Chapitre 13

FISH COMMUNITIES IN THE EAST AFRICAN GREAT LAKES

PEUPLEMENTS ICHTHYOLOGIQUES DES GRANDS LACS D'AFRIQUE DE L'EST

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Many fish communities of the East African Great Lakes (Lakes Victoria, Tanganyika and Malawi) are under intense pressure of exploitation to meet Man's escalating needs for animal protein. Indeed, the requirement for fish protein is rising exponentially with the rapidly accelerating increase in human populations and one can confidently predict that these fish communities will be subjected to even greater fishing pressure in the future. A frightening aspect of this exploitation is that so little is known of the structure of the communities, or of the interactions within and between them, that it is impossible to predict, except in the broadest outline, the outcome of man-induced perturbations of such multispecific fisheries. There is already evidence of the effects of Man's exploitation and manipulation of these resources (Fryer, 1972; Coulter, 1976; Turner, 1977a, 1977b; Sharp, 1981; Witte, pers. comm.) and it is clear that the fish communities of these lakes are particularly sensitive to exploitation. There are indications that in Lake Malawi several of the larger species of fish are either locally extinct or, by virtue of the patchy distribution of most species (see below), totally extinct (Turner, 1977a).

The most basic ecological data consist of counts of individuals and of the species to which these individuals belong, of the trophic and habitat relations between these species and of the way that the counts and relations vary with time. Research on the Great Lakes of Africa is still in the exploratory phase. For example, more than 50 % of the discovered species in Lakes Victoria (Van Oijen *et al.*, 1981) and Malawi (Ribbink *et al.*, 1983a) are undescribed and an unknown proportion in Lake Tanganyika await description (Brichard, 1978). There is no doubt that many additional species will be discovered as a result of further exploration and research. Since many of the component species of the fish communities of the African Great Lakes are still undescribed with very little ecological data available concerning any of these species, it is clear that our understanding of the structure of and interactions within and between communities is in its infancy. Despite this, modern techniques are used to harvest these stocks and the impact of these fishing methods is of such a magnitude that it is now likely that we shall never know the communities in an undisturbed state. Indeed it is possible that species which are unknown to science are being or have already been lost as a result of over-exploitation. Fisheries biologists have an unenviable task of trying to conserve the unique species diversity while simultaneously endeavouring to satisfy the ever increasing demand for protein. Any general discussion on fish communities of the Great Lakes of Africa will be superficial since no detailed data base exists. Furthermore, those communities which are subject to heavy fishing pressure are undergoing considerable change at present and are likely to experience further changes in the future. This means that a true baseline is unobtainable.

It has been appreciated since the earliest scientific explorations of these lakes that each has a rich species diversity and that each major habitat (rocky, sandy, weeded, open water etc.) is frequented by numerous species which constitute the communities characteristic of those habitats. In this chapter each of these communities will be dealt with in turn. However, the communities of the three lakes are not given an equal coverage. Those of Lake Malawi are discussed in greatest detail and then parallels between its communities and those of the other lakes are drawn fairly briefly, but with reference to the appropriate literature.

THE LAKES AND THEIR MAJOR HABITATS.

Lakes Malawi and Tanganyika are long, narrow and deep Rift Valley Lakes with clearwaters and permanent stratification, the water below about 200 m being slightly cooler than the surface waters and totally anoxic (Fryer & Iles, 1972; Lowe-McConnell, 1975; Beadle, 1981). Lake Victoria, which was formed by warping, with consequent backflooding of rivers (Fryer & Iles, 1972) and is not in the Rift Valley, has a squarish shape and a larger surface area than the Rift Valley Lakes, but is shallower and turbid (Greenwood, 1974; Van Oijen *et al.*, 1981).

Although the lakes differ topographically and historically from one another, the major ecological habitats of each are essentially similar, but Lake Victoria has relatively more muddy and vegetated substrata and less rocky substrata than do the two Rift Valley Lakes. Lake Victoria has numerous sheltered bays and inlets as well as a gradually sloping bottom which is in contrast to the steep profile and paucity of bays along much of the coastlines of the Rift Valley Lakes. Further details of physiography are given by Greenwood (1974), van Oijen *et al.*, (1981), Poll (1956), Marlier (1959), Brichard (1978), Fryer & Iles (1972), Jackson (1961) and Ribbink *et al.*, (1983a). Sandy beaches are less numerous than rocky shores in Lake Tanganyika (Lowe-McConnell 1975), while in Lake Malawi about 25% of the coastline is rocky.

The major habitats may be broadly classified as follows : rocks, sediments, macrophytic vegetation and open water. In each habitat further subdivisions are recognised, thus sediments may range from coarse gravel to a fine silt of mineral or organic origin. Similarly, rocky shores may be composed partly, or entirely, of small pebbles, rocks, boulders or huge rocky slabs. Vegetated areas differ according to whether the macrophytes are emergent or submergent as well as to which species of plant dominates an area. With increasing depth there is a change in the predominant plant species. A point is reached, at about 10 m in the Rift Valley Lakes but shallower in the more turbid Lake Victoria, below which macrophytes disappear completely. On sedimented substrata, or in the interstices of rocky areas, sand predominates in the shallows and may extend quite deeply on exposed shores before being covered by an increasingly thick mantle of ooze or mud with varying proportions of organic matter. The depth to which a permanent muddy mantle extends up a sandy bottom is determined by the physical characteristics of the bay or inlet. In sheltered bays in which the scouring effects of waves and currents are minimal the sandy region is covered by mud in shallow water. For example, within Monkey Bay in southern Lake Malawi, mud overlying sand is found in water less than a metre deep in sheltered regions while in the centre of the Bay, at a depth of about 15 m, the gelatinous ooze covering the sand is 120-140 cm thick. By contrast, the entrance of Monkey Bay is exposed to wave action and currents which clean the shallows so effectively that the muddy mantle is first found at 6-8 m depth; at 40 m depth it is still thin, being no more than 2-3 cm deep. At the less sheltered Nkhata Bay, the muddy mantle is usually in deeper water. Wave action and currents clean sediment from rocky shores and, since their effects are greatest in shallow water, the shallows generally are sediment-free. Once again, the degree of exposure of such shores to these elements determines the depth at which the sediment layer commences.

THE FISHES COMMUNITIES OF THE GREAT LAKES.

The fishes of the Great Lakes of Africa are drawn from nineteen families (Table 1). A feature of each lake is that it supports unique species flocks which have evolved and diversified within its confines. In Lake Tanganyika there are species flocks in five families; the Bagridae, Centropomidae, Cichlidae, Clariidae and Mastacembelidae. Lake Malawi has flocks in two families, the Cichlidae and Clariidae, while in Lake Victoria only the Cichlidae have speciated widely. The Cichlidae is the only family which has produced species flocks in each of the three Great Lakes, and it has also given rise to the greatest number of species (Table 1, and Chapter 2), colonised the largest number of habitats and displayed the greatest degree of adaptive radiation. Not surprisingly, therefore, the fish communities of these lakes are dominated by cichlids in all habitats except the open pelagic waters which are dominated by the Clupeidae and Centropomidae in Lake Tanganyika (Coulter, 1981), and by the cyprinid *Engraulicypris sardella* and the Clariidae in Lake Malawi.

Table 1 : The number of species in each family of the three Great Lakes. Data from Lowe-McConnell (1975), Van Oijen *et al.* (1981) and Ribbink *et al.* (1983a).

	Lake Victoria	Lake Tanganyika	Lake Malawi
Anabantidae	1	-	1?
Anguillidae	-	-	1
Bagridae	2	11	1
Centropomidae	-	5	-
Characidae	2	4	1
Cichlidae	250^+	200^+	400^+
Citharinidae	-	1	-
Clariidae	6	5	13
Clupeidae	-	2	-
Cyprinidae	12	11	10
Cyprinodontidae	3	2	1?
Distichodontidae	-	2	-
Malapteruridae	-	1	-
Mastacembelidae	1	7	1
Mochokidae	2	5	1
Mormyridae	7	-	5
Polypteridae	-	1	-
Protopteridae	1	1	-
Schilbeidae	1	-	-

The understanding of the fish communities of littoral rocky shores is better than that of communities in any other habitat. Accordingly, this discussion is devoted mainly to rock-dwelling fishes, then attention is focussed on communities in other habitats.

1 - COMMUNITIES OF LITTORAL ROCKY HABITATS.

Lake Malawi. The rocky habitats of Lake Malawi are dominated by small, brightly or darkly coloured cichlids which show striking anatomical and behavioural specializations for feeding (Trewavas, 1935; Fryer, 1959; Fryer & Iles, 1972). Most of these fishes are closely associated with the rocky zones, some never venturing more than a metre from the rocky substatum (Fryer, 1959).

In Lake Malawi a group of 10 closely related endemic genera collectively referred to as Mbuna dominate the rocky zones. It is estimated that more than 200 species of Mbuna occur in Lake Malawi (Ribbink *et al.*, 1983a). A survey of these fishes demonstrated that the Mbuna community at each site differs from that at other sites in both species composition and numerical abundance of constituent species. This was even true of areas which were no more than a few hundred metres apart. A further feature is that many species are endemic to a single small part of the lake (Ribbink *et al.*, 1983a). Similarly, the non-Mbuna of the rocky shore communities varied from one site to the next in species composition and in numbers of individuals, though there are among these fishes several species which have a lake-wide distribution (e.g. *Cyrtocara polystigma* (Regan), *Cyrtocara kiwinge* (Ahl), *Labeo cylindricus* Peters, *Barbus johnstonii* (Günther), *Opsaridium* (= *Barilius*) *microcephalus*, *Bathyclarias worthingtoni* Jackson, and others).

Thus, the intralacustrine endemicity demonstrated by many results in unique communities around the lake comprising endemics plus contributions from the more widespread species. Although this feature has been demonstrated most clearly for communities of rocky habitats, the studies of fishes of other habitats indicate similar geographic effects on community structure (Ribbink *et al.*, 1983a; Chapter 2).

