# AN ECOLOGICAL STUDY OF TERRITORIALITY IN FOUR CICHLID SPECIES RESIDENT ON ROCKY SHORES NEAR MONKEY BAY, LAKE MALAWI.

by

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CONTENTS

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## ABSTRACT

This study centres on a diverse assemblage of epilithic algal grazing fish (17 cichlids and 2 cyprinids) found on the rocky shores near Monkey Bay, Lake Malawi. Diet overlap among these species is large, but competitive exclusion is apparently avoided by the species having different feeding structures, behaviour and distribution on the shore.

In many respects the ecology and behaviour of the cichlid fishes inhabiting the rocky zones of Lake Malawi parallel those of coral reef fish. In both communities there are species which are highly territorial, resulting in resource subdivision and, in some cases, the development of algal gardens. As this behaviour has not been previously reported for cichlid species, this thesis describes the territoriality of the rock-dwelling cichlids of Monkey Bay, Lake Malawi, and poses three specific questions:

1. What is the function of territoriality?
2. How do the territorial species subdivide the space resource?
3. What prevents one species taking over all the available space?

It is suggested that interspecific territoriality evolved in response to a shortage of food, and, at present, serves principally to defend an algal garden i.e. a food supply of high standing crop.

The species studied are extremely site specific. The rocky shore is subdivided among the four species according to the rock configuration, size, algal mat composition and position on the shore, of the available sites.

An experimental study of the space utilization of the two common territorial species, referred to as '*Pseudotropheus* orange cheek' and '*Pseudotropheus* aggressive', showed that suitable territory sites are in short supply and that these species are in competition for some sites.

These results do not support those of Fryer (1959) who suggested that a superabundance of food enabled fish to coexist by sharing the same food resource. Indeed it now appears that a shortage of food may have been a major driving force during the recent evolution of the species studied.

# CHAPTER 1

## INTRODUCTION

A recent survey of the fishes of the rocky shores of Lake Malawi (Ribbink et al., in press) and current trawl sampling programmes of the Fisheries Department in Malawi (Ribbink,pers.comm.) indicate that Lake Malawi may contain more than 400 species of cichlid. Knowledge of the ecology of most of these species is extremely limited and the data which are available pertain principally to economically important food fish (Lowe, 1953; Turner, 1977; Tweddle & Turner 1977).

One group of Lake Malawi fish which has been largely overlooked until recently is an assemblage of fish which grazes on epilithic algae found on the rocky shores. This group will be referred to as the epilithic algal grazing guild. The term 'guild' was introduced by Root (1967) and is defined as 'a group of species that exploit the same class of environmental resources in a similar way'.

In an early study of the ecology of the epilithic algal grazing fish of Lake Malawi, Fryer (1959) recognised 14 species in this guild at Nkhata Bay. Of these, twelve were cichlids and two were cyprinids. Eleven of the cichlids belonged to a generic complex which is commonly known by its local (Chitonga) name 'Mbuna' (Fryer, 1959)[*1]. One of the remarkable features of this guild is the large diet overlap of its member species. Although Fryer did not quantify stomach content analyses, it is clear that several species have almost identical diets and no species is ecologically segregated from all others on the basis of diet alone. Apart from small differences in diet and slight differences in distribution of the species,

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[*1] Recent studies by Holzberg (1978) and Ribbink et al. (in prep) have shown that several of the colour morphs which Fryer (1959) grouped as a single species in fact represent separate taxa. 'Species' which show this characteristic include Pseudotropheus zebra (Boulenger), P. tropheus Regan, Petrotilapia tridentiger Trewavas and Cynotilapia afra (Günther).

no other means of ecological segregation was found by Fryer. This is in apparent contravention of the competitive exclusion principle which, in a simple form, states that 'complete competitors cannot coexist.' (Hardin, 1960). Fryer (1959) concluded that the competitive exclusion principle did not apply to this community because a superabundance of algae made it unnecessary to compete for food and that high predation levels suppressed fish populations sufficiently to allow this superabundance to develop.

Recent theoretical and field studies of assemblages of co-habiting species suggest that species with similar diets may coexist despite a food limitation. Roughgarden (1974) developed a mathematical model in which species with high diet overlaps may coexist if their resource utilization curves are leptokurtic (thick-tailed) i.e. if they use a broad spectrum of food resources. Another theory which relates to the coexistence and resource partitioning of coral reef fish states that assemblages of fish present on coral reefs are not in equilibrium, and that chance plays an important role in dictating species composition and abundance on a given reef (Sale, 1977; 1978a and b; 1979; 1980a & b; Sale & Dybdahl, 1978). Although the full implications of this theory have yet to be worked out it is possible that under these conditions a fine partitioning of the available resources is not necessary for coexistence.

Smith & Tyler (1973) point out that how and where a fish feeds is often more important to resource partitioning than the items on which it feeds. Relevant literature reveals that there are at least three ways by which food resource partitioning may occur by means other than differences in diet. These are considered below and will be referred to as subdivision by microhabitat, subdivision by habitat zonation and subdivision by territoriality.

## Subdivision by microhabitat

Subdivision by microhabitat may occur when morphological specializations allow species access to different microhabitats from which they may collect similar food items without being in competition. For example, small fish or species with elongate rostra may have access to narrow cracks which larger co-habiting species cannot utilize (Smith & Tyler, 1972; Robertson *et al*., 1979).

