# Chapitre 16

# FISH COMMUNITIES OF SOUTH EAST AFRICAN COASTAL LAKES

# *PEUPLEMENTS ICHTYOLOGIQUES DES LAGUNES DU SUD EST DE L'AFRIQUE*

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Due to their relatively large size coastal lakes form the bulk of the estuarine area of Africa and are hence the most important category of estuarine system with regard to fish. They are found in several regions of the continent but among the most extensive are a chain along the east coast from Lagoa Poelela in Mocambique to St Lucia in Natal (Fig.l) and along the west coast from Cameroun to Guinea. St Lucia, which has an area of 300 $km^2$,is the largest estuarine system in Africa. Coastal lakes differ from other lakes because they are usually brackish and have some connection, however tenuous, with the sea. They fit the definition of coastal lagoons given by Barnes (1980) but to quote this author «.....Lagoons, therefore as one might expect, grade into other coastal habitat types : into semi-enclosed marine bays, into freshwater lakes, and into estuaries; and some of these intergradations may represent stages in an evolutionary sequence.....»

Almost all intergradations are shown by the coastal lakes of south east Africa and the present state of each, both physically and biologically, is a result of their geological history, their degree of isolation from the sea, the number of inflowing rivers and, if they are totally isolated, the length of time they have been cut off. The salinity of these lakes therefore varies from freshwater to seawater and higher. The degree of isolation from the sea, the amount of fresh water entering the system and the surface to volume ratio control the salinity. It is impossible to generalise about the salinity conditions of African coastal lakes, as some, such as Lake Nhlange (1-4 ‰) and L. Poelela (4-7 ‰) are stable for long periods whereas others change more rapidly. Lagos lagoon shows both diurnal fluctuation due to tidal effects and much greater seasonal changes caused by the influx of freshwater in the rainy months. During the dry season the salinity is high (25-35 ‰) and brackish conditions extend inland for about 35 km. In the rainy season the salinity falls and almost freshwater conditions prevail (0-10 ‰) (Hill & Webb, 1958). In contrast at St Lucia lake in Zululand, salinity fluctuates widely on a long term basis according to climatic cycles, usually of five to seven years : during wet cycles salinities are 10-25 % but in drought periods may reach 102 % (Day 1981). It is evident therefore that salinity plays a major role in influencing the fish communities of coastal lakes, although it is by no means the only factor which has to be considered. Turbidity, depth and substratum are also important (Blaber & Blaber, 1980). Factors which many coastal lakes have in common and which are relevant to fish faunas are : their relatively large size, the sheltered nature of their waters and often high productivity. These phenomena have also made them attractive to man in terms of their economic value as harbours and fishing grounds. Hence problems concerned with pollution, overfishing and conservation are important practical considerations pertinent to the fish communities of coastal lakes.