A typical permanent community of a rocky habitat in Lake Malawi comprises mainly Mbuna species with contributions from other cichlids and from several noncichlids. In addition, there are temporary members of the community in every rocky habitat. These include (i) semi-pelagic planktivorous *Cyrtocara* spp., referred to locally as «Utaka» (Iles, 1960), which move inshore to breed or to feed on plankton which is present in water currents around rocky outcrops and reefs , (ii) sand-dwellers which release and guard fry among rocks, and (iii) fry and juveniles of numerous species which shelter among rocks until they are large enough to live in the more open habitats for which they are adapted as adults. Rocky habitats are also frequented by fishes which visit from adjacent habitats and, as the setting of each rocky zone is unique, the input of species from surrounding habitats is variable. For example, in southern Lake Malawi the island of Thumbi East is situated at the entrance to Monkey Bay. On the north-eastern side of the island, which is exposed to the open lake, the rocky zone extends to a depth of 35-40 m, but on the sheltered south-western side which faces into Monkey Bay the purely rocky zone terminates between 3-8 m depth. On the shallow side the rocky zone merges along its base with the vegetated, sandy and/or muddy habitats and the members of the communities of each of these habitats range some distance into the provinces of other communities. The base of the rocky zone on the exposed shore is too deep for macrophytes and appears to be beyond the depth range of the shallow-dwelling species found in sandy and muddy habitats within Monkey Bay. Consequently, these rocky habitats are visited by an entirely different group of sand-dwelling fishes as well as different intermediate zone species e.g. *Aulonocara* spp. and *Trematocranus* spp.

Small isolated rocky outcrops, such as the islands of Chinyankwazi, Chinyamwezi and Zimbawe, which are separated from other rocky habitats by deep water and by substrata which are inimical to lithophilous fishes, are characterised by having few Mbuna species (Zimbawe 9 species; Chinyamwezi 12 species; Chinyankwazi 14 species; Ribbink *et al.*, 1983a). By virtue of the exposure of these islands to the scouring effects of wave action and strong currents, the substratum is essentially free of sediment to 30-40 m depth, and fishes which are normally associated with sediment-rich zones are rare or absent. Similarly, fishes characteristic of the intermediate habitats in the 0-40 m depth band are also absent. In contrast to these small islands of purely rocky habitats in deep water which are inhabited by a few species, large islands usually have a variety of habitats in both shallow and deep water and their faunas are speciose e.g. 49 Mbuna at Likoma Island; 32 at Chisumulu Island; 34 at Maleri Island; 29 at Mbenji Island (Ribbink *et al.*, 1983a). Such findings are consistent with some aspects of the theory of island biogeography (MacArthur & Wilson, 1967). From the foregoing it is apparent that the faunal composition, especially the Mbuna, the overall species richness and the number of individuals of each species differs from one locality to the next. Such insularity of species is largely explained by the highly sedentary nature of many of them, some of which may have their entire distribution restricted to a few thousand square metres (Ribbink *et al.*, 1983a). An implication is that relatively widespread species, such as *Labeotropheus fuelleborni* Ahl, would find themselves within a different species assemblage at each locality, where they are likely to be subject to different interspecific interactions (Ribbink *et al.*, 1983b). It follows that immigrants and founders may need to adapt to a new set of environmental factors (biotic and abiotic) which might differ quite considerably from those of their area of provenance. This sets the scene for speciation in allopatry (see Chapter 2).

The geographic isolation of communities fosters change between such communities so that the species composition of each becomes less alike with time, particularly as the component species diverge from sister species in communities elsewhere. Those species which are most closely adapted to life in rocky habitats and which partition the resources of these habitats most finely are the Aufwuchs feeders, most of which are Mbuna. These are also the fishes which are likely to be affected most by the environmental differences existing between geographically isolated rocky zones. The allopatric populations of Mbuna species which are common to a number of sites differ from one another in coloration (Ribbink *et al.*, 1983a) and size which suggests a sensitivity to environmental pressures. In contrast, predatory species are less sensitive to a variation in the composition of a rocky shore community and the topography of such a shore because they feed on a variety of prey species. Thus, provided that the general characteristics of prey species are the same or similar from one area to the next, no locality-dependent specializations to piscivory are necessary. Indeed, the predatory species found most commonly in rocky habitats (*Cyrtocara kiwinge*, *Cyrtocara macrostoma* (Regan), *Cyrtocara polystigma*, *Cyrtocara linni* (Burgess & Axelrod), *Aristochromis christyi* Trewavas and *Rhamphochromis? esox*) show no clearly discernible geographical variation. However, a possible reason for this is that, relative to the Aufwuchs feeders, the piscivores are mobile and gene flow between populations is probably sufficient to stabilize species specific characters over a wide geographic area.

The marked insularity exhibited by most rock-dwelling cichlids reflects their tendency to remain within the rocky habitats for which they are adapted. Examination of communities at 121 different parts of the lake showed that in each community species are adapted to different microhabitats (Ribbink *et al.*, 1983a). Some species are narrowly adapted (stenotopic) while others are more catholic (eurytopic). Eurytopic species may range over a wide variety of rocky substrata, perhaps venturing into intermediate zones and may also occur over a broad depth range, but stenotopic species are usually restricted to a particular substratum, such as patches of small rocks among medium-sized or large rocks, and to narrow depth ranges (Fig. 1 and 2). The preferred or normal habitat of a species is that part of the environment in which most of its individuals live and breed. Such a general definition does not account for the observation that the preferred habitat of a species varies with the age of the individuals, nor does it account for the fact that some species may spend most of their adult lives in a particular area where they feed, but occupy an entirely different habitat during the breeding season. With regard to the Mbuna, sexually mature fishes live, feed, hold territories and breed within their preferred habitat throughout the year and so the broad definition is adequate. The discussion which follows applies to adults only.

Normally, only small species are permanent residents among small rocks (20-50 cm diameter) and pebbles (> 20 cm diameter). Since large individuals cannot fit into the small gaps between such rocks, these areas are unsuitable to them as refuge and spawning sites. In addition to being inhabited by larger species, habitats comprising large rocks are also tenanted by small fishes, particularly nonterritorial species of *Labidochromis*, the scale-eater *Genyochromis mento* Trewavas and cave-dwelling species such as *Pseudotropheus elongatus* "yellow-tail" (Ribbink *et al.*, 1983a). Habitats of medium-sized rocks (50-150 cm diameter) are inhabited by a wide variety of species some of which habitually frequent upper surfaces of prominent rocks, some occur most frequently at the base of such rocks and others which remain in cracks or crevices between and among rocks.

The caves, holes and crevices among rocks provide protective privacy from eggeaters and other fishes which might interfere with spawning and so areas of broken rocks and rubble are most suitable for territoriality. In contrast, exposed surfaces of huge boulders and rocky slabs which do not provide shelter are seldom used by territorial fish, but they do support large numbers of juveniles, sub-adults and non-territorial adults which harvest the Aufwuchs growing on the rock surfaces. These fishes are, however, at risk when feeding and have to dash for shelter when threatened by predators.

Most lithophilous species occur within the upper 10 m, but the distribution of some Mbuna extends beyond 40 m depth (Figs 1 & 2). The ability to penetrate depth was studied experimentally on eight species of Malawi cichlid and it was found that all were limited to relatively shallow water by functional constraints imposed by their swimbladders (Hill & Ribbink, 1978; Ribbink & Hill, 1979; Marsh & Ribbink, 1981; Ribbink *et al.*, 1983b). However, field observations showed that these species live well within their potential physiological range, for example, *Melanochromis joanjohnsonae* Johnson has the ability to compensate to 25 m depth but normally lives between 1-3m and is rare beyond 4.5 m depth (Hill & Ribbink, 1978). It appears, therefore, that although depth *per se* may limit the vertical distribution of species, other factors which alter with changing depth probably affect depth distribution to a greater extent. These factors include the effects of wave action and currents, light penetration and productivity as well as thickness of sediment on the rocks and the nature of the substratum.

Many species share restricted areas. Habitats of medium-sized rocks in shallow water are particularly rich in species, many of which appear to use similar resources (Fig. 2). Studies of space requirements of these fishes are in their infancy, but enlightening results have been obtained. Holzberg (1978) found that two sympatric species of the *Pseudotropheus zebra* species-complex at Nkhata Bay have territories which overlap. There was, however, no intraspecific overlap of territories (Fig. 3a). Similarly, Marsh (1981) found that the territories of three sympatric species of *Petrotilapia* often showed considerable overlap, but conspecific territories abutted or overlapped only slightly. The territories of *Petrotilapia* spp. are large (mean size : 22.2 m^2 for *Petrotilapia tridentiger* Trewavas; 19.9 m^2 for *Petrotilapia genalutea* Marsh; 6.8 m^2 for *Petrotilapia nigra* Marsh) and frequently the territories of a variety of other cichlid species are included within their boundaries (Fig. 3b).

The degree of territoriality exhibited by Mbuna varies from species to species. *Petrotilapia* spp., members of the *Pseudotropheus zebra* species-complex and many others are highly aggressive towards conspecifics and their territories may abut but do not overlap. They are, however, fairly tolerant of heterospecifics.

There are species such as *Pseudotropheus elongatus* «aggressive» which are so highly aggressive that all potential intruders are excluded from their territories under normal circumstances; territories of these fishes never overlap and usually do not abut (Fig. 3c). Since the Aufwuchs in these territories is not harvested by any fishes other than the resident, it grows longer than that of surrounding areas. These areas of long Aufwuchs are referred to as «algal gardens» (Sharp, 1981; Ribbink *et al.*, 1983a) and are attractive food sources to a number of species which are normally excluded. Occasionally large schools of *Petrotilapia* feed in algal gardens and by virtue of the size of these fishes and the number of individuals in a school the territorial fishes defending the gardens are overwhelmed (Sharp, 1981; Marsh, 1981; Marsh & Ribbink, 1986). At the other end of the scale from these highly aggressive species are those which do not hold territories at all (e.g. several of the *Labidochromis* spp., Ribbink *et al.*, 1983a).

Evidence of species-specific requirements for space was provided by removing individuals from their terrritories. Such individuals were soon replaced by conspecifics, but removal of several successive replacements led to a situation in which territorial heterospecifics became established in the vacant space (Sharp, 1981). This indicates that intraspecific competition for territorial space which fulfils the topographical requirements of the species is strong, and also that in the absence of the normal resident its preferred territorial habitat may be occupied by another species.