## Subdivision by habitat zonation

Members of a community may be partially segregated by having peak densities in different habitat zones. Zonation of species has been reported for several fish communities in both fresh water (Zaret & Rand, 1971; Gibbons & Gee, 1972; Tramer & Rogers, 1973; Werner *et al*., 1977) and in the sea (Gosline, 1965; Jones, 1968; Tyler, 1971; Emery,1973; Clarke,1977; Williams,1979). Whether this separation is considered to occur within or between habitats depends on how the term 'habitat' is defined. For the purpose of this study I consider the rocky shore to be a single habitat and any further subdivisions, on the basis of water depth or rock size, shall be referred to as habitat zones.

## Subdivision by territoriality

It has recently been realised that interspecific territoriality may result in the subdivision of feeding areas. When individuals of a territorial species drive off potential competitors for food they thereby reserve the food within their territory for their own use (literature reviewed in Chapter 3).

The above aspects of the ecology of the epilithic algal grazing guild were not studied by Fryer (1959) as he did not have the facilities for prolonged underwater observation, consequently his conclusions are based almost exclusively on gut content analyses. Fryer did note, however, that some species were common close inshore while others occurred farther out. He also suggested that *Pseudotropheus minutus* Fryer may be able to feed in narrower cracks than the ecologically similar *Pseudotropheus fuscus* Trewavas by virtue of its narrower mouth.

Underwater observations by the author revealed that interspecific competition appeared to play an important role in the subdivision of epilithic algal grazing resources. This thesis therefore tests the hypothesis that 'subdivision by territoriality' is an important means of food resource partitioning in the four species of Mbuna studied.

In order to achieve this aim, the thesis is divided into three parts:

1. a general overview of community structure in the epilithic algal grazing guild with particular attention to food and space resource subdivision,
2. a description of the ecological aspects of territoriality in four interspecifically territorial cichlids resident on the rocky shores near Monkey Bay, and a discussion of the function of territoriality in these species,
3. an investigation to determine which factors are important in the subdivision of the space resource between the four interspecifically territorial species, and an experimental examination of the possibility of interspecific competition between the two most common of these species.

## CHAPTER 2

## A NOTE ON THE TAXONOMY OF THE MBUNA

The majority of species of the epilithic algal grazing guild belong to a group of cichlids known as the Mbuna. Although this group has no formal systematic standing, Fryer (1959) considers them 'worthy of at least tribal rank'.

The Mbuna are small cichlids, seldom more than 20cm in total length and frequently smaller. The body is moderately elongate with split lateral lines, denticulate scales and the nape covered with a large number of scales. Dentition varies but there is always a short series of three to nine conical, postero-lateral teeth on each side of the upper jaw. There are always several rows of teeth anteriorly which may be conical, or, more usually, bi-cuspid or tri-cuspid. The dorsal fin has fifteen to nineteen (usually seventeen to nineteen) spines and seven to eleven soft rays. The anal fin has three spines and seven to eleven soft rays (Fryer, 1959). The left ovary of the female is markedly atrophied and only the right is functional. All Mbuna genera are known to be mouth brooders.

Many Mbuna species are undescribed. This is partially a result of difficulties of catching these small rock-dwelling fish prior to the development of SCUBA, partly because many species are highly localised in distribution and difficult to obtain because of poor access to much of Lake Malawi's shores, and partly because of the great and still largely unresolved taxonomic complexity of the recently evolved species flock of Lake Malawi as a whole (Greenwood, 1979). Even at the well worked and accessible Monkey Bay sites, there are at least nine undescribed species of Mbuna, eight of which are included in the annotated list which follows. Fortunately these species fall into three groups with apparent ecological and taxonomic affinities with described Mbuna species, so it is possible to give them an informal identity by comparing them with these known species. The taxa to which these fish appear to relate are Petrotilapia tridentiger Trewavas, Pseudotropheus tropheops Regan and Pseudotropheus fuscus Trewavas. Representative samples of all the species worked on at Monkey Bay have been lodged with the J.L.B. Smith Institute of Ichthyology, Grahamstown and at the Fisheries Research Station, Monkey Bay.

Important details about the undescribed Mbuna species are given on a foldout inside the back cover. The four undescribed interspecifically territorial species shall, for the purposes of this thesis, be referred to as 'Pseudotropheus orange cheek', 'Pseudotropheus aggressive'; 'Pseudotropheus broad mouth' and 'Pseudotropheus sky blue'. The taxonomic complexities of Malawi cichlids make it impractical to describe these species for the purpose of this study.

## CHAPTER 3

## A REVIEW OF INTERSPECIFIC TERRITORIALITY

A territory has been defined as 'any defended area' (Noble, 1939; Myrberg & Thresher, 1974) or an 'exclusive area' (Schoener, 1968) or a 'fixed area with the presence of defence that keeps out rivals' (Brown & Orians, 1970). These are general definitions which cover all forms of localised aggression and ritualised defence of an area. Territories as defined above are common in most vertebrate and several invertebrate groups (see Davies, 1978 for an excellent review).

Since this study is concerned with territoriality which results in interspecific resource subdivision, it is only relevant to consider those forms of territoriality in which the territory owners obtain their essential food and shelter resources within the territory boundaries and, at the same time, exclude all potential competitors (conspecifics and others) from their territories. Therefore, in this dissertation, I define a territory as 'an interspecifically defended area which contains the food and shelter resources required by the owner'. The individuals defending such territories are said to be interspecifically territorial.

Two vertebrate groups which commonly exhibit interspecific territoriality are birds and coral reef fish. In birds this behaviour was recorded at least as early as 1920 (Howard, 1920) when a number of instances were cited. Despite Howard's review, subsequent workers often ignored the concept or dismissed it as either a transitory phase in the divergence of sibling species, or as a case of mistaken identity in which the species chased somehow resembled a conspecific intruder (Murray, 1971). It is only in the last two decades that the full significance of interspecific territoriality as an adaptive trait has been realised (Orians & Wilson, 1964; Clarke, 1970 & 1971; Myrberg & Thresher, 1974; Robertson, et al., 1979).