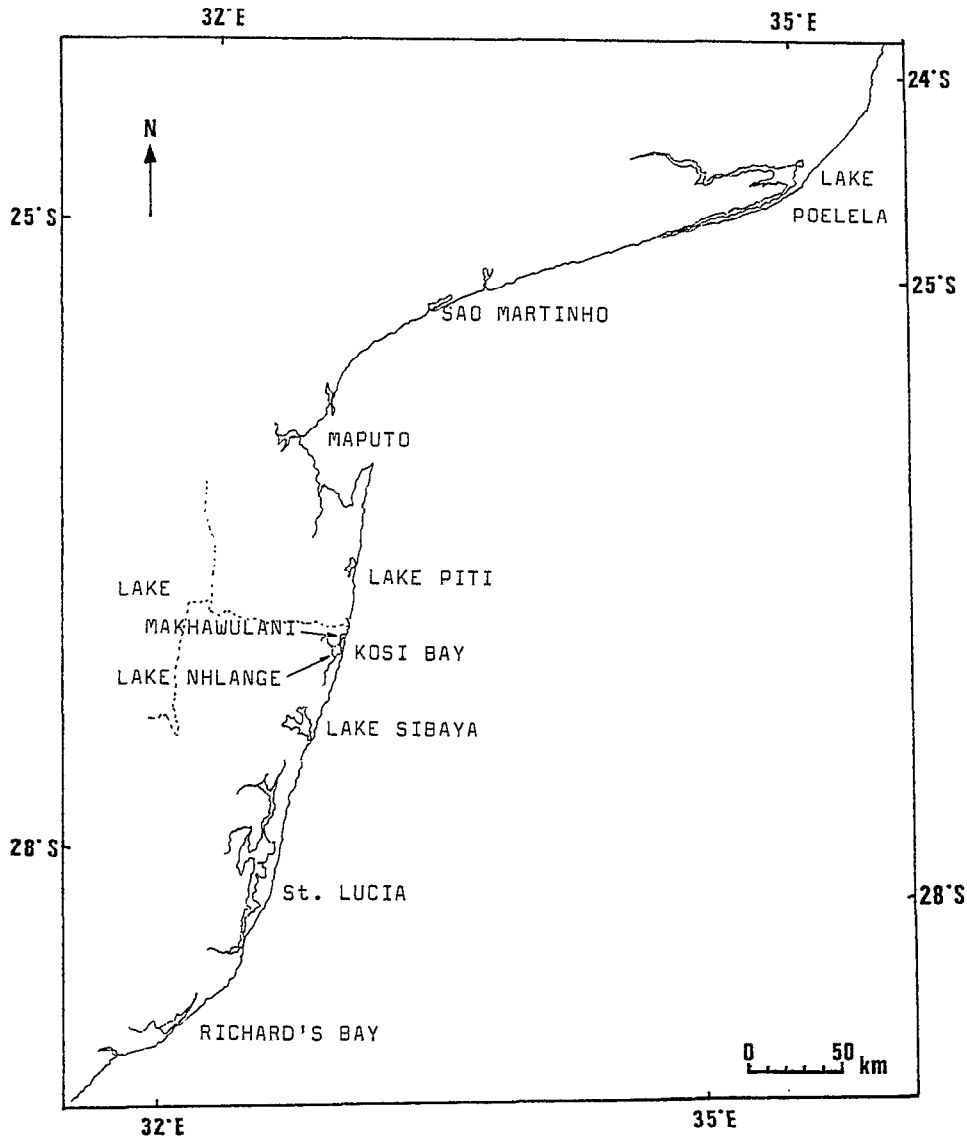


**Fig. 1** : The coastal lake system of south east Africa. (..... = international border).

The fishes of coastal lakes are treated separately from those of other African lakes because they are mainly marine species or of marine origin. Coastal lakes are frequently referred to as a type of estuary and certainly their fauna is most closely related to that of estuaries. The fish communities of coastal lakes may be divided according to their origin. In most cases the dominant species are euryhaline marine ones which enter the system either as juveniles in search of nursery areas, or as adults looking for food (Blaber & Blaber, 1980). Other groups occurring in these lakes are a euryhaline freshwater component and an estuarine group consisting of species which complete their life cycle in the lake. A stenohaline marine component usually occurs in the mouth area of open coastal lakes where the salinity does not fall below that of seawater; but should not be considered as part of the coastal lake community although the fish may play a significant predatory role in a limited area.

## 1 - FISH COMMUNITIES OF SOUTH EAST AFRICAN COASTAL LAKES

The chain of lakes from Poelela to Swartvlei exhibit a variety of types in terms of their isolation from the sea, depth and salinity. The chief characteristics of these lakes have been reviewed by Allanson (1981). Their fish communities differ markedly from one another.

The main physical features of the five largest lakes together with their dominant fish faunas are shown in Table 1. The species diversity varies but for different reasons. Lake Sibaya, which is totally isolated, deep and oligotrophic (Allanson, 1981), has a relatively impoverished fauna of freshwater species and estuarine "relict" species (Bruton 1979a) Lake Poelela has an even lower species diversity despite an intermittant connection with the sea, although it should be noted that the species numbers shown in Table 1 are based on a single sampling period (Hill *et al.*, 1975). Lake Poelela has a 75 km long tenuous connection with the sea via a system of channels and lakes, is relatively deep and has a low salinity. It probably represents an example of a coastal lake just prior to total isolation, with freshwater species becoming dominant over marine ones. Lake Nhlange is permanently connected to the sea through the Kosi system and much movement of euryhaline marine fish takes place between it and the neighbouring parts of Kosi and the sea (Blaber & Cyrus, 1981). The relatively low numbers of species in Nhlange can be attributed to the low salinities which restrict the numbers of marine species together with the deep oligotrophic nature of the lake. Depths in excess of 20 m over much of their area in Lakes Poelela, Sibaya and Nhlange (Hill, 1975) render much of the bottom unsuitable for fish due

**Tableau 1.** The main physical features and dominant fish faunas of the large coastal lakes of south east Africa.

| LAKE | Poelela | Nhlange (Kosi) | Sibaya | St Lucia | Swartvlei |
|---|---|---|---|---|---|
| ISOLATION | 75 km tenuous link with sea | estuary linked | isolated | estuary linked | estuary linked |
| MAX.DEPTH (m) (X̄) | 24 (13.7) | 31 (7.2) | 40 (13) | 2 (<1) | 16 (6.7) |
| AREA km² | 65 | 31 | 65 | 300 | 11 |
| SALINITY (‰) | 6.5 - 8.0 | 0 - 5.0 | 0 | 20 - 110 | 1.0 - 20.0 |
| TURBIDITY (secchi m.) | 7 | 1 - 2 | 3 | <0.5 | 0.5 - 4.5 |
| DOMINANT FISH GROUP | euryhaline freshwater | euryhaline marine | freshwater & estuarine relict | euryhaline marine | euryhaline marine |
| DOMINANT ILIOPHAGOUS SPECIES | *Oreochromis mossambicus* | Mugilidae & *Chanos chanos* | *Oreochromis mossambicus* | Mugilidae | Mugilidae |
| DOMINANT FILTER FEEDER SPECIES | none recorded | *Gilchristella aestuarius* | *Gilchristella aestuarius, Hepsetia breviceps* | *Thryssa, Hilsa, Gilchristella* | *Gilchristella* |
| DOMINANT INVERTEBRATE BENTHOS FEEDING SPECIES | *Glossogobius, Croilia, Pseudocrenilabrus* | Gerreidae, *Pomadasys, Rhabdosargus* | *Glossogobius, Croilia, Pseudocrenilabrus* | wide variety | *Lithognathus lithognathus* |
| DOMINANT PISCIVOROUS SPECIES | *Tylosurus leiurus* | Sphyraenidae, *Caranx ignobilis, C. sexfasciatus* | *Clarias gariepinus* | *Argyrosomus hololepidotus, Elops machnata* | *Lichia amia* |
| No. SPECIES OF FISH RECORDED | 12 (1) | 37 (2) | 18 (3) | 108 (4) | 25 (5) |