Feeding behaviour, trophic interrelationships and feeding space requirements are largely unexplored. Data collected thus far indicate that most Mbuna species feed upon loose Aufwuchs, a small proportion feed upon filamentous algae and several, such as *Genyochromis mento* (a scale and fin-eater) and *Melanochromis crabro* Ribbink & Lewis (an ectoparasite and egg-eater), have unusual diets. The *Cynotilapia* spp. appear to be specialized to feed upon plankton (Fryer, 1959). Although Mbuna are trophic specialists (Fryer, 1959), it appears that all are opportunists which will feed on other resources (e.g. plankton) when available (Ribbink *et al.*, 1983a). As virtually

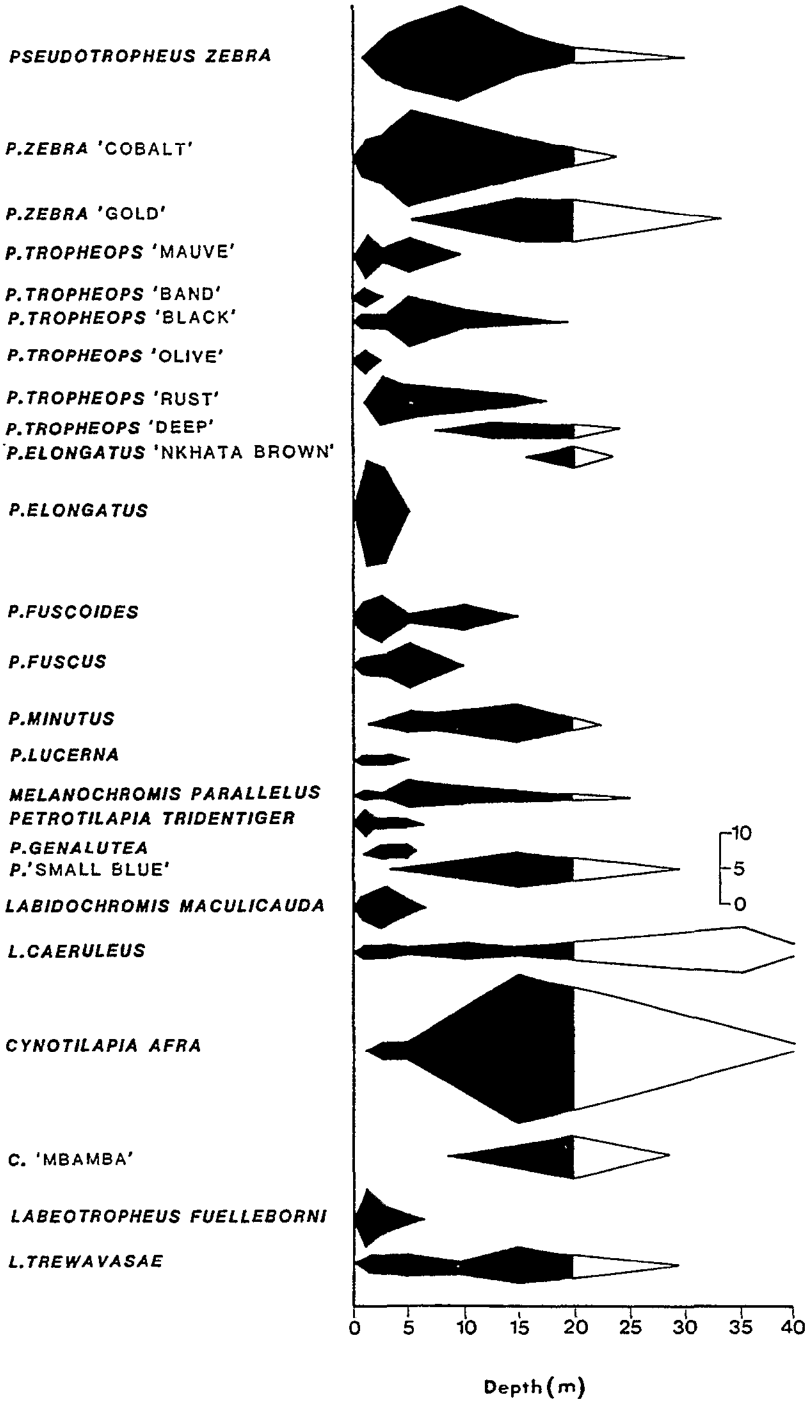

Fig. 1 : A transect at the point of the Nkhata Bay peninsula, Lake Malawi, giving the depth distribution and numerical abundance of Mbuna species. Solid black areas indicate counts of individuals in 50 m^2 (2 x 25 m) grids laid at selected depth contours to 20 m ; beyond 20 m numbers were estimated. Most species occur in the shallows, but several extend beyond 40 m. Territorial males of each species were counted (after Ribbink *et al.*, 1983).

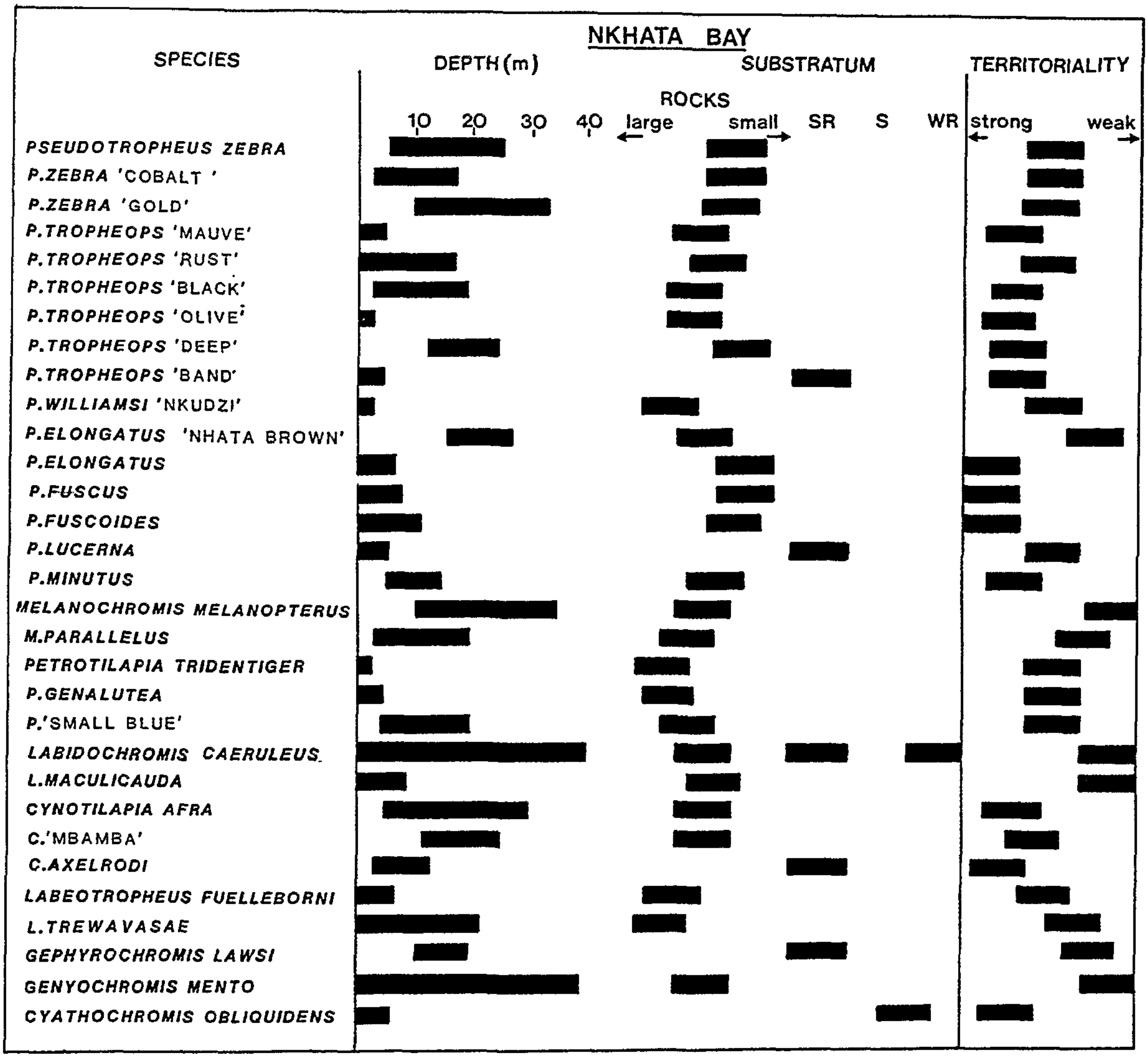

Fig. 2 : Resource utilization by the Mbuna community at Nkhata Bay after Ribbink *et al.* (1983a). Blocks indicating preferred depth are based on quantified data. Those indicating a habitat preference are based on unquantified observations. Preferences for habitats of rocks of a particular size, intermediate zones of sand-rock (SR) or weed-rock (WR) or sandy environs (S) are indicated. Blocks do not indicate the full depth range of species, nor absolute restriction to a particular habitat; they give the preferred depth and habitat types.
An assessment of the degree of territoriality is given by the position of blocks in a range from non-territorial fishes (extreme right) to strongly territorial species with algal gardens (extreme left). Those species which are centrally placed are aggressive almost entirely to conspecifics. The evaluation of the degree of territoriality is largely subjective. The positioning of the blocks was relative to the three reference points given above (i.e. left, right or central).