Although there are many similarities in behaviour and territories of birds and coral reef fish there is one important difference which should be mentioned. Whereas fish commonly defend their territories from a large variety of species of many forms, colours and sizes, territoriality in birds usually involves only two closely related species which defend mutually exclusive territories but do not attack other species (Orians & Wilson, 1964; Rice, 1978; Catchpole, 1972).

Humming birds are an interesting exception to this rule. They hold territories centred around the flowers from which their nectar is obtained. These territories are defended against all humming bird species as well as passerine 'nectar robbers' and, in a few instances, large nectar feeding insects (Stiles & Wolf, 1970; Snow & Snow, 1972; Feinsinger, 1976; Kodric-Brown & Brown, 1978).

Prior to the present study, there were no well-documented records of fresh water fish exhibiting interspecific territoriality with the possible exception of the darters (Percidae) which defend their territories against other species of darter when they are housed together in aquaria (Winn, 1958). The ecological significance of this behaviour is not known.

Etho-ecological studies of interspecific territoriality generally aim at answering one (or both) of the following questions (a) what is the adaptive function of territoriality and (b) when two or more species defend mutually exclusive territories, how is the space resource subdivided?

There are two theories for the evolution of interspecific territoriality in birds. (a) that it is a maladaptive error in identification (Murray, 1971) i.e. the territorial birds chase conspecifics and, by mistake, sibling species which are similar in appearance to conspecifics, and (b) that it is adaptive and evolved to subdivide resources by the subdivision of space where the species involved are similar (Orians & Wilson, 1964; Catchpole, 1972; Rice, 1978).

There are strong arguments for both theories and it seems probable that either may be true, depending on the particular instance under consideration.

Researchers on coral reef fish tend to favour a multifunction hypothesis of interspecific territoriality in fish. Possible hypotheses are that territoriality (a) is a non-adaptive error in species identification, (b) functions to protect a nest or eggs, (c) functions to preserve a refuge and, (d) functions to protect food resources from competitors.

The first of these is unlikely to apply since, as mentioned before, territorial reef fish interact with many species of a large variety of sizes, body forms and colours. That they should consistently make such obvious mistakes is difficult to accept (Myrberg & Thresher, 1974). The other three hypotheses are adaptive functions any of which could result in the evolution of territoriality since they will benefit the defendant as an individual. Of these three, the defence of a food supply stands out as being the most important and universally applicable theory for coral reef fish. For instance, although the defence of substrate spawned eggs and of a conspicuous nest site for mate attraction is of obvious value to those species which have them, this function cannot apply to the many territorial species which spawn in mid-water and do not have a nest (Robertson et al., 1979). Similarly, several authors (Myrberg & Thresher, 1974; Moran & Sale, 1977) have argued the importance of defending refuge sites. It seems unnecessary to defend a complete territory merely to prevent other fish from occupying a shelter hole. Furthermore some species defend territories which do not contain adequate shelter (Robertson et al., 1979) and many species are non-territorial yet require shelter holes (Smith & Tyler, 1972).

On the other hand the majority of interspecifically territorial reef fish studied exclude species with similar diets (usually benthic algae) from their territories and, in many, the territoriality results in increased standing crops of algae within the territories (Vine, 1974; Belk, 1975; Brawley & Adey, 1977; Robertson et al., 1979). Thus, although the defence of nest, eggs and shelter hole may add impetus to the selective pressure for interspecific territoriality, the available literature suggests that these functions may be of secondary importance only and that the main function of interspecific territoriality among coral reef fish is the defence of a food supply.

Population regulation as a function of territoriality presupposes group selection (Wynn Edwards, 1962). Since group selection is an unlikely eventuality (Maynard Smith, 1964, 1976), it shall not be considered further.

The second question often asked in connection with interspecifically territorial animals is: how do two or more species which defend mutually exclusive territories subdivide the space resource? There are at least three mechanisms by which this may occur: chance, specialization and competitive exclusion.

## Chance

Sale (1974, 1975, 1976, 1977, 1978b), studying four species of a guild of territorial coral reef fish, found little evidence of any organized pattern in the subdivision of the space resource. Instead, individuals were apparently randomly distributed throughout the habitat and vacated territories were often re-occupied by a different species from that of the previous owner. Sale proposes a "lottery hypothesis" whereby the pelagic larvae of the fish are analogous to tickets in a lottery and whether or not an individual gains a territory is a chance process - the fish in the correct position when a territory becomes vacant takes the 'prize'. Only unpredictable changes in the terrain, lack of correlation between fish recruitment and population size and the pelagic nature of the fish larvae (and hence high migration between patches) prevents one species gaining complete dominance and excluding all others from the habitat.

The mechanism of coexistence by chance may be unique to coral reef fish since only these meet the stringent requirements for coexistence listed above. However, Rice (1978) reports that two interspecifically territorial vireos (class Aves) defend mutually exclusive territories which also appear to be randomly distributed within a single habitat. He concludes that the ecological similarity of the two species prevents one from excluding the other from the habitat. Thus, as for the lottery hypothesis, the species occupying a given site depends on chance, but the factor(s) which prevent competitive exclusion are different.

## Specialization

McKaye (1977) found that the cichlid fishes of the neotropical Lake Jiloa subdivide breeding sites (which are interspecifically defended) on the rocky shores according to hole size and water depth. The size of hole used is proportional to the size of the fish. In this instance size may be considered as a specialization which appears to result in sites being more suitable for one species than another.