1 : from Hill *et al.* (1975)
2 : from Blaber & Cyrus (1981)
3 : from Bruton (1980)
4 : from Whitfield (1980)
5 : from Whitfield (1983)

to low light levels (Hart & Allanson,1976) and lack of suitable benthic food (Boltt, 1975a).Thus most fish in these lakes occur in comparatively shallow shelf areas or in open waters (Bruton, 1979a). Migrations of fish to and from Lake Nhlange take place around the marginal shelf areas (Blaber, 1978).

St Lucia is a shallow lake with a large surface area and, except during periods of drought, is permanently connected to the sea. Unlike Lakes Poelela, Nhlange and Sibaya its whole area is available to fish. Benthic and planktonic production are high (Boltt, 1975b; Blaber *et al.*, 1981) and most euryhaline marine fish can tolerate the prevailing salinities (Whitfield *et al*, 1981). The species diversity in St Lucia is therefore high (Table 1). St Lucia also differs from the three lakes previously mentioned in that it is primarily a turbid water system. High turbidities are an important factor influencing the distribution of inshore and estuarine fish, many of which, especially during the juvenile phase, exhibit a preference for turbid waters (Blaber, 1981).

Swartvlei is included in this review although it is geographically distant from the subtropical east coast lakes and has a different origin (Hill, 1975). It is located on the south Cape coast in a temperate latitude and is adjacent to a relatively cool sea. The low species diversity in Swartvlei, which has been extensively sampled (Whitfield, 1983), is probably due to the restricted number of euryhalime species in the cool Cape waters.

The dominant fishes of each of the coastal lakes grouped according to their trophic status are shown in Table 1. With increasing isolation from the sea, freshwater species become dominant. Of particular interest is the role of iliophagous species, that is those which feed by ingesting the surface layer of the substrate together with associated detritus and micro-organisms. In lakes dominated by freshwater influences, such as Sibaya and Poelela, the cichlid *Oreochromis mossambicus* is the chief iliophagous species. It can survive very high salinities (Whitfield *et al*, 1981) and is present in Lakes St Lucia and Nhlange where it may be numerous, especially at low salinities, but in these lakes,grey mullet (Mugilidae) of at least 10 species are the predominant iliophagous fish. The distribution of *O.mossambicus* in estuaries and coastal lakes in relation to competitors such as Mugilidae and the milkfish, *Chanos chanos*, was reviewed by Whitfield & Blaber (1978a, 1979). It is probable that *O. mossambicus* is limited not only by its breeding requirements of sheltered littoral waters but by competition with other iliophagous species and the presence of faster swimming marine piscivores.

Zooplankton densities in most of the coastal lakes of south east Africa are relatively low and hence numbers and diversity of filter feeding fish are low. None were recorded in Poelela (Hill *et al.*, 1975) where plankton biomass was very low. The estuarine clupeid, *Gilchristella aestuarius*, is an important planktivore in coastal lakes and in Nhlange, Sibaya and Swartvlei is the only planktivorous species apart from small numbers of *Hepsetia breviceps* in Sibaya and Swartvlei. In St Lucia, where zooplankton densities are at least twenty times greater than in the other lakes *G. aestuarius* filter feeds but in Sibaya, Nhlange and Swartvlei it feeds by selecting individual zooplankters (Blaber *et al.*, 1981). *G. aestuarius* from St Lucia have a significantly different growth pattern from those in other coastal lakes. In St Lucia *G. aestuarius* is not the only filter feeder and is outnumbered by the larger anchovy *Thryssa vitrirostris* and the kelee shad, *Hilsa kelee.*

Lakes Poelela and Sibaya have a similar benthic community consisting of small gobies and cichlids. The same species, *Glossogobius ciuris, Croilia mossambica* and *Pseudocrenilabrus philander* are present in Lake Nhlange but are overshadowed by marine species such as *Rhabdosargus sarba* and *Pomadasys commersonni* and the Gerreidae. The number of marine benthic species entering lake Nhlange is apparently limited by the salinity. The majority of the large number of species in St Lucia are marine invertebrate benthos feeders. The shallow waters of St Lucia with their abundant benthos (Boltt, 1975b) favour a wide array of benthic fish from small soles (*Solea bleekeri*) and small sciaenids (*Johnius belengeri*) to larger prawn and mollusc feeders such as *Pomadasys commersonni.* The commonest benthic feeder in Swartvlei is *Lithognathus lithognathus*, although *Pomadasys commersonni, P. olivaceum* and *Glossogobius giuris* are present.