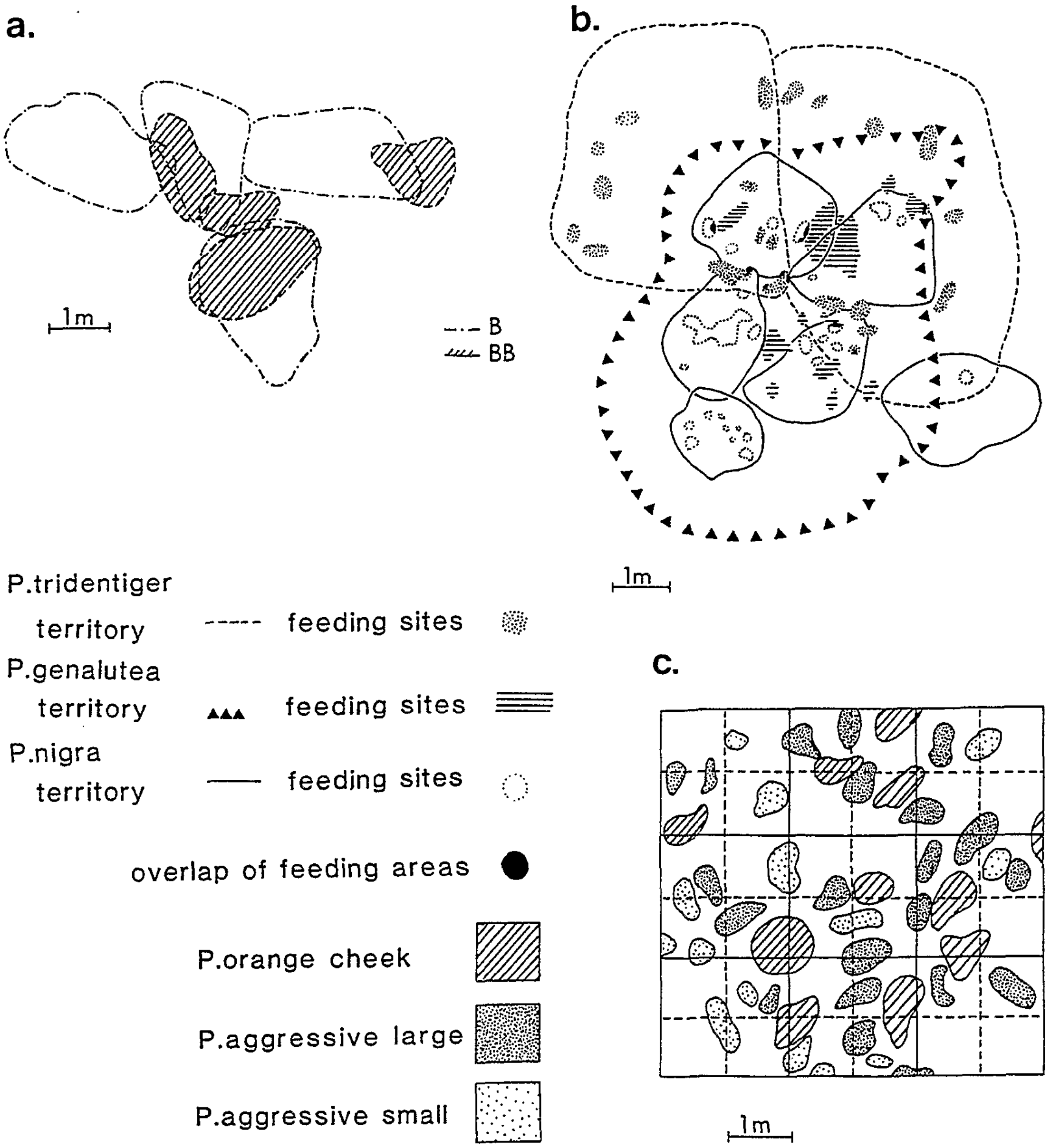

Fig. 3 :

a) Territories of two members of the *Pseudotropheus zebra* species-complex overlap, but those of conspecifics abut without overlap (after Holzberg 1978). BB = *Pseudotropheus zebra* B = *Pseudotropheus zebra* «cobalt» (names after Ribbink *et al.*, 1983a).

b) Territories of three species of *Petrotilapia* overlap, but those of conspecifics abut without overlap. Individuals feed most frequently from specific sites within their territories with little heterospecific overlap of feeding sites (after Marsh, 1981).

c) Territories of highly aggressive species show no overlap. These species feed from algal gardens, within their territories which they defend (after Sharp, 1981). Territories of *Pseudotropheus tropheops* «orange cheek» *Pseudotropheus elongatus* «aggressive» larger than 75 mm SL smaller than 75 mm SL. Names after (Ribbink *et al.*, 1983a). The scale for all three figures is identical permitting a comparison of the size of territories of different species.

all Mbuna feed upon Aufwuchs, one questions how this resource is shared. Fryer (1959) suggested that, due to the apparent high productivity of the rocky shores, Aufwuchs is present in superabundance and there is sufficient for all. A stable superabundance is unlikely to persist and Sharp (1981) found that, while a superabundance of Aufwuchs may be present for short periods, in general there is a shortage of food on rocky shores.

Superficially, the members of lithophilous communities appear to co-exist with considerable overlap of space and food requirements (Fryer, 1959; Fryer & Iles, 1972). Close examination shows, however, that many species are adapted to live within a particular depth range and show preferences for rocks of a certain type. Syntopic species usually have differing microhabitat preferences and those fishes which ingest the same food collect it from different parts of the habitat (Marsh, 1981; Sharp, 1981, Ribbink *et al.*, 1983b). Furthermore, peculiarities of dentition and jaw structure enable species or groups of closely-related species to harvest components of the Aufwuchs which are inaccessible to other Mbuna. For example, Fryer (1959) records that the long forceps-like teeth of members of the genus *Labidochromis* enable these fishes to feed from within narrow cracks and grooves whereas the broad mouths and relatively short teeth of the *Labeotropheus* spp. would restrict their feeding to the prominences on the rock surfaces. Similarly, *Pseudotropheus tursiops* Burgess & Axelrod appears to be able to use the side of its elongate jaw to collect Aufwuchs from narrow cracks and crevices which cannot be used by fishes of similar adult size which lack the elongate snout (Ribbink *et al.*, 1983a).

Labeotropheus species have subterminal mouths and so individuals are able to feed in a position which is almost parallel to the rock surface (Fig. 4a), allowing them to graze in water which is shallower than that which can be used by similar sized fishes with terminal mouths (e.g. *Pseudotropheus zebra* (Boulenger), *Petrotilapia* spp.) It also enables them to maintain position and feed in wave-washed areas more effectively than terminal mouthed species which feed at right angles to the substratum (Fig. 4b).

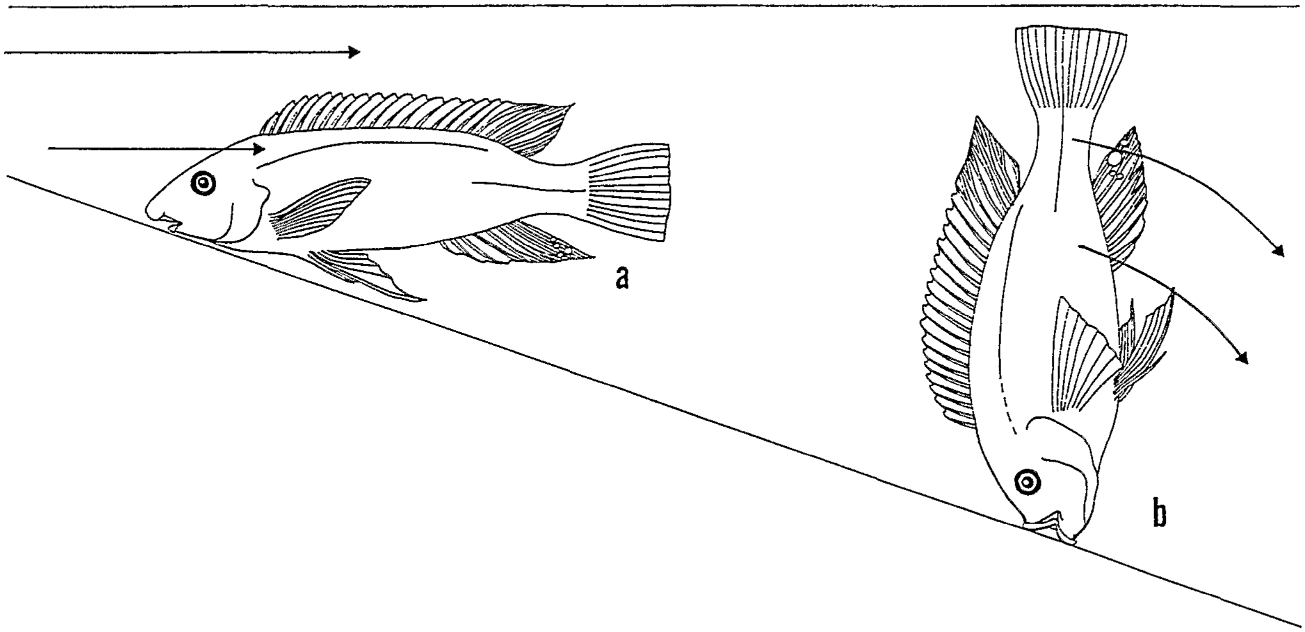

Fig. 4 : see text above.

Lakes Victoria and Tanganyika. Both Lakes Tanganyika and Victoria have Mbuna-like fishes dominating their rocky shores. The recently discovered communities of rock dwelling fishes in Lake Victoria resemble the Mbuna in many respects, namely : they are small darkly or brightly coloured fishes; they have small deeply embedded scales on the chest and nuchal area; they exhibit similar trophic adaptations and appear to be geographically restricted (Van Oijen *et al.*, 1981; Witte, 1984).

The structural and ecological similarity between the lithophilic fish faunas of Lakes Malawi and Tanganyika has been noted frequently (Regan, 1921; Fryer, 1959; Marlier, 1959; Matthes, 1962; Fryer & Iles, 1972; Mayland, 1978) and behavioural similarities were also emphasized recently (Kawanabe, 1981; Yamaoka, 1982; Hori, *et al.*, 1983; Takamura, 1983 a & b).

The rock-frequenting fishes of Lake Tanganyika, also like those of Lake Malawi, are darkly or brightly coloured, and strongly lithophilous with microhabitat preferences for depth and substratum; they are territorial and sedentary showing philopatric tendencies and geographical restriction - which is marked in some instances - and they are trophic specialists. Similarly some species are numerous in the rocky habitat while others are rare with a gradation of numerical densities between these two extremes. The community comprises a variety of species, many with Mbuna-like characteristics, but contributions from other species, including predatory and planktivorous groups, may be large. In both these Rift Valley lakes the density of fishes is high with Lake Tanganyika having a slightly greater density (18 individuals m^{-2} at Uvira in Lake Tanganyika, Hori *et al.*, 1983, vs 6-14, rarely 20 individuals m^{-2}, in Lake Malawi, Ribbink *et al.*, 1983a).

The overall parallels between the rock-frequenting fishes of Lakes Malawi and Tanganyika are striking, although the species composition of the two lakes is entirely different and, while all the lithophilous cichlids of Lake Malawi are maternal mouthbrooders, a fairly high proportion of those of Lake Tanganyika are substratum spawners.

2 - COMMUNITIES OF SEDIMENTED AREAS.