Space subdivision by specialization may also result from species having different requirements which have to be met within their territories. For instance species which differ in diet preferences will choose territories in which the preferred food predominates. These preferences usually result in the species involved separating into different habitats and hence they only occur side by side in the zone of overlap. This is often the case for interspecifically territorial birds (Murray, 1971; Catchpole, 1972) and may also be true of coral reef fish (Robertson *et al*.,1979).

## Competititve exclusion

Interspecific competition is defined here as: competition which exists between two or more sympatric populations when they seek a common essential resource which is in insufficient supply to meet their combined needs. Thus the presence of one population reduces the potential abundance of the other and/or *vice versa* (Vance, 1972; Feinsinger, 1976).

Miller (1964) studied species of pocket gopher (family Geomyidae) which defend their territories (burrows) interspecifically. All four species have a preference for deep sandy soils but differ in their tolerance of soil coarseness (Figure 1) and respective abilities to obtain and defend territories. These abilities are ordered such that the species with the narrowest soil tolerance is the strongest competitor for space and the species with the broadest soil tolerance is the weakest competitor for space. Those with intermediate tolerances and competitive abilities follow an intermediate pattern. This results in the competitively superior species occupying the preferred zone while the subordinate species occupy sequentially less suitable habitats in order of dominance. The only reason one or more species is not excluded is because each species can occupy some part of the habitat which competitively superior taxa cannot utilize (Figure 1).

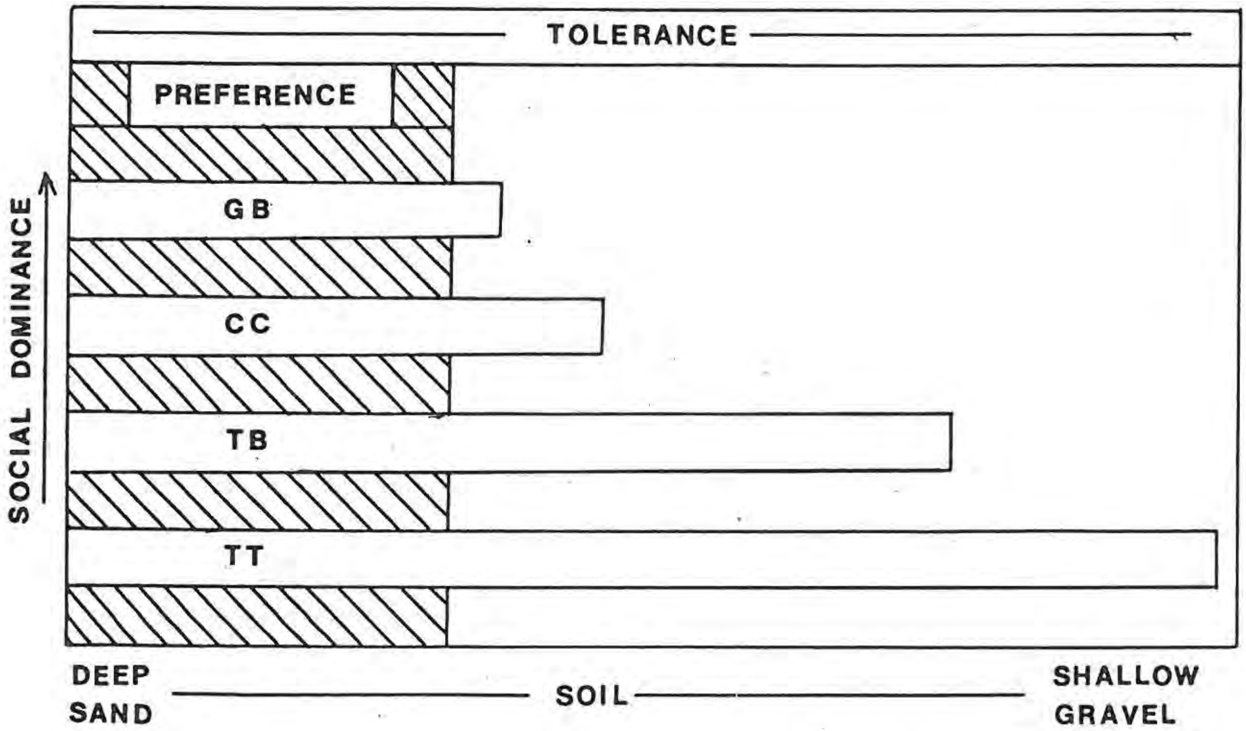

Figure 1. Soil preferences and tolerances of Geomys bursarius (GB), Cratogeomys castanops (CC), Thomomys battae (TB), and T. talpoides (TT). (Family Geomyidae). Adapted from Miller (1964).

A similar situation has been recorded for barnacles (Connell, 1961 a & b) which, although not territorial, are nonetheless in competition for space. The height above sea level which each species occupies in the intertidal zone is restricted by the presence of the other species in accordance with their respective abilities to obtain space.

Although there are no definite instances of this form of space subdivision occurring among fish, Robertson et al. (1979) discuss the possibility that competitive exclusion occurs between three territorial surgeon fish on Aldabra Atoll. They state 'We think that there is an interspecific dominance hierarchy among the three species, a hierarchy which can determine which of them takes control of disputed areas of substrate'.

From the above it appears that the principal function of interspecific territoriality among fish is the defence of a food supply. Where two or more coexisting species defend mutually exclusive territories, it is necessary to subdivide the space resource. This may occur by chance processes, specialization or competitive exclusion.