The differences between the lakes are again illustrated by the piscivores. No piscivore, of either freshwater or marine origin, occurs in Lake Sibaya where *Clarias gariepinus* is the main fish eater. *C. gariepinus* also feeds on a wide variety of other foods (Bruton, 1979b). The clear

waters of L. Nhlange favour the barracudas (Sphyraenidae) and kingfish (Carangidae) which hunt by sight and eat a variety of species. In contrast, the turbid waters of St Lucia attract large numbers of the sciaenid *Argyrosomus hololepidotus* as well as *Elops machnata* which prey mainly on filter feeding species (Whitfield & Blaber, 1978b).

It is apparent from the foregoing that due to the individual nature of each of the coastal lakes, their fish communities are peculiar and must be considered separately.

## 2 - COMPARISONS OF COMMUNITY STRUCTURE

The structure of the fish communities of Lakes Nhlange, Sibaya and St Lucia are very different and have been sufficiently well studied to permit useful comparisons in terms of energy flow.

**Lake Nhlange.** This estuary-linked lake is dominated by euryhaline marine fish but the relatively low diversity of benthos (Boltt, 1975a) and zooplankton (Blaber & Cyrus, 1981) together with low salinities restricts the species diversity. Most of the information given here is taken from the review by Blaber (1986). Two main habitats are recognisable : the open water shelf areas with sandy substrata and the sheltered littoral areas with extensive *Phragmites* beds and sandy substrata covered with plant detritus. Few fish occur over the deep basin. The basic food web for the fishes is shown in Figure 2.

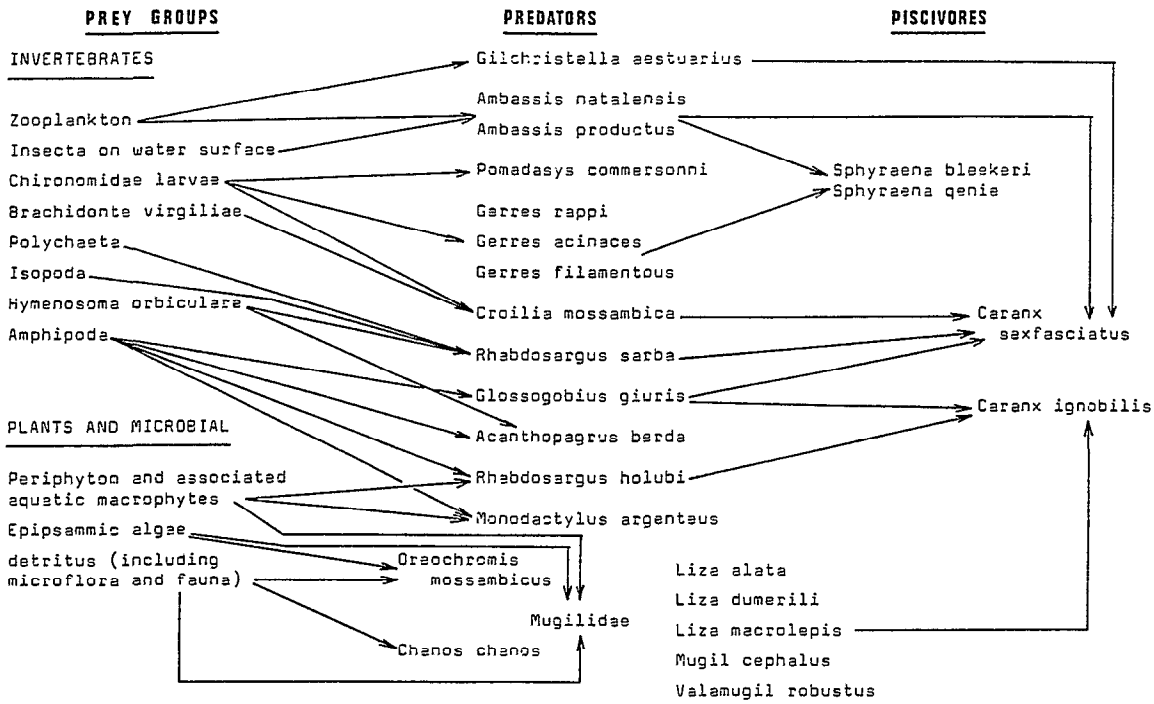


**Fig.2** : Outline of the food web of the fish community of Lake Nhlange (after Blaber, 1986).

The Mugilidae (grey mullets) are the dominant iliophagous fish. Five species, *Liza alata, L. dumerili, L macrolepis, Mugil cephalus* and *Valamugil robustus*, occur in Lake Nhlange (Blaber & Cyrus, 1981) but they segregate the resource by their different substrate particle size preferenda (Blaber 1977). The cichlid *Oreochromis mossambicus* occurs mainly in and adjacent to the extensive *Phragmites* reed beds and does not venture into the more open areas where mullet abound. Small numbers of the planktivore *Gilchristella aestuarius* are found in the open

