be stenophagous |
| Other favoured factors | <ul style="list-style-type: none"> ● Rapid turnover, ● High rate of natural increase 'r'- max, ● Early reproduction, and ● Small body size | <ul style="list-style-type: none"> ● Slow turnover, ● Low resource threshold, ● Delayed reproduction, and ● Large body size |

Data from North America indicate that fish biomass in reservoirs is higher than in natural lakes (Cooper, 1966). This also appears to be the case in African waters (Paugy, 1979). A recent study (Marshall, 1984b) compared 11 reservoirs with the 11 intensively-fished African lakes listed by Henderson & Welcome (1974). In both groups fish yields were related to MEI (Fig. 4) but the reservoirs were more productive, especially when the MEI was low. The reasons for this are unclear, but may be linked to the relative youth of man-made lakes and the fact that their ecosystems have not stabilised. Since their inflows are greater than their volumes they must receive more nutrients annually, per unit volume, than natural lakes which sustain high production. Our understanding of nutrient dynamics in man-made lakes and their effects on fish populations is still poor and is one of the gaps in our knowledge of these systems. In some cases yield (kg/ha/yr) might be better in man-made lakes than in natural ones because of the greater density of fishermen, due to resettlement or fisherman being attracted to a fishery where the yield is high, though such results often need qualification. Since most man-made lakes are of recent construction much of their catch data were obtained shortly after closure, enhancing the possibility that sustainable yields were over-estimated due to high initial fish production. Besides this, during the first years following closure, fluctuations in catches frequently occur due largely to variations in fishing effort in the unsettled circumstances surrounding the creation of a new dam. So, at the beginning, the very high fish production produces an abnormal increase in the numbers of fishermen who are often not professionals but «amateurs», such as resettled agriculturalists who are encouraged to take up this occupation (Chambers, 1970; Butcher, 1971). During the decline of the initial high productivity there is a decrease in fish catches, and «occasional fishermen» stop their activity, perhaps finding other employment as conditions around the new dam stabilize.

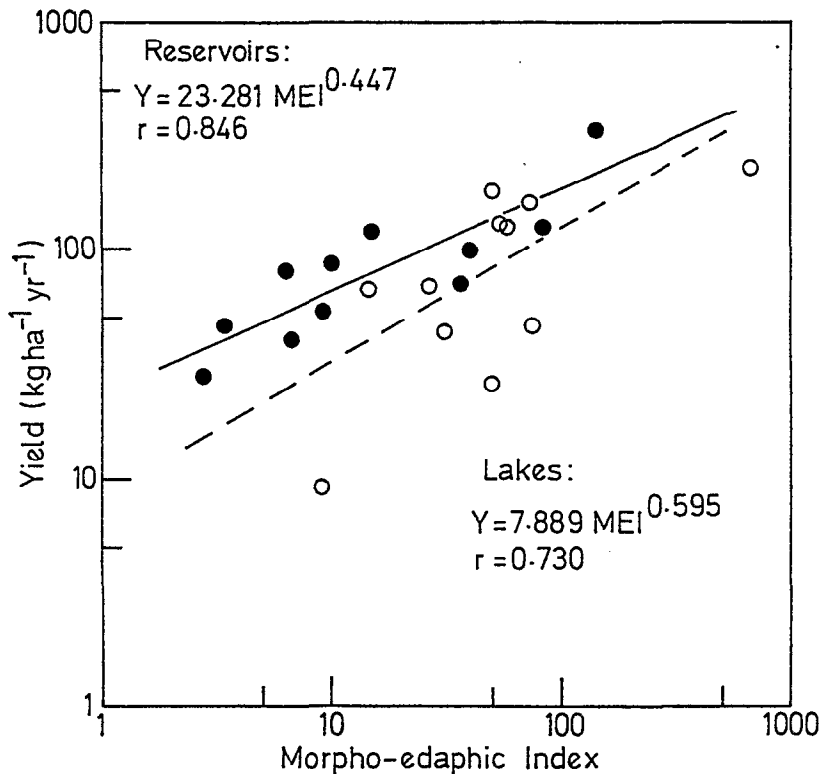


Fig. 4 : The relationship between morphoedaphic index and fish yield in some African reservoirs (●) and lakes (○). From Marshall (1984)

Claims of high initial productivity should in any case be treated with some reserve since the temptation, in some cases may exist to claim initial as continuing productivity in order further to justify the costs of dam building. The only factor, in the stabilization phase, which might allow for a higher production in a man-made rather than a natural lake is where more nutrients are brought in by affluent rivers due to a higher water replacement rate (Beauchamp, 1966).

5 - DISCUSSION

The most important factor common to man-made lakes is that they are all, even the oldest, in a relatively rapid state of change. By this is not meant the physical changes common to all lentic water bodies, that they are filling up with silt and will sooner or later cease to exist, a process considerably more rapid with man-made lakes, so none of them have a life of more than a few hundred years. Rather, it is the biological changes which are relevant, as each lake harbours an assemblage of aquatic organisms which is never constant either in terms of its biomass or its composition. Thus we cannot predict the ultimate nature of their fish communities; probably we never shall be able to do so with any great degree of precision because, apart from the changes in the biota which are continually occurring, the fishes themselves immediately begin to adapt as considered above. Evolutionary pressures start to operate from the very beginning, populations may become isolated, often cutting off gene flow between previously homogenous groups, and very little remains that is in any way static in any man-made lake fish community.