## CHAPTER 4

## THE STUDY AREA

Lake Malawi, situated between latitudes 9° and 15°S, is the most southerly of the African Rift Lakes (Figure 2). As a result of its tropical situation, temperatures are high and the annual temperature fluctuation of the surface waters is small, usually between 23° and 28°C (Eccles, 1974; Ribbink et al., in press). Summer rains result in an annual fluctuation of the lake level of 0,7-1,5m, the highest level being reached in April or May and the lowest in November or December. The prevailing winds in the dry season (March - October) are south-easterly and may develop speeds of 40km $hr^{-1}$, generating surface waves 3-4m high (Eccles, 1974). This wind may blow uninterrupted for several days in succession. By contrast, the northerly wind which dominates the rainy season seldom exceeds a gentle breeze for more than a few hours at a time.

Detailed observations and experimental work were carried out at two rocky shore sites near Monkey Bay (14°4'S, 34°56'E, Figure 3). The Thumbi East site, situated on the exposed side of Thumbi East island, is subject to swells generated by both south-easterly and northerly winds. These create an almost continuous turbulence which keeps the rocks free of visible sediment down to 5m depth. Below this, sediment becomes increasingly thicker with depth and from 8m downwards accumulations of fine organic sediment are found in low lying pockets between the rocks. Rock extends down to 35m where it gives way to a sandy plain (Figure 4). The slope of the shore is approximately 1 in 4. Rock size varies from small pebbles to huge boulders 20m or more across. The distribution of these rocks is apparently random except for patches of small rocks (< 30cm diameter) which may be found in between large boulders and at the base of underwater cliffs. Underwater visibility is good, seldom being less than 5m and occasionally exceeding 10m. The nearby Harbour Island (Figure 3) has a similar terrain.

Figure 2. Map of Lake Malawi showing sites visited during the course of this research. N.B. = Nkhata Bay; C.I. = Chisimulu Island; L.I. = Likoma Island; T.W. = Thumbi West Island; M.B. = Monkey Bay; Z = Zimbabwe Rocks.

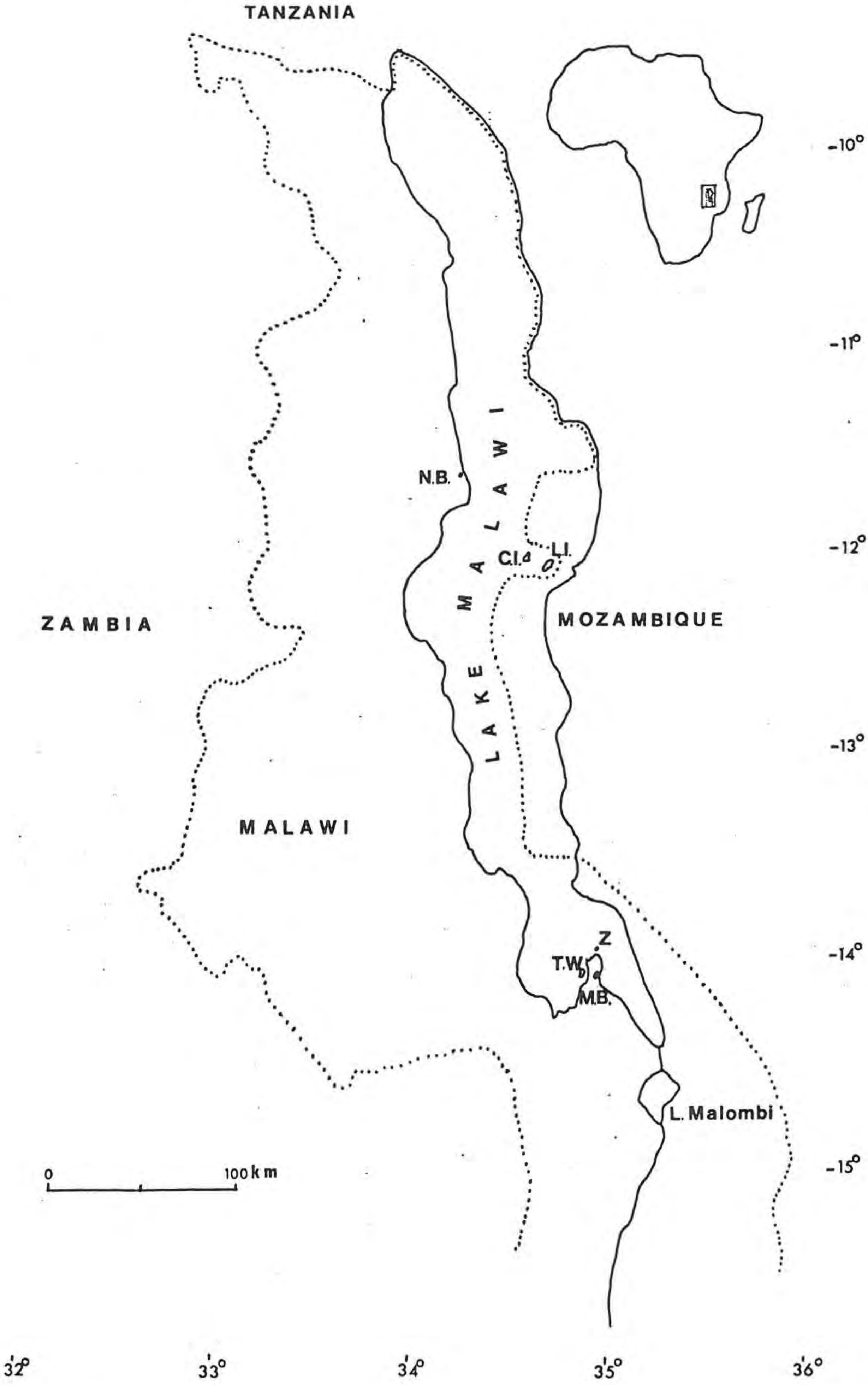
TANZANIA
-10°
-11°
N.B.
LAKE MALAWI
C.I.
L.I.
-12°
ZAMBIA
MOZAMBIQUE
-13°
MALAWI
Z
T.W.
-14°
M.B.
L. Malombi
0
100 km
-15°
32°
33°
34°
35°
36°

Figure 2.