Lake Malawi. The complexity of the communities of rocky shorelines can, in part, be ascribed to the fact that they offer a wide variety of micro-habitats, reflecting differences in rock type, weathering, slope, depth and exposure to wave-action and currents. Isolation of rocky areas offers further scope for diversification of their faunas as a result of differing opportunities for colonisation. Sandy and muddy substrata, superficially at least, appear to offer fewer opportunities for resource partitioning yet they too contain large numbers of species peculiar to them.

The most obvious factors which could affect the distribution of species in such areas are the presence of macrophytes, depth and the grain size and organic content of the substratum. While beds of macrophytes show sharp boundaries, the other characters usually show gradients, the different biotopes merging into each other with no obvious barriers to the movement of fish. Furthermore, level or evenly sloping bottoms of sediment are usually continuous, while rocky slopes generally have a lower limit where they are bounded by sediments (Ribbink *et al.*, 1983a).

A classic example of ecological segregation of fishes is that of the five tilapiine species which live over sedimented substrata in southern Lake Malawi. Lowe (1952, 1953) found that these tilapiine species are distributed differently with regard to depth, substratum type, feeding requirements and also with regard to breeding seasonality and the locality of breeding sites (see also Fryer & Iles, 1972 : 265). Little can be added to this study and so in the discussion which follows attention is focussed upon the haplochromine species of sedimented areas.

A demersal trawl survey of more than 70 stations, at depth increments of 18 m between 18 and 180 m was carried out in Lake Malawi south of 13°30' and recorded over 180 species. Although the catfish *Bagrus meridionalis* Gunther and *Synodontis njassae* Keilhack were recorded from most stations, the individual cichlid species had restricted distributions, so that the composition of the catch at any station was predictable, usually containing from 20 to 30 cichlid species and 2 to 10 non-cichlids. Lewis (1981) examined the catches from three adjacent stations in the South East arm at depths of 18, 36 and 54 m. He reported a total of 51 cichlid species, of which only three were found at all depths (Table 2). One of these three, a planktivore (*Cyrtocara eucinostoma*), was the most abundant species at 18 m where it formed almost 40 % of the catch, but it formed only 0,3 % of the catch from 54 m. The other two were rare predators, on only one occasion forming over 1 % (1.7 %) of the catch. Although two thirds of the fauna at 18 and 36 m were common to both depths, and almost 30 % of the species at 54 m also occurred at 36 m, the composition of the catches was completely different. Chaika (1976) stated that, while depth was important for the distribution of the demersal cichlids, bottom type had little effect. Lewis, however, noted that Chaika's analysis was based on presence or absence, and took no account of abundance. An analysis of Lewis' data (Table 3) shows that the species which constitute the bulk of the catch at any depth form only a small proportion at the other depths, so that although the faunal lists of adjacent stations may look similar the community structure and ecological interactions are very different.

Lewis' data on the three stations off Nkope are typical of the pattern of trawl catches in Lake Malawi. The trawling survey sampled most stations 3 or 4 times a year over a period of 3 years. Every increment of 18 m showed a different but characteristic species assemblage. Outside the regular survey area a single haul off Nkhota Kota at a depth of 220 m, near the limit of dissolved oxygen, yielded a small catch including 1.5 kg of cichlids belonging to 7 species never

Table 2 : Number of species occuring at each of three adjacent trawling stations at 10 fathom (ca 18 m) depth increments in Lake Malawi, with number and percentage by weight of species occuring at one, two or three depths (data from Lewis, 1981).

Depth	10 fthm (ca 18 m)	20 fthm (ca 36 m)	30 fthm (ca 54 m)
Total number of species	30	30	17
Number restricted to one depth	9	7	12
(% of catch by mass)	(11.7)	(2.2)	(55.5)
Number common to 10 and 20 fthm	21	21	-
(% of catch by mass)	(88.3)	(95.2)	
Number common to 20 and 30 fthm	-	5	5
(% of catch by mass)		(2.9)	(42.3)
Number common to all depths	3	3	3
(% of catch by mass)	(39.8)	(2.6)	(2.2)

Table 3 : Percentage by mass of the most abundant species in demersal trawl catches at each depth and their contribution by mass to the catch at other depths at three adjacent trawling stations separated by 10 fathom (ca 18 m) depth increments off Nkope in southern Lake Malawi (data from Lewis, 1981). *Probably *L. microdon*, see text.

Depth	10 fthm (ca 18 m)	20 fthm (ca 36 m)	30 fthm (ca 54 m)
Two most abundant at 10 fthm (*Cyrtocara eucimostoma*, *Pseudotropheus livingstonii*)	58.3	6.5	0.3
Two most abundant at 20 fthm (*Lethrinops parvidens*, *C. argyrosoma*)	9.8	69.8	0
Two most abundant at 30 fthm (*L. cf aurita*, **L. stridei*)	0	0.1	73.3

seen in previous hauls (pers. obs., D.H. Eccles). The trawling survey was normally restricted to water of a depth of 18 m or more, but a few shallow stations were studied and again showed a distinctive species composition, being dominated by species other than those common at 18 m or those characteristic of inshore seine net catches (Eccles & Lewis, 1978).

While the species composition of the communities changes with depth, the trophic interrelationships remain similar, although the decrease in light leads to the disappearance of macrophytes, and later of actively photosynthesising algae and thus the components of the fish community which exploit these resources. Physical changes in the environment are accompanied by changes in the morphology of the fish. An apparent adaptation to decreasing light intensity is the development, in the sub-orbital region, of hypertrophied pores and canals of the cephalic lateral line system. This feature characterises the genera *Aulonocara* and *Trematocranus*. Some species of these genera occur in shallow water, and may be extremely abundant at the rock-sand interface where they inhabit caves and crevices. Other species are important components of sediment communities between about 25 m and 80 m. Probably the inflation of the lateral line canals serves to amplify the signals detected by these organs and thus enables the fish to locate their prey by their motion, independent of visual cues.

The nature of the sediment has an important influence on communities. For example, the structure of the teeth of species which take food from the bottom appears to be associated more with the coarseness of the sediment than with the nature of their food. There is thus a tendency for the teeth to become smaller and often more numerous, but in fewer rows, as the substratum becomes finer with increasing depth. This trend reaches a conclusion with an undescribed cichlid species which is a major component of the community between 145 and 180 m and in which the adult is often completely toothless.

A further adaptation to increasingly fine sediments is found in an undescribed species figured as «*Cleithrochromis bowleyi*» by Axelrod & Burgess (1977). This species is common between 70 and 90 m on substrata overlaid by thick diatomaceous ooze. It is characterised by the possession of large, broad-based, pectoral fins, and by the hypertrophy of the cleithrum which forms a conspicuous prominence in the profile. It has a sharp, somewhat elongated, snout and inflated cephalic lateral line canals. The most likely explanation for the extraordinary development of the cleithrum is that this fish buries its head in the sediment while feeding and that it uses the thrust from its broad-based pectorals to reverse out of the mud, the cleithrum forming the base for the muscles which erect these fins.

The replacement of one species by another exploiting a similar ecological niche as depth increases is well exemplified by a series of molluscivorous species. In water of less than 10-15 m small gastropods are exploited largely by *Barbus eurystomus* Keilhack and *Cyrtocara placodon* (Regan). At 20 m depth these are replaced by *C. anaphyrmus* (Burgess) which resembles *C. placodon.* This species is replaced, in turn, below about 50-60 m by *Lethrinops mylodon* Eccles & Lewis.

Similar examples of species replacement could be given for many groups. *C. eucinostoma,* which occupies large inshore areas during the breeding season (McKaye, 1983), is replaced in deeper water by *C. mloto* (Iles), an important constituent of trawl catches from 10 to 36 m. The pike-like piscivore *Rhamphochromis leptosoma* is replaced in deeper trawl catches by *R. macrophthalmus* Trewavas. *Clarias gariepinus* (Burchell) which is common down to about 10 m is replaced by various species of the endemic genus *Bathyclarias,* one of which, *B. atribrancus* (Greenwood) appears to be confined to depths of over 90 m. Its food is uncertain but its gut is usually packed with tubes which appear to be produced by oligochaetes, although such species have not yet been found in the lake.

Although cichlids normally dominate the demersal habitats, this is not always the case. Usually about 10 %, and rarely up to 50 % or 60 %, of a trawl catch belong to other groups, mainly catfish. The only niche which is dominated by catfish is that of the major piscivore in deeper water, which is filled by *Bagrus meridionalis* Gunther. In shallower water, however, this role is largely taken over by cichlids such as *Cyrtocara nototaenia* (Boulenger) in about 25 m, *C. leptura* (Regan) in 18-27 m and *Serranochromis robustus* (Günther) in vegetated inshore areas, although even here *Bagrus* is active at night.

As was noted in the case of the rock-frequenting communities, local conditions affect the depth range of individual species so that, for example, *Chilotilapia rhoadesii* Blgr., which is common down to 20 m but is not found below 30 m in the south east arm, was trawled at 50 m off Nkhota Kota in the less productive central part of the lake.

A further similarity between distribution patterns of communities of sedimented and of rocky habitats is that, although the former are less fragmented than the latter, a certain degree of geographical variation occurs in their component species. Thus *Lethrinops mylodon* Eccles & Lewis is represented by recognisably distinct sub-species in the south and off Nkhata Bay in the north-central part of the lake (Eccles & Lewis, 1979). Similarly *Lethrinops longimanus* Trewavas and *L. macracanthus* Trewavas, which coexist and are readily distinguished from each other in the south east arm, are represented near Sungu at 13°31'S by an intermediate form which can be assigned to neither species (Eccles & Lewis, 1979). Again, although *L. stridei* Eccles & Lewis occurs in both the southeastern and southwestern arms of the lake there are small recognisable but not quantifiable differences between fish from the two populations which are separated by the rocky Nankhumba Peninsula.

Even more marked differences are found between the benthic communities of the southern and northern extremities of the lake. Catches from comparable habitats in the two areas have few species in common. *Lehthrinops longipinnis* Eccles & Lewis, which is a major component of catches at about 50 m in the south, is absent from the north where *L. argenteus* Ahl occurs. Similarly the genus *Gephyrochromis*, described from the north, is not known from the south where its place appears to be taken by *Pseudotropheus elegans* Trewavas.