Nevertheless, the trends which become apparent in most reservoirs can be broadly analysed. It is useful to recapitulate the uses to which the nutrient load, is put, as well as considering its rates of inflow from the affluent river and outflow from the impounded system. Initially, for a brief period, the impounded water is enriched by ions leaching from the newly inundated substrate and from the decay of drowned terrestrial vegetation. Very soon there is a dense bloom of algae, particularly though not exclusively of the pioneering nitrogen-fixing blue-greens, followed shortly by an increased of zooplankton. After that floating macrophytes multiples if such plants were originally present. Temperature can limit plant growth if the lake is situated in an area with a distinct winter. A more serious, year-round limitation to algal growth is turbidity from silt brought in from eroded land surfaces. These suspensoids reduce light penetration, limit heat input, slow production by preventing photosynthesis and, by limiting radiant energy from the sun to the upper surface layers only, accelerate cooling by wind action (Allanson *et al.*, 1983). In such circumstances most nutrients are either permanently sealed in bottom silt or lost through the dam's outflow.

Where floating aquatics are present they may absorb much of the nutrient store within a short time. If several species are present the larger tend to shade out the smaller, as in Lake Cahora Bassa, where the exotic *Eichhornia crassipes* shaded out and dominated all others (Bond & Roberts, 1978). Floating weed mats, especially of exotics lacking their natural biological control agents, can rapidly reach large proportions and take up most of the available nutrient (Mitchell & Rose, 1979). This leads to attempts at chemical and biological control (Bowmaker, 1973; Bowmaker *et al.*, 1978), but quite soon another change may take place when rooted aquatic macrophytes such as *Ludwigia* and *Phragmites* become the dominant plants leading to a diverse benthic community (McLachan, 1974).

This, as well as the establishment of pelagic fish communities such as the freshwater sardines, may lead to the decline of the floating aquatics which once threatened to overwhelm the reservoir (Marshall & Junor, 1981). Less nutrients are therefore bound in the floating aquatics and more become available for other uses such as an increase again in the phytoplankton and so of the zooplankton and fish such as the sardines. Such fish become numerous which leads to an increase in the numbers of predators such as tigerfish and Nile perch. Apart from such variations upon the theme of how different organisms, and ultimately the fish, use the nutrients within the lake, the question of nutrient input must be considered. This is especially important in man-made lakes where the replacement time of the water is very much shorter than in large natural lakes. The complete volume is capable of being replaced by inflowing water usually

within one to four years at most which makes the fish community extremely sensitive to annual fluctuations in river flow and the consequent amount of nutrient which each year enters the man-made lake. These are variables affecting either the fish of the entire reservoir or of a local area near the mouth of the affluent river. In Lake Kariba these effects have been quantitatively studied by Marshall (1982) who showed that commercial catches of the sardine *Limnothrissa miodon* were significantly higher in the Sanyati Basin after strong flows in the Sanyati river. The commercial catches indicate the size of the population, and short-term fluctuations probably take place in other pelagic species which are at the end of a short planktonic food chain.

A final aspect of nutrient supply that is of importance in many man-made lakes, especially those near large conurbations, is eutrophication caused by industrial or sewage effluent. In small quantities it may be beneficial, increasing aquatic populations, but in excess can lead to gross hypertrophy, over-production of blue-green algae and pollution, as in Hartbeespoort, South Africa (CSIR, 1976). A less extreme example is Lake McIlwaine, Zimbabwe, where striking changes have taken place because of eutrophication and a subsequent improvement in water quality (Fig. 5). By 1966 the lake had become highly eutrophic and an introduced tilapia, *Oreochromis macrochir*, became important, feeding on blue-green algae (Minshull, 1978). The endemic *O. mossambicus* virtually disappeared and the introduced *T. rendalli* declined possibly because it destroyed aquatic macrophytes (Junor, 1969), although the increasingly dense algal blooms may also have contributed to its decline. Efforts to control eutrophication began in 1968 and were highly successful (Thornton, 1982), which probably contributed to the next fish population change. *Labeo altivelis* had steadily declined until 1972 but then began to increase so that in 1979 it made up 45% of the total catch. This may have been caused by the decline in blue-green algae population which improved water transparency, and in turn led to an increase in benthic diatoms, a major food item for *L. altivelis* (Munro, 1967).

It is of interest to note that, at the time of writing, exactly twenty five years have elapsed since the closing of the Kariba dam wall, bringing the first of the big tropical African man-made lakes into being. Much has been learned of the fish communities of this and other big reservoirs since then, but much remains to be done. In particular, managers of fish communities in these lakes should use this experience to quantify and predict future trends.