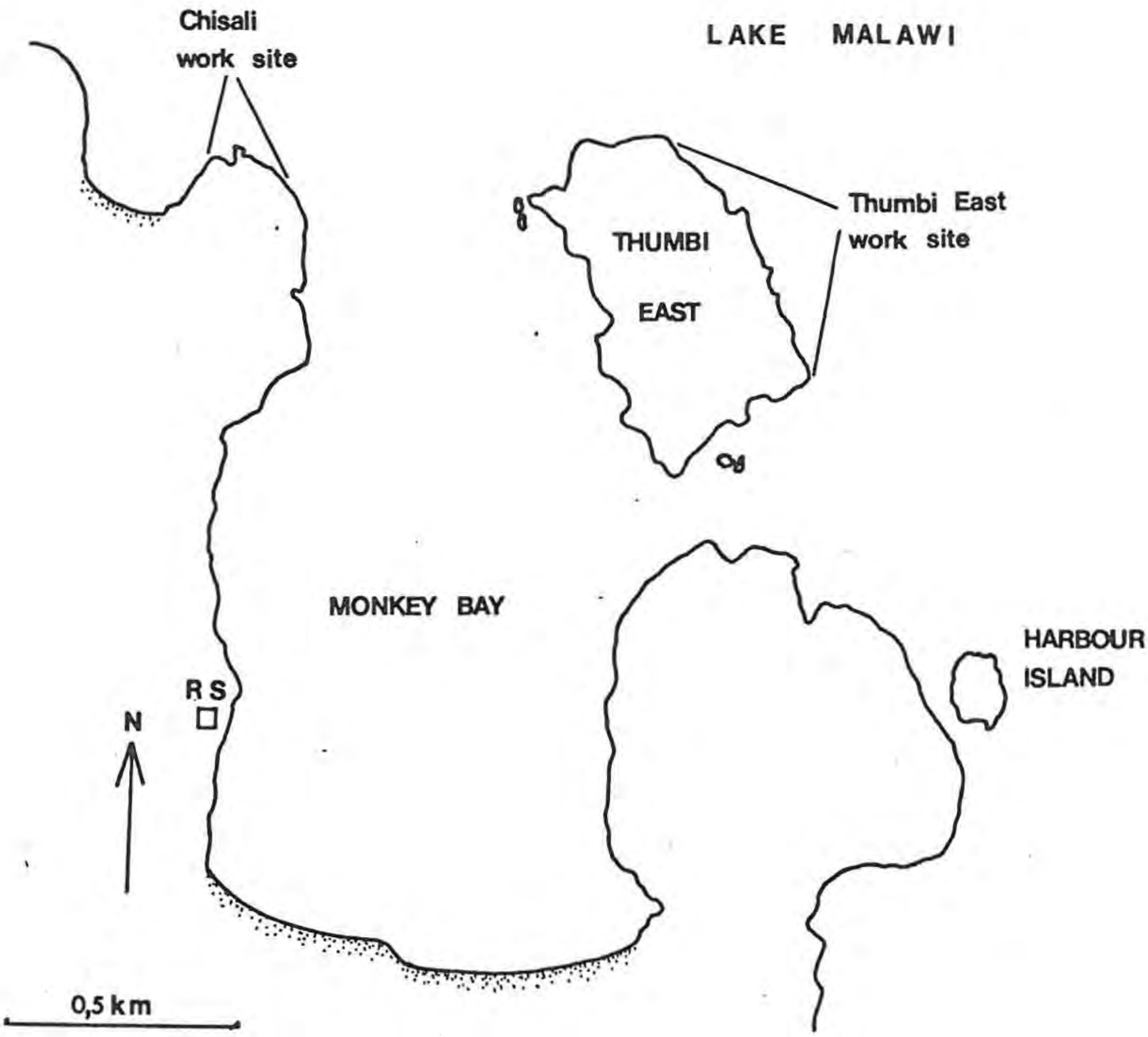

Figure 3. Map of Monkey Bay showing the exposed Thumbi East site and the Chisali site which is sheltered from the prevailing south-easterly winds. Beaches are represented by stipling. The remainder of the shore is rocky. Rs = research station.