The species composition varies not only with depth, but also with the area in which the catch is made. The north east corner of the south east arm is characterised by relatively high numbers of the sponge *Malawispongia echinoides* Brien and of a species of *Aulonocara* which is rare elsewhere, while one undescribed species of *Cyrtocara* was taken on several occasions but is restricted to a single station near Mbenji Island. Eccles & Lewis (1977) noted that *Lethrinops microdon* is associated with diatomaceous ooze and that movements of this species appear to be affected by incursions of cool water along the bottom under the influence of southerly winds (Eccles, 1974). Where the species forms a large component of the catch, as with *L. microdon,* such factors have important implications for fisheries management.

Turner (1977a, 1977b) studied the effect of demersal trawling on the species composition of catches in the south east arm of Lake Malawi. He found that after 7 years of commercial exploitation the proportion of species in the catch had changed, the larger species having declined while the smaller ones had become more abundant. The magnitude of change was related to the difference between the normal adult size of the species and the mean adult size of all species in the catch. He pointed out that this result would be expected since small species are vulnerable to fishing mortality for a smaller proportion of their life and are thus at a competitive advantage.

Eccles & Lewis (1977) noted that the abundance of *Lethrinops stridei* had shown a greater decline than would have been expected from its size. This was one of the most abundant species in early exploratory catches (Eccles, pers. obs.), but is now rare in the area studied by Turner. They suggested that a further factor in the decline of this species might be the effect of extensive trawling on the structure of the bottom deposits, with the disturbance of the sediments and epipelic algae and the stirring of nutrients from the mud into the water column. They speculated that this might have led to a redistribution of primary production between the plankton and the benthos, with consequent effects on the demersal fish species.

While the marked decline of *L. stridei* from the shallower trawling grounds is real, changes in its apparent abundance in deeper water may be taxonomic artefacts. The separate identity of *L. stridei* and *L. microdon* was not recognised until the programme of exploratory trawling had been under way for some time so that earlier records could refer to either species. Such an error is apparent in the case of the fauna of the Nkope stations referred to by Lewis (op. cit.). In this area the inshore edge of the bottom type with which *L. microdon* is associated lies at about 50 m so that the most abundant species from the 65 m station, recorded as *L. stridei,* was probably in fact *L. microdon.* This contention is substantiated by the fact that two of the paratypes of *L. microdon* were obtained from this station at an earlier date (Eccles & Lewis, 1977).

Lakes Victoria and Tanganyika. Both Lake Victoria and Lake Tanganyika resemble Lake Malawi in that they contain unique assemblages of sediment-associated species. Van Oijen *et al.* (1981) reported on a survey of the cichlids of the Mwanza Gulf in southern Lake Victoria. They recorded over 200 species, of which more than 150 were undescribed and noted that these were usually restricted to specific habitats so that every habitat has its own peculiar assemblage. Although their trawl survey in the Gulf extended only to a depth of 18m, they found that most species had very restricted depth ranges. In many cases this was related to reduced oxygen concentrations below 10 m and, in others, to the nature of the substratum. The similarity to the Lake Malawi situation extends to the fact that in both lakes the species with the widest depth range was a zooplankton feeder, which is explained by the fact that they are not dependent on the nature of the substratum for feeding.

Less information is available for demersal sedimented habitats in Lake Tanganyika, although Poll (1956) noted that a number of benthic cichlid species occur at depths down to 100 m. From his data, however, it appears that the depth ranges of individual species are greater than those of their equivalents in the other two lakes. As in Lake Malawi, hypertrophied cephalic lateral line canals are found in the genera *Aulonocranus* and *Trematocara*, some of the latter occurring at depths of as much as 100 m. A similar adaptation is found in the deep water *Thoracochromis mcconnelli* (Greenwood) of Lake Turkana.

Coulter (1967) set gill nets between 20 and 180 m at the south of Lake Tanganyika and found that, while the different species recorded usually covered wide depth ranges, there was a degree of niche separation in the diet of the predatory species. These wide depth distributions contrast with the situation in Lakes Malawi and Victoria. The probable explanation lies in differences in the basin morphology and physical regime of the lakes. Both Lake Malawi and Lake Tanganyika have completely anoxic hypolimnia (Eccles, 1974), while Lake Victoria mixes completely in most years (Talling, 1966) so that anoxic conditions occur only occasionally in the deepest parts. The two former lakes show regular marginal upwelling but, while in Lake Malawi a depth of 250 m is not found closer than 100 km to the southern end of the lake and upwelling at the south is from the intermediate layer, in Lake Tanganyika this depth is encountered within 15 km of the southern end. Coulter (1963) found upwelling of hypolimnetic water in his study area, recording anoxic conditions at a depth of 80 m and only 1 mg 0_2/l at 60 m on one occasion in the cool season.

Although low oxygen concentrations are found near the bottom in sheltered gulfs of Lake Victoria at modest depths, these are limited to the interface between the water and fine silts (Van Oijen *et al.*, 1981) and anoxic conditions occur rarely in the main water mass where they are confined to deep waters (Talling, 1966). Thus, as in Lake Malawi, conditions are favourable for the development of a range of species adapted to low light intensities and relatively low oxygen concentrations.

The fact that at the south of Lake Tanganyika depths below 50 metres are likely to experience wide seasonal fluctuations in oxygen concentrations and even completely anoxic conditions, precludes the evolution of stenotopic forms with preferences for deep waters. This offers an explanation for the differences between the structures of the benthic communities of Lake Tanganyika, on the one hand, and Lake Malawi and Lake Victoria on the other.

3 - INTERMEDIATE HABITATS.

Lake Malawi. At the interface between two major habitats, such as rocky or sandy zones, there is a region where the two are mixed. Fryer (1959) referred to these mixed areas as intermediate habitats. The mixed rock-sand belt is very narrow in regions where rocky shores descend steeply to meet abruptly the sandy plains, or the belt may be broad where rocky shores shelve gradually, eventually giving way to a purely sandy substratum. Most rocky shores of the Great Lakes shelve steeply and so, in general, the area of mixed rock-sand habitat is very narrow.

Inevitably a narrow ribbon of intermediate habitat will have contributions from the fauna of the two habitats which flank it, but in addition these regions are occupied by a number : of species which occur nowhere else. Included among these species are brightly coloured members of the genera *Aulonocara* and *Trematocranus*, several Mbuna species and a variety of *Cyrtocara* spp., including members of the Utaka group, which nest in the sand alongside or beneath rocks (Ribbink *et al.*, 1983 a). Similarly, *Oreochromis shiranus* (Boulenger) and *Tilapia rendalli* excavate nests in these intermediate zones beneath rocks in 1-9 m depth.

In shallow regions the mixed zones may have macrophytes growing in sand between rocks. Such intermediate habitats have species contributed from sandy, rocky, vegetated and intermediate zones and the fishes which dominate such an area are usually those of the predominant habitat in the mixed area. Thus the community of such an area is governed by the circumstances of the area - its depth, relative proportions of rocks, sand and macrophytes, and its proximity to any of these major habitats. Wave action and currents will also influence the species composition of a community of such habitats since organic sediment will be prevalent in sheltered areas, but absent in areas exposed to scouring by waves or currents. Similarly the nature of rocks, sand and macrophytes would dictate to some extent which species occupy the region. There are no species known to be exclusive to this mixed zone although several species such as *Cyathochromis obliquidens* Trewavas, *Pseudotropheus* cf. *novemfasciatus*, *Cyrtocara kirkii* (Günther) and *Astatotilapia calliptera* (Gunther) appear to be more common than in sand-rock or sand-macrophyte habitats.

Lakes Tanganyika and Victoria. Intermediate habitats of Lake Tanganyika and Victoria are alluded to in the writings of Brichard (1978), Hori *et al.* (1983) and Van Oijen *et al.* (1981). It is likely that a study of fish communities of such habitats in these lakes will show that they parallel Lake Malawi in having species adapted to and characteristic of mixed zones.

4 - PELAGIC AND SEMI-PELAGIC COMMUNITIES OF THE THREE GREAT LAKES.

In Lake Tanganyika and Lake Malawi there are distinct pelagic communities exploiting the plankton. In the former these communities are relatively simple, consisting mainly of two clupeid species, a cyprinid and a cyprinodont, a cichlid which feeds on plankton, and four centropomid predators. In Lake Malawi the zooplankton are exploited by a range of cichlid species (Iles, 1959) which are found mainly inshore, a cyprinid *Engraulicypris sardella* and a number of catfish species such as *Bathyclarias loweae* (Jackson, 1959). The associated predators are cichlids of the genera *Rhamphochromis*, particularly *R. longiceps* (Günther), and *Diplotaxodon.* In inshore areas and in the southern part of the lake where upwelling results in extensive phytoplankton blooms (Eccles, 1974), phytoplankton is utilised directly by semi-pelagic species of *Oreochromis* (= *Tilapia*; Lowe, 1953).

Coulter (1970) showed that exploitation of the pelagic community of Lake Tanganyika led to a large decline in the abundance of predators, but that total catches increased slightly, the reduction in predator biomass in this case being compensated for by increased survival of the short-lived rapidly-reproducing prey.

Turner (1982) stated that, while levels of primary production in Lake Malawi and Lake Tanganyika were broadly similar, the pelagic fish biomass of the latter was, on an area basis, from 1.6 to 10 times greater than that of Lake Malawi. He also noted that both *Cladocera* and the larvae of the midge *Chaoborus* are absent from the zooplankton of Lake Tanganyika but are common in Lake Malawi, where swarms of adult *Chaoborus* are a striking feature of the central area of the lake. He considered that in Lake Malawi *Chaoborus* must play a significant role as a predator of the zooplankton and suggested that this was possible because, in contrast to the clupeids *Limnothrissa miodon* (Blgr.) and *Stolothrissa tanganicae* Regan, *Engraulicypris* is relatively inefficient at utilising this resource.

Turner's study was centred at Nkhata Bay, near the north-central part of Lake Malawi, and his information on lake-wide distribution was obtained from two surveys, during one of which larval density was studied. He found higher total fish biomass towards the ends of the lake, and larval densities off Nkhata Bay were at least an order of magnitude lower than those at the extreme north and south. In the south, where *Engraulicypris* populations are greatest, *Chaoborus* swarms are rare, but are seen occasionally between November and March.