waters feeding chiefly on the calanoid *Pseudodiaptomus stuhlmanni* (Blaber *et al.*, 1981). These copepods are also consumed by Ambassidae in and adjacent to the reed beds but the main foods of *Ambassis productus* and *A. natalensis* are chironomid larvae and flying insects, the latter taken from the water surface (Martin & Blaber, 1983). Among the benthic species, three species of *Gerres* are common and feed predominantly in open areas on chironomid larvae. Their preferred food in other parts of the Kosi system is bivalve siphons but bivalves other than the small *Brachidontes virgiliae* are absent from Lake Nhlange (Cyrus & Blaber, 1983). The major foods of the other benthic feeders, *Pomadasys commersonni, Rhabdosargus sarba* and *R. holubi* are shown in Figure 2. The gobies *Croilia mossambica* and *Glossogobius giuris* are abundant. The former burrows in open sandy areas while the latter lives mainly in the marginal reed zones. *Croilia mossambica* feeds mainly on the bivalve *Brachidontes virgiliae* (Blaber & Whitfield, 1977a) while *G. giuris* is omnivorous. The burrowing habit of *C. mossambica* helps it escape predators although it is extensively eaten by piscivores (Blaber & Cyrus, 1983). At the top of the food chain are *Caranx ignobilis* and *C.sexfasciatus* together with the two barracudas, *Sphyraena bleekeri* and *S. qenie. Caranx ignobilis* preys mainly on Mugilidae, *R. sarba, Croilia mossambica* and *G. giuris*, while *C. sexfasciatus*, although consuming these species, also feeds on large numbers of *Gilchristella aestuarius* and Ambassidae. The *Sphyraena* species in Lake Nhlange consume Ambassidae and Gerreidae. The majority of the euryhaline marine fish in Nhlange are juveniles and sub-adults which utilise the lake as part of the estuarine nursery and feeding ground. Mugilidae of all ages are present; the fry and juveniles spend at least a year in the lake system (Blaber & Whitfield, 1977b) while the adults appear to move randomly in and out of the lake. With the exception of *Croilia mossambica, Gilchristella aestuarius* and *Glossogobius giuris*, together with the freshwater species, all the species in Lake Nhlange spawn in the sea.

**Lake Sibaya.** This lake has received more attention from biologists than any other in southeast Africa due to the establishment of a research station on the shore in 1965 by Rhodes University. This served as a base for an integrated research programme.The structure of the fish community has recently been reviewed by Bruton (1979, 1980) the following data are taken largely from his paper.

The fish fauna consists of 18 species and is dominated by cichlids (4 species) and gobiids (3 species). Although freshwater species predominate, five species (*Gilchristella aestuarius, Hepsetia breviceps. Croilia mossambica, Glossogobius giuris* and *Silhouettea sibayi*) have marine affinities, thus reflecting the marine origin of the lake. The distribution of the fishes of Sibaya in relation to the feeding niches available is shown in Figure 3. Noteworthy are, firstly, the lack of specialist piscivores, probably due either to the absence of a well-developed pelagic fish community, or because marine piscivores such as occur in Lake Nhlange could not adapt to isolation; secondly, the low numbers of plant eaters, which may be a reflection of the low primary productivity of the lake (Allanson & Hart, 1975); and thirdly, the poor condition and small adult size of *S. mossambicus*, the most abundant species in the lake. Bowen (1976, 1978, 1979, 1980) showed that food quality was probably responsible for the dwarfing of the adults. Juveniles feed on benthic detritus further from nearshore sandy areas but adults feed on benthic detritus further from the shore. The protein content of the food decreases with increasing depth.

Bruton (1980) states that the extensive deep offshore and open water zones of Lake Sibaya are comparatively lifeless compared wit the littoral fringe as far as fish populations are concerned. This is a similar situation to that in Lake Nhlange although the structures of the two communities are different.

**Lake St Lucia.** This estuarine linked system has a very diverse fish fauna due to its physical characteristics and strong connection with the sea. The fish community is dominated by marine species, either as juveniles or adults, or both. An outline of the composition of trophic levels of the fish community is shown in Figure 4. The complexity of the interrelationships is illustrated by the pelagic food web involving zooplankton, filter feeding fish and piscivores (Fig.5). The shallow nature of St Lucia together with relatively high turbidities are major factors making the system attractive to inshore marine species (Blaber & Blaber, 1980). Due to