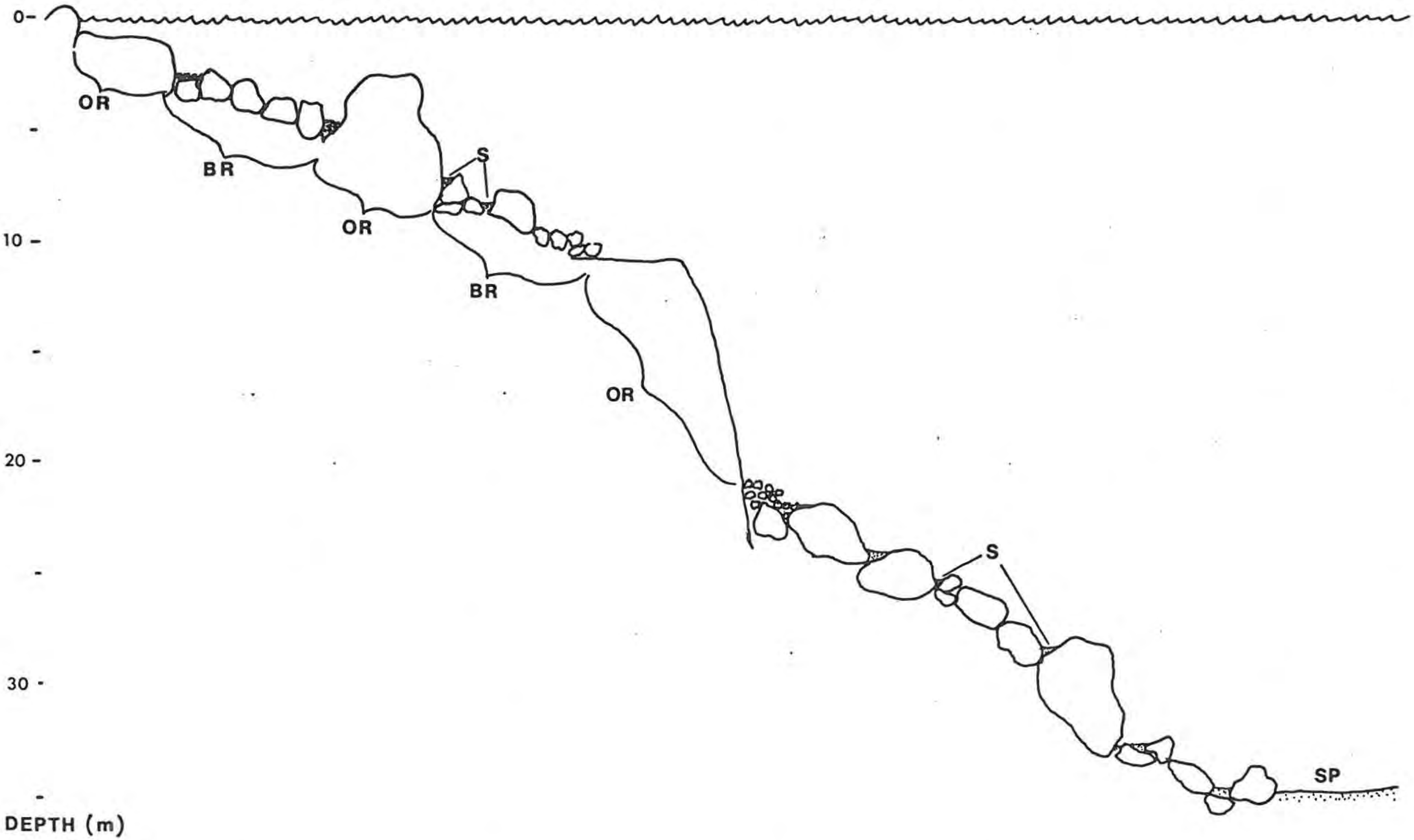

Figure 4. Cross section of a typical rocky shore on Thumbi East. OR = open rock; BR = broken rock;S = sediment; SP = sandy plain.

The second site, Chisali, is situated on a north-facing shore which is completely sheltered from the south-easterly winds but is exposed to the occasional, brief northerly winds. Although quantitative data are not available, this site is noticeably more silted than Thumbi East. Sediment is often visible on rocks in the extreme shallows and pockets of organic sediment are found in hollows in only 4m of water. The rock extends to 11m depth where a thick uninterrupted bed of filamentous blue-green algae (genus Lyngbia) covers the bottom. The nature and size of rocks is similar to that at Thumbi East except that accumulations of small rocks, where present, are invariably covered by a layer of sediment. Underwater visibility is slightly less than at Thumbi East and, during a strong northerly wind, may be reduced to a metre or less by suspended sediment.

For comparative purposes, further observations were made at the following rocky shore sites in the southern and central parts of the lake (Figure 2): Chisimulu Island, Likoma Island, Nkhata Bay, Thumbi West Island and Zimbabwe Rocks.

The following terms are used to refer to particular habitat zones on the rocky shore (see also Figure 4):

Open rock: a rock face larger than 2m in diameter which does not provide shelter.

Broken rock: patches of rock with an average diameter of between 20cm and 2m. This zone provides innumerable crevices and refuge holes.

Small rock: rock patches in which the average rock diameter is less than 20cm.

Extreme shallows: those portions of the littoral zone over which the water is less than one metre deep.

Shallows: those portions of the littoral zone over which the water is between one and five metres deep.

Intermediate depths: those portions of the littoral zone over which the water is between five and ten metres deep.

Deep water: rocky shore in the 10 to 20m depth range. Only brief observations were made below 20m.

# CHAPTER 5

## THE FOOD RESOURCE

In the study sites, all exposed rock surfaces down to at least 40m are covered by a thin algal mat comprising attached filamentous blue-green algae and an assortment of diatoms, unicellular and multicellular algae, bacteria and detritus. In deep water and sheltered bays a layer of sediment may cover the rocks and its associated algae. Invertebrates including mites, copepods, ostracods and larvae of chironomids, Trichoptera and Ephemeroptera are found in the algal mat and derive shelter and food from it (Fryer, 1959). To distinguish the various components of this mat in analyses of stomach contents, the terms used by Fryer (1959) are followed:

Aufwuchs: All epilithic organic matter except benthic invertebrates.
'Calothrix': All attached, filamentous blue-green algae.

Fryer recognized two species of blue-green algae of the genus *Calothrix* at Nkhata Bay. He compares these with the trees in a woodland since their filaments are firmly attached to the rocks and between them (and on them) grow numerous other algae which constitute, as it were, the undergrowth. Fryer does not mention which species of *Calothrix* were present, nor does he distinguish between the two in stomach content analyses.