Although Turner states that primary production in the two lakes is comparable, his figures, based on a year's records, are similar to the lower of the figures given by Hecky (1978) for his surveys of Lake Tanganyika in April and October. It is possible that the primary productivity of Lake Tanganyika may be greater than that of Lake Malawi on an annual basis. Such a situation could result from the limnological regime of the lakes. The basin of Lake Tanganyika has steep shores, and the nutrient-rich anoxic hypolimnion in most areas is found within a short distance of the shore. Upwelling in the south of Lake Tanganyika is often accompanied by simultaneous fish mortalities since anoxic water is involved (Coulter, 1963). This water is extremely rich in nutrients. In Lake Malawi, the upwelling at the south involves intermediate, less nutrient-rich water. Thus the respective forms of the lake basins may lead to a greater annual turnover of nutrients in Lake Tanganyika than in Lake Malawi.

It is possible that the dominance of *Chaoborus* as a predator of the zooplankton in the central part of Lake Malawi may be the result, not of the relative inefficiency of *Engraulicypris* in this role, but of a lower production and standing stock of zooplankton in this area. *Chaoborus* is an ambush predator which adjusts its density by the use of air bladders, and seizes prey which approach it. Such a passive predatory strategy is more efficient, in energetic terms, than is active hunting and is also adopted in the resource-poor mesopelagic zones of the ocean by fish such as the snipe-eel, *Nemichthys* (Meade & Earle, 1970).

An alternative explanation for the absence of *Chaoborus* from Lake Tanganyika may lie in abiotic factors. Verbeke (1957a) reported that these midges were completely absent from both Lake Tanganyika and Lake Kivu. At that time Lake Kivu contained no zooplankton-feeding fish and he suggested (1957b) that clupeids from Lake Tanganyika should be introduced to utilise the resource. This was done in 1958-1960 and *L. miodon* has become established although, even by 1980, it did not appear to have affected the composition of the zooplankton (de Iongh *et al.*, 1983). Hecky (1978) stated that Lake Kivu and Lake Tanganyika differed from the other African lakes in having unusually high concentrations of magnesium and potassium. Further chemical differences may arise from inflow of water associated with vulcanism. Degens *et al.* (1973) stated that hydrothermal discharges provide about 0.5 km^3 of water annually to Lake Kivu. Such discharges are often highly mineralised and may contain heavy metals. The Ruzizi River, which drains Lake Kivu, is the main inflow to Lake Tanganyika, so that any chemical species present in its waters in abnormally high concentrations would also enter Lake Tanganyika and it is possible that chemical characteristics common to the two lakes may adversely affect *Chaoborus.*

DISCUSSION

An inevitable consequence of the acquisition of new information is that it modifies existing concepts, either by reinforcing them or by departing from them. In the discussion which follows we substantiate some of the earlier work, but in several instances we use newly acquired information to suggest alternative interpretations.

Size and complexity of the communities. The use of mechanised fishing techniques and of SCUBA, and the exploration of areas not previously studied, have led to the discovery of hundreds of undescribed species in the last 15 years. The current rate of discovery of new species is still high and so there is no knowing how many fish species are supported by each lake. Now, more than ever before, it is apparent that the adaptive radiation and speciation of these fishes within each lake has no equal among other vertebrates. It is also apparent that the communities are far more speciose than previously imagined and, accordingly, the complexity of interspecific relationships is greater than envisaged. It is abundantly clear that, with the work on the fishes of these lakes still in its exploratory and descriptive phase, the effects of unfettered exploitation of these largely unknown multispecific communities cannot be comprehended at present.

Intralacustrine geographical restriction. For some time it has been apparent that the lithophilous fishes of the Rift Valley Lakes are narrowly distributed within each lake (Fryer, 1959; Marlier, 1959). Recently this was forcefully substantiated (Brichard, 1978; Ribbink *et al.*, 1983 a) and a similar situation was found in Lake Victoria (Van Oijen *et al.*, 1981). Fishes of other habitats appeared to be more mobile and the general impression was that, with few exceptions (Trewavas, 1935; Fryer & Iles, 1972), they enjoyed lake-wide distribution. It is becoming apparent, however, that fishes of sedimented substrata, of vegetated regions and from pelagic or semipelagic habitats of the Rift Valley Lakes often have geographic distributions which are limited to specific areas (Eccles & Lewis 1978; 1979; Brichard, 1978; Lewis, 1981). In addition unpublished data from demersal trawl samples show that the species composition of catches taken in northern Lake Malawi are considerably different from those of the southern lake (Lewis pers. comm; Tweddle pers. comm.).

In contrast to the Rift Valley Lakes it was believed (Fryer & Iles, 1972; Greenwood, 1974) that Lake Victoria populations enjoyed a lake-wide distribution, but Van Oijen *et al.* (1981) and Witte (1984) have shown that populations of Lake Victoria are spatially isolated. Thus, in these African Great Lakes, allopatry of species is an important way in which the resources of each lake are utilized non-competitively by its fishes.

Temporary components of communities. As noted earlier, short-term exchange of members between adjacent communities is a frequent occurrence. However, there are also regular daily or seasonal migrations between habitats for feeding or reproduction. Thus, although *Cyrtocara eucinostoma* (Regan) and *Cyrtocara mloto* (Iles) are common constitutents of demersal trawl catches between 20 and 50 m in Lake Malawi, they are not dependent on the bottom for food as they are zooplankton feeders.

Longer-term feeding migrations between different areas of Lake Malawi have been demonstrated for the phytoplankton-feeding *Oreochromis* and several «Utaka» species. Reproductive migrations were discussed by Fryer & Iles (1972) and an example of such behaviour in *C. eucinostoma* was described by McKaye (1983).

Migrations are often of importance with regard to commercial exploitation, the best known examples being trap fisheries for cyprinids on their spawning migrations upstream from a number of lakes. They are also of importance in the lakes themselves. Thus, in Lake Malawi the fishermen follow the shoals of Utaka from the south east arm to the south west arm and Domira Bay. Another species which appears to migrate is *Cyrtocara leucisca* (Regan) («silibanga»); this is an important constituent of demersal trawl catches in about 20 m in the area near Monkey Bay during the period November to February, after which it becomes rare. Although it is asssumed that it has migrated out of the area, it does not appear in trawl catches elsewhere.

Stenotopy. In each lake there are numerous stenotopic species some of which are adapted very narrowly to particular depth zones, substrata and other environmental attributes. Although microhabitat preferences are most apparent in lithophilous communities, there is growing evidence of a similar stenotopy among fishes of other habitats (Fryer & Iles, 1972; Eccles & Lewis, 1977, 1978, 1979; Brichard, 1978; Lewis, 1981; Van Oijen *et al.*, 1981; Witte, 1984). Species specific adaptations to particular microhabitats effectively restrict species to sections of each environment. Such stenotopy enables a greater number of species to be packed into the habitat under consideration, particularly if the fishes are narrowly stenotopic.

Stenotopy has been recognised among the fishes of the Rift Valley Lakes for some time, but only recently has it been realized that some of the fishes of Lake Victoria are also as narrowly adapted (Witte, 1984).

Feeding. In each lake there is a large number of species, but a limited number of different food resources. There are, for example, more than 250 haplochromine species in Lake Victoria, but only 11 main trophic categories are recognized (Witte, 1984). A degree of dietary overlap is inevitable and occurs widely (Fryer, 1959; Van Oijen *et al.*, 1981; Ribbink *et al.*, 1983 a). On first discovering this, Fryer (1959) concluded that at least certain food items Aufwuchs) must be present in a superabundance and both he (Fryer, 1959; Fryer & Iles, 1972) and Greenwood

(1974, 1981) suggested that fishes with identical requirements negated the competitive exclusion principle. Virtually nothing is known about interspecific competition among fishes of the African Great Lakes, but research is beginning. For example, Takamura (1983 a) observed that the more similar the food type the greater is the interspecific aggression among certain lithophilous species of Lake Tanganyika. In another paper, Takamura (1983 b) suggests that an interspecific feeding symbiosis has developed between two Aufwuchs feeders, *Petrochromis polyodon* and *Tropheus moorei,* in Lake Tanganyika. Furthermore, evidence arising from more detailed studies of community members shows that fishes which superficially appear to have identical requirements are either separated physically (i.e. occupy different depths or substrata) or take food from different sites (Ribbink *et al.,* 1983a, 1983b; Hori *et al.,* 1983). The tendency of these detailed examinations is to expose the ecological segregation of species, thus departing from the notions of Fryer & Greenwood which suggested that some community members co-exist in a negation of the competitive exclusion principle.

Fryer's suggestion that there is a superabundance of algal food and a consequent lack of competition in the inshore rocky areas is negated by recent observations. While the lake is undergoing its dry season fall its level drops about 15-20 cm per month. At this time, dense algal mats, with filaments in excess of 15 cm in length, develop in shaded spots in the splash zone where wave action is sufficient to keep them continuously wet but where they cannot be grazed by fish. Such mats are never observed under water or above the surface when the level is rising, although the conditions for algal growth just below the surface must certainly be less harsh than in the splash zone where exposure to drying and to the sun is a hazard. Despite the absence of conspicuous mats, the rocky zones show a good growth of algae; but this is heavily grazed and kept short.

Such a situation does not evidence a lack of competition but, rather, a very intense utilisation of a rapidly reproducing resource. Certainly, if particular resources are temporarily abundant they are utilised by a wide range of species including many not specifically adapted to feed upon them. Thus, most Mbuna species feed on zooplankton when this is abundant (Ribbink *et al.,* 1983 a). However, the value of trophic specialization is not in periods when a resource is super-abundant, but at such times when resources are scarce (McKaye & Marsh, 1983). It is at these times that natural selection may act most harshly upon the individuals within a species to promote trophic specialisations.

Communities. The concept of the community is useful only if it has descriptive or predictive value, but the problems are considerable. Certainly the concept of a community, as exemplified by the rocky or sandy bottom communities of Lake Malawi, has descriptive value but is too broad to have any value in predicting the effects of perturbations. Where fishing causes changes in ecological interactions such as those demonstrated by Coulter (1970) for pelagic fish in Lake Tanganyika. or by Turner (1977a, 1977b) for the demersal fishes of Lake Malawi, a more narrow definition of the community is needed, restricting the concept to one where the component species show actual or potential interactions. If actual, or potential, interaction between component species is accepted as a characteristic of a community, those species assemblages which are sufficiently separated that they share no common species, or where species which are abundant in the one are present as rare outliers in the other, are in effect separate communities, although they have no definable boundaries and merge with intermediate assemblages.

Since the species composition of the catch from a particular combination of depth, exposure and bottom type is predictable, this array of species might be considered a community. However such a community defies definition since it merely reflects the result of a number of overlapping discrete distributions, each with its individual pattern. Because of this overlapping of distributions there are no definable boundaries to the species assemblages except in the widest sense as, for example, between phytophilous, lithophilous and psammophilous species.