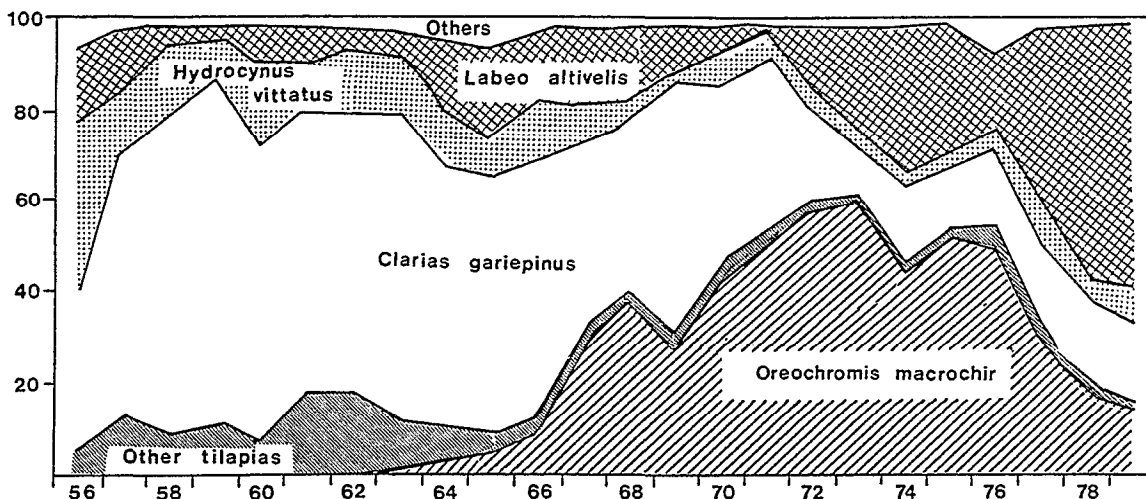


Fig. 5 : Changes in composition of the commercial fish catch in Lake McIlwaine, Zimbabwe, 1956-1978. Redrawn from Marshall (1982b).

RESUME

Il existe actuellement des réservoirs artificiels sur de nombreuses rivières africaines. Leur construction a modifié les conditions écologiques (facteurs édaphiques, apports en éléments nutritifs) et changé la composition des peuplements ichtyologiques. Dans un premier stade, l'eau des réservoirs s'enrichit en sels minéraux provenant des sols nouvellement submergés et de la décomposition de la végétation. Il en résulte un développement algal très important, une augmentation du zooplancton et une multiplication des macrophytes flottants. La turbidité des eaux et la température hivernale peuvent limiter la productivité qui en tout état de cause diminue avec le temps en raison d'un apport moins important en éléments nutritifs qui sont en partie utilisés par une communauté benthique plus variée qu'à l'origine et comprenant des macrophytes enracinés et des invertébrés.

Etant donné que le chalutage benthique est rarement pratiqué, il n'est pas recommandé de couper les arbres avant la mise en eau car les troncs immergés sont de bons substrats pour le développement d'une flore et d'une faune épiphytiques servant de nourriture aux poissons. Les plantes flottantes prolifèrent d'abord exagérément mais diminuent par la suite lorsque le système se stabilise et que les apports en éléments nutritifs diminuent. L'évolution de la nature de la biomasse végétale sous l'effet de divers facteurs biotiques ou abiotiques a un impact important sur les communautés ichtyologiques des lacs de barrage.

Le barrage lui-même peut être un obstacle pour des poissons tels que les anguilles ou les mulots migrant depuis la mer et entraîner la disparition de ces espèces en amont. Les espèces potamodromes qui se reproduisent de manière saisonnière dans les tributaires ou les plaines inondées sont abondantes après la mise en eau car elles ne subissent plus une forte mortalité en saison sèche, mais régressent ensuite dans la mesure où elles ne trouvent plus de zones favorables à leur reproduction. Les espèces benthiques comme les Mormyridae peuvent devenir moins abondantes du fait de la désoxygénation des eaux près du fond et les espèces affectionnant les eaux courantes disparaissent en général complètement. Mais les espèces, comme les *Tilapia*, qui étaient adaptées aux eaux stagnantes dans l'ancien cours d'eau, se développent abondamment dans ce nouveau contexte.

Les lacs de barrage ont une vaste zone pélagique favorable au développement des espèces planctonophages comme les Clupeidae. Dans le Zambèze où les poissons pélagiques étaient absents, l'introduction de la sardine du lac Tanganyika fut un grand succès économique. Des prédateurs comme les *Hydrocynus* ont modifié leur comportement habituel pour pénétrer en pleine eau à la recherche de proies et constituent ainsi une part non négligeable de la pêche pélagique.

Les adaptations de différents poissons aux conditions lacustres ont été discutées. Elles peuvent donner des informations sur la manière dont débute les phénomènes de spéciation - bien connus dans le cas des communautés de Cichlidae des grands lacs africains - dans ces milieux de grande taille et sans obstacles physiques.

En ce qui concerne la production piscicole et la pêche dans les lacs de barrage, il faut souligner qu'elles peuvent évoluer très rapidement, notamment durant les années qui suivent la mise en eau. Un modèle de production de la pêche en fonction de l'indice morpho-édaphique est proposé.

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