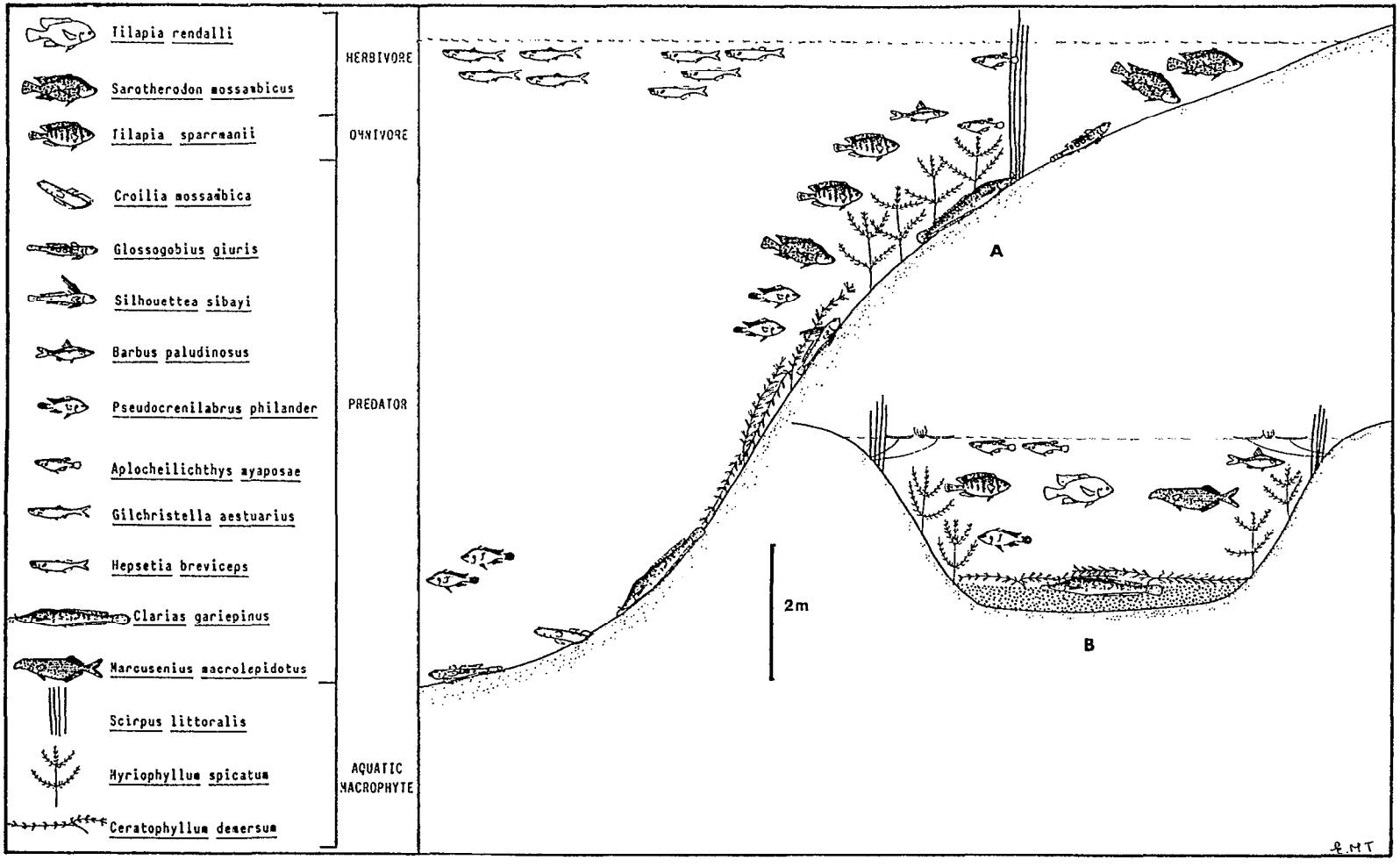


**Fig. 3 :** Diagrammatic representation of the distribution of fishes in the major feeding niches in Lake Sibaya. A. exposed shore. B. sheltered bay (from Bruton, 1980).