To restrict the recognition of communities to such assemblages would be to reduce the predictive value of the concept. Furthermore, while changes to the population structure in one depth range within a fairly uniform habitat may affect other species at that depth as shown by Turner (1977b), these effects are local and are largely restricted to the depth range of the affected species though some repercussions for a broader spectrum of the biotope are likely.

There is a danger, from the point of view of fisheries management, that the acceptance of a broad definition of communities might lead to the conclusion that fishing in a restricted area would not lead to overfishing since the stocks could be replaced by immigration from areas out of the range of exploitation. The implications for management are serious, in that the over-simplified approach which has, of necessity, been adopted in the case of the trawl fisheries of Lakes Malawi and Victoria, is not really tenable. The demonstrated existence of large stocks of broad taxonomic groupings such as «*Haplochromis*» or «*Lethrinops*» in these lakes does not necessarily mean that these groups can be treated as single entities for management purposes, even where the species are extremely similar. This belief would be fallacious if presumed «reservoir» areas differ in depth or bottom type from those being exploited.

The changes in species composition of the catch in southern Lake Malawi noted by Turner were confined to the depth range at which pair trawling using fibre warps was feasible (i.e. to about 35 m). *L. stridei* in this area was not replaced by the similar *L. microdon* which occurs nearby but at greater depths and over a somewhat different bottom type, and which remained abundant off Nkope until at least 1978 (D Eccles, pers. obs.).

Before the fisheries of these lakes can be regulated to provide optimum long-term benefits to the people of the area, a knowledge of the species composition of the catches in different depths and over different bottom types is necessary. This requires exploratory trawling with careful taxonomic evaluation of catches and the survey and mapping of bottom deposits. Once these data are available it should be possible to monitor catches and to manage individual stocks. However the taxonomic background for such work is still far from complete and, were it available, the costs of monitoring would be considerable.

In the absence of detailed knowledge of the species composition of exploited communities a practicable management approach might be to regulate fishing effort on the basis of the whole catch, as has been done in Lake Malawi for the trawl fishery. Here, when demersal trawl catches fell to an undesirably low level, the fishery was closed for a period of six months. The result was substantially increased catches when fishing was resumed. While such an approach is feasible in the case of a trawl fishery which has been developed by Government, and where the right to fish has been expressly granted by a licence, it is more difficult in the case of fisheries where there are traditional rights.

A further method of control which has been attempted in Malawi is the restriction of trawling to particular depth ranges or distances offshore. Such an approach is theoretically effective but, since the cost of patrolling is high, in practice it cannot readily be enforced unless there is a detailed knowledge of the taxonomy and distribution of the species so that fishing areas can be identified by examination of the species composition of the catch. Widespread contravention is likely to prevail if the rewards are high and the risks of detection are low.

A more effective method of protecting stocks from over-exploitation by trawling might be to select representative areas of each ecological type and to physically render them unsuitable for demersal trawling. This could be readily done by scattering over the bottom obstacles large enough to interfere with the nets and so spaced that there was a high probability of encounter in a days's fishing. Such physically closed areas would require little policing, and the obstructions could be so widely spaced (of the order of 100 to 200 m apart) that they would have little effect on the composition of the fauna. These areas would serve as refuges in which stocks of the exploited species could be retained, and from which continuous re-colonisation of the adjacent exploited areas could occur. The existence of such refuges might be useful in reducing the replacement of larger species by smaller, and often less desirable, ones.

A further option which has often been suggested is the introduction of new species to the ecosystem. Eccles (1975) argued that, in the case of newly established artificial impoundments, fish catches could be enhanced by the introduction of suitable specialised lacustrine species. Such an approach has also been advocated for the Great Lakes. In the 1950's and early 1960's there was controversy about the desirability of introducing the large predatory Nile perch (*Lates* spp) into Lake Victoria to «utilise» the «undesirable» haplochromines. Despite the fact that the criteria of «desirability» were based on foreign values which placed a premium on angling and on large fillets or cutlets, the introduction was effected. The introduction "succeeded" and now large *Lates* form part of the trawl catches in the north. In the absence of baseline data on the haplochromine community of Lake Victoria the impact of the introduction of *Lates* cannot be assessed. It is likely that many haplochromine species will disappear, or become much less abundant. Not only would this result in reduced catches, but the loss of these species would be considerable in aesthetic or scientific terms, although it cannot be evaluated as a cost. However, it is debatable whether *Lates* really is a desirable species. While a mechanised fishery with sophisticated refrigeration and marketing facilities can handle such fish, the industry on the Great Lakes is likely, for the foreseeable future, to be based largely on small-scale artisanal fisherman who would lack such facilities and to whom a large fish might well be a liability. Meanwhile, the development of a trawl fishery for small cichlids in Lake Malawi has shown that, far from being «undersirable», these are a valuable resource which can readily be sun-dried and which now form the basis of a considerable export trade.

Lates was also introduced to Lake Kyoga, where it has contributed greatly to the catch without apparently affecting the tilapia populations (Gee, 1969). The reason for this success is unclear, but it is possible that in this swampy lake *Lates* can more effectively exploit small species than can the local fishermen, and that it converts these small fish to a form which is accessible to fishing gear.

More recently Turner (1982) has suggested that clupeids from Lake Tanganyika be introduced to Lake Malawi to utilise the plankton which, he suggests, is not efficiently exploited by *Engraulicypris*. While such an introduction into Lake Kariba was successful, the likelihood of success of an introduction into Lake Malawi is lower, due to the presence of successful plankton-feeding species. Furthermore, it is still open to question whether the pelagic plankton resource base is sufficient to support an offshore fishery. An additional uncertainty is introduced by the possibility that the absence of *Chaoborus* from Lake Kivu and Lake Tanganyika may be the result of abiotic factors. A greater knowledge of the physical background and the seasonal cycle of production in both Lake Tanganyika and Lake Malawi is necessary before this question can be answered. In the interim, it would be very unwise to introduce a new species to an already closely adapted ecosystem consisting of a number of complex communities.

RÉSUMÉ

Les communautés de poissons des grands lacs d'Afrique de l'Est sont encore très mal connues car les recherches en sont encore au stade descriptif et exploratoire. En raison de la demande croissante en protéines animales, plusieurs de ces communautés ichtyologiques sont soumises à une exploitation intense. Cette pression de pêche a déjà modifié la structure des communautés et il est probable qu'il n'existe plus maintenant de communautés non perturbées.

On appelle communautés, des groupes d'espèces caractéristiques de différents habitats. Les communautés des zones rocheuses sont les mieux connues. Dans le lac Malawi, le Mbuna est le poisson le plus abondant dans les biotopes rocheux, mais d'autres Cichlidés, ainsi que des espèces appartenant à d'autres familles, cohabitent avec le Mbuna et l'ensemble de ces poissons constitue les membres permanents de la communauté. Des visiteurs temporaires venant de biotopes voisins, ainsi que des poissons venant pondre dans les zones rocheuses ou les utilisant comme nurseries avant de regagner leurs biotopes habituels, viennent compléter cette communauté.

Les poissons lithophiles sont à ce point sédentaires que beaucoup d'espèces sont endémiques d'une seule localité. Il en résulte que les groupes d'espèces composant la communauté de chaque côte rocheuse est différent de celui des autres côtes. Dans bien des cas, des espèces ayant apparemment des exigences identiques sont isolées géographiquement et ne peuvent entrer en compétition. La plupart des espèces lithophiles ont une préférence marquée pour des microha-

bitats très particuliers, et leur répartition est liée étroitement à la présence de ces microhabitats. C'est dans les zones de moins de 10 m de profondeur, avec des rochers de 0,5 à 2 m, que l'on observe le plus grand nombre d'espèces. Inversement, la faune est la plus pauvre dans les grands rochers en eau profonde (plus de 40 m).

Différents types de comportements territoriaux et des spécialisations trophiques caractéristiques pour chaque espèce permettent d'utiliser au mieux les ressources disponibles. Bien que l'essentiel des travaux mentionnés dans ce chapitre ait été réalisé dans le lac Malawi, les communautés de poissons lithophiles des lacs Victoria et Tanganyika sont très similaires. Dans le lac Tanganyika, cependant, une grande partie des Cichlidés pondent sur un substrat alors que chez les Cichlidés des deux autres lacs, les mères pratiquent l'incubation buccale.

En général le passage d'un type de sédiment (sable grossier par exemple) à un autre (boue par exemple), se fait graduellement et il n'y a pas de frontière bien nette. Néanmoins, les espèces se répartissent en fonction de la profondeur et de la nature du fond. Le partage des ressources se fait également par une spécialisation du régime alimentaire et une adaptation aux eaux profondes, ainsi que par l'isolement géographique d'espèces présentant des exigences similaires, voire identiques. Les poissons des biotopes intermédiaires (mélange de sable, de rochers, et d'hydrophytes dans les zones peu profondes) sont caractéristiques de ces zones d'interfaces du lac Malawi. Il en est probablement de même dans les lacs Victoria et Tanganyika.

Les communautés pélagiques ou semi-pélagiques ne sont pas autant spécialisées que les communautés démersales ou littorales. Dans le lac Tanganyika, les Clupéidés pélagiques font l'objet d'une pêche importante, mais dans le lac Malawi, la pêche pélagique est relativement peu productive. Turner a suggéré d'introduire les Clupéidés du lac Tanganyika dans le lac Malawi. Les auteurs pensent que cette proposition est très dangereuse dans la mesure où la limnologie du lac Malawi est encore très peu connue et que l'on ne possède pratiquement aucune information sur les communautés ichtyologiques et leurs relations avec le milieu pélagique.

Une telle introduction serait irréversible et potentiellement catastrophique. L'introduction d'espèces allochtones dans des lacs artificiels peut être bénéfique, mais il est peu probable qu'il en soit de même dans les milieux naturels. Il est donc recommandé de ne pas effectuer ces introductions.

Une bonne connaissance des peuplements ichtyologiques est indispensable pour gérer une pêcherie multispécifique. Cette connaissance étant loin d'être suffisante actuellement, il est proposé de répartir des obstacles sur les fonds chalutables dans certaines zones préalablement sélectionnées, afin de les préserver de la pêche. La recolonisation des zones adjacentes pourrait alors s'effectuer à partir de ces zones refuges.

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