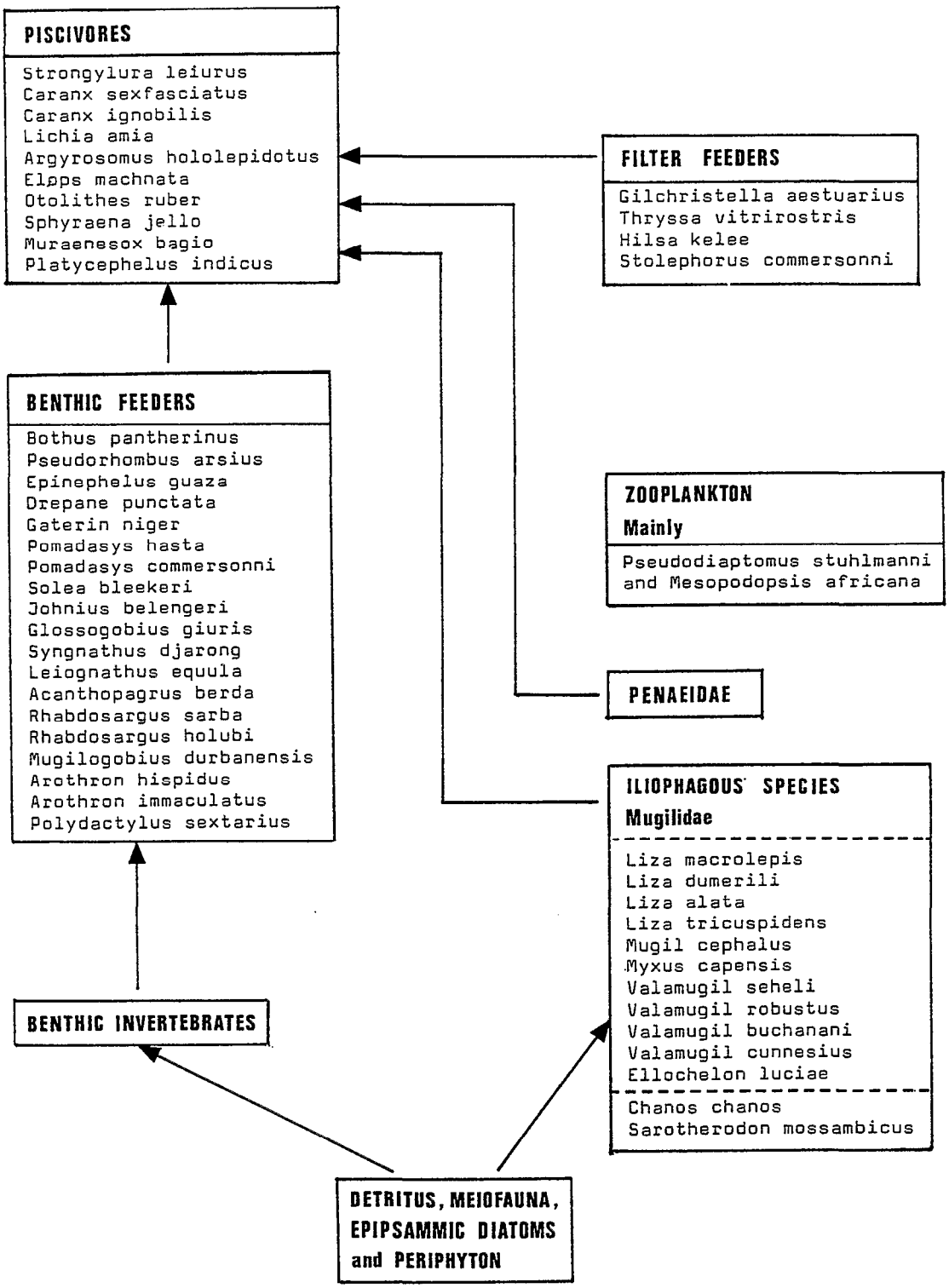


**Fig. 4** : An outline of the composition of the different trophic levels of the fish community of Lake St Lucia (after Blaber, 1986).

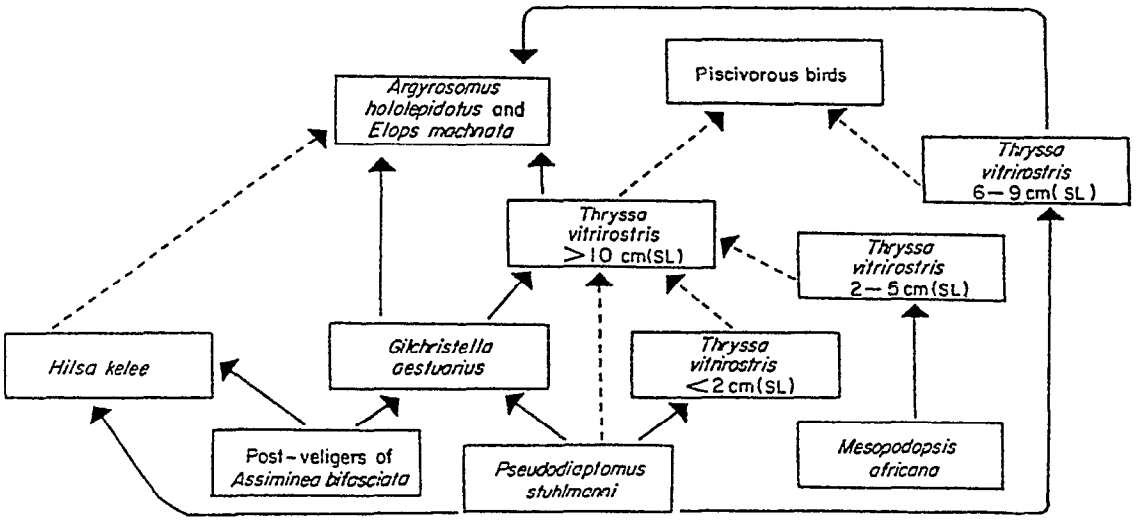


Fig. 5 : The pelagic food web in Lake St Lucia (after Blaber, 1979).

the large scale salinity fluctuations which have taken place at St Lucia (Millard & Broekhuysen, 1970) and the public concern generated by the effects of hypersaline conditions on plant and animal life, a great deal of biological research has been undertaken. A checklist of the fish fauna in 1948 was published by Day *et al.* (1954) and further checklists resulted from the Commission of Inquiry during the years 1964 — 1966 (Millard & Broekhuysen, 1970). The first detailed research on the fishes of St Lucia was that of Wallace (1975) and Wallace & van der Elst (1975) during the hypersaline years from 1969 to 1972. Wallace (1975) recorded the salinity ranges of most species (later extended under low salinity conditions by Whitfield *et al.* (1981) and demonstrated an inverse relationship between species diversity and salinity in the North Lake compartment of the system. Wallace and van der Elst (1975) showed that vast numbers of juvenile marine fish of small size migrate into the lake and spread along the length of its shores. Wallace (1975) also showed that a greater proportion of large adult fish occur in St Lucia than in most estuaries, particularly *Argyrosomus hololepidotus, Mugil cephalus, Pomadasys commersonni* and *Rhabdosargus sarba.* There is an annual movement of *P. commersonni* which feed mainly on bivalves, into St Lucia in spring and summer (Wallace, 1975). The shoals of this commercially important species which move in and out of St Lucia consist of pre- and post-spawners, but those which migrate into the furthest parts of the system have already completed their spawning.

Two main piscivorous food chains exist in the fish comunity (Whitfield & Blaber, 1978b), firstly, that of zooplankton feeding anchovies and clupeids to the predatory *Elops machnata* and *Argyrosomus hololepidotus*, in which it has been shown that the whole pelagic food web is supported largely by the calanoid *Pseudodiaptomus stuhlmanni* (Fig.5); secondly that of mullet and other fish to the less common Carangidae, Sphyraenidae and sharks.

As in Lake Nhlange few species spawn within the lake with the exception of those small estuarine species already discussed. The anchovy *Thryssa vitrirostris* also spawns in St Lucia and its life cycle is closely related to the annual cycles of zooplankton.

## 3 - EXPLOITATION AND CONSERVATION

The nature and geographical location of coastal lakes has made them useful and important to the human economy as harbours and waterways, as fishing grounds and as conservation areas. The lakes of west Africa form several important harbours such as those at Lagos and Abidjan and all are heavily exploited for fish (Pillay, 1967). The major commercial fishes are species

of *Sphyraena, Lutjanus. Pomadasys* and *Tachysurus* together with those of the families Sciaenidae, Sparidae and Mugilidae. The clupeid *Ethmalosa fimbriata* is also the basis of an important fishery. Fish yields as high as 8000 kg/ha/y are reported from-the lagoons of Dahomey (Lowe-MacConnell, 1977). The migrations of grey mullet between lagoons and the sea support a lucrative fishery in Ghana (Pillay, (1967).

The south east African coastal lakes are less utilised than those of west Africa although that which existed at Richards Bay on the Natal coast has been converted into a deep water harbour. A local gill net fishery based on cichlids exists at Lake Poelela in Mocambique but no yield figures are available. Lakes Nhlange and Sibaya are fished on a small scale by the local people. Lake St Lucia forms part of a game reserve containing large numbers of hippopotamuses and crocodiles although sport angling is permitted in certain areas. Of all the south east African coastal lakes St Lucia has the highest potential fish production. The importance of St Lucia from a conservation viewpoint cannot however be overemphasized; it is the most important juvenile fish nursery on the coast of south east Africa, forming not only a nursery for fish spawned near St Lucia, but also for those from a large area of the continental shelf adjacent to the Tugela Bank and Richards Bay area (Wallace & van der Elst, 1975). The crocodiles and piscivorous birds of St Lucia are dependent on the fish populations. Without doubt the tourist and angling value of St Lucia rely upon adequate conservation of the fish fauna. Obviously it would be difficult if not impossible to allow an economic commercial fishery and at the same time try to retain St Lucia in its present etate. Thus the coastal lakes of south east Africa are in a relatively unspoiled state and their economic value at present lies in the tourist industry and their value as centres for basic scientific research. The coastal lakes of west Africa on the other hand are of great economic importance, both nationally as in the case of Lagos harbour in relation to oil exports, and locally for large numbers of fishermen whose livelihood depends on exploitation of the fish communities.

## RÉSUMÉ

Les lagunes côtières constituent un ensemble hétérogène de milieux, où la salinité des eaux notamment, est un facteur écologique important. La salinité peut être plus ou moins stable ou varier fortement en fonction de cycles saisonniers ou climatiques.

La composition des peuplements ichtyologiques dépend de différents facteurs et notamment de l'existence de communications importantes avec le milieu marin. Lorsque les lagunes sont isolées de la mer les espèces d'eau douce sont dominantes, alors que c'est le cas des espèces euryhalines d'origine marine lorsque les uryhalines d'origine marine lorsque les communications avec la mer sont permanentes. Par exemple, parmi les espèces se nourrissant de la pellicule superficielle du sédiment, *Oreochromis mossambicus* est l'espèce dominante dans les lagunes d'Afrique du sud-est sous forte influence des eaux douces. Il est remplacé par les Mugilidae dans les milieux en liaison permanente avec la mer.

Les structures des peuplements ichtyologiques de quelques lagunes (Nhlange, Sibaya, St Lucia) sont brièvement présentées en insistant sur les chaînes trophiques propres à chacun d'eux.

Les milieux lagunaires sont en général très productifs et la pêche y est importante. Les lagunes d'Afrique du sud-est sont cependant moins exploitées que celles d'Afrique de l'ouest et l'intérêt économique de certaines d'entre elles est basée sur l'industrie du tourisme.

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