Samples of '*Calothrix*' collected on the rocky shore near Monkey Bay and sent for identification contained many species of blue-green algae (Lazarek, pers.comm., see below). Several of these do not belong to the genus *Calothrix* but this general term is nonetheless retained, as a common noun (calothrix) for lack of a more suitable one.

Three major calothrix subdivisions are made in which those species commonly found together on rock faces and in stomach contents are grouped.

Calothrix 1: This group includes principally Cladophora and Oedogonium species but also Calothrix brevissima and C. kosinkajae. They are characterised by green coloration and long branching filaments.

Calothrix 2: This group includes Calothrix castetti, C. epiphytica, Oscillatoria amphibia and Lyngbia species. These species have fine non-branching filaments which are often closely packed and are brown or red when seen in the field or viewed under a compound microscope.

Calothrix 3 : An unidentified blue-green alga which possibly belongs to the genus Cladophora or Oedogonium. It is confined to rocks covered in thick sediment in water of 10m and deeper.

Loose Aufwuchs: All particulate organic matter associated with the rock i.e. free living and epiphytic algae, diatoms, bacteria and detritus, but not calothrix or benthic invertebrates. In the field it is possible to distinguish two categories of loose Aufwuchs: (a) that found between and on strands of calothrix and (b) that which lies loose on top of the calothrix mat. Under normal conditions the latter is principally organic sedimentary matter. In stomach content analyses it is not possible to separate these two categories.

Benthic invertebrates: Since the fish species dealt with are predominantly Aufwuchs feeders, no attempt has been made to classify invertebrates to species level. Mention is, however, made of any invertebrate groups which appear frequently in the stomach contents of a particular species. Some of the benthic invertebrates associated with the rocky shores of Lake Malawi have been listed by Fryer (1959).

Phytoplankton: The south of the lake is subject to large fluctuations in phytoplankton abundance, probably caused by seasonal wind and upwelling conditions (Eccles, 1974). Dense blooms of a blue-green algae of the genus Anabaena occasionally form in the shallows during calm weather in winter.

Zooplankton: During the course of this research zooplankton appeared very infrequently in the stomachs of the epilithic algae grazers. This food item is therefore considered to have been of little importance to the members of the epilithic algae grazing guild in Monkey Bay during the period of this study.

## Validity of food categories

When grouping similar food items into categories there is always a danger of overlooking an important difference between the diet of two species which occur within one such category. Unfortunately neither the facilities nor the expertise were available to subdivide food categories further than has already been done. The author would like to stress that the inherent dangers associated with this have been borne in mind at all times.

## CHAPTER 6

## METHODS

### General

All field work was carried out using open circuit SCUBA (Self Contained Underwater Breathing Apparatus) as well as a snorkel and mask. While the use of SCUBA was essential to the research program, it is unfortunately a very time consuming method of collecting data. Preparation for a dive may take several hours because both experimental and diving apparatus must be prepared and checked. In addition it was often necessary to synchronise the dives of two researchers, thus further lowering individual efficiency. Finally the length of each dive is limited by the available air, the divers' resistance to cold and, in the case of dives below 10m, decompression time. Depending on the nature of the job at hand it was generally found that dives were limited to 1½ - 2½h periods.

During the two years spent on research in Lake Malawi (November 1977 - December 1979) approximately 800 SCUBA hours and 50 snorkel hours were logged, 85% of which were directly involved with the present study. A breakdown of the distribution of this diving time is given in Table 1.

Although some marine fish are apparently disturbed by the exhaled bubbles from SCUBA (Earle, 1972a), this was not obvious in the majority of Mbuna. The presence of a diver even as close as two metres did not appear to affect the behaviour of the fish in any way. Observations were further facilitated by the good visibility (5-10m). All data collected underwater were recorded with pencils on roughened perspex sheets.

Fish for stomach content analyses or measurement were collected individually,

Table 1

Approximate distribution of diving time between the various research projects undertaken.

| | Hours |
|---|---|
| Preliminary observations | 75 |
| Fish catching | 50 |
| Transects | 100 |
| Removal experiments | 125 |
| Mapped quadrates | 40 |
| Field trips & photography | 100 |
| Activity counts | 50 |
| Tagging | 40 |
| Standing crop | 10 |
| Calothrix distribution | 5 |
| Exclusion chambers | 20 |
| Fish enclosure | 80 |
| Relative aggression | 50 |
| Miscellaneous | 50 |
| TOTAL | 795 |

usually by driving them into a 15mm stretched mesh monofilament nylon net in which they were entangled but not gilled. Occasionally more elusive species had to be speared with a small, light multi-pronged spear shot from a conventional speargun.

Fish distribution and density

Two techniques, underwater counts and poisoning, are commonly used to census fish over coral reefs, rocky shores and other areas unsuitable for the use of seine nets.

To obtain a quantitative estimate by poisoning it is essential to demarcate the area from which the dead fish are collected either with nets or by choosing spots sufficiently isolated from other populated areas e.g. coral patch reefs (Smith, 1973). Attempts were made to estimate fish densities on the rocky shores of Lake Malawi by poisoning with rotenone. This was done within a 4 x 4m enclosure made of mosquito netting and supported at the corners by floats. This enclosure was lowered into position and held down by lead weights and rocks (Figure 5). Two divers entered the net through a hatch in the roof and dispersed rotenone.

Unfortunately this technique proved to be of little value, principally because the disturbance made by placing the net and distributing rotenone drove the fish into the innumerable holes in the rocky bottom. It was evident that many fish seen within the net prior to poisoning either escaped or were trapped below the rocks. These attempts did however confirm the presence of many fry which normally remain hidden from sight.

A technique which proved to be far more successful, both during the present study, in other lakes (Keast & Harker, 1977; Mc Kaye, 1977) and on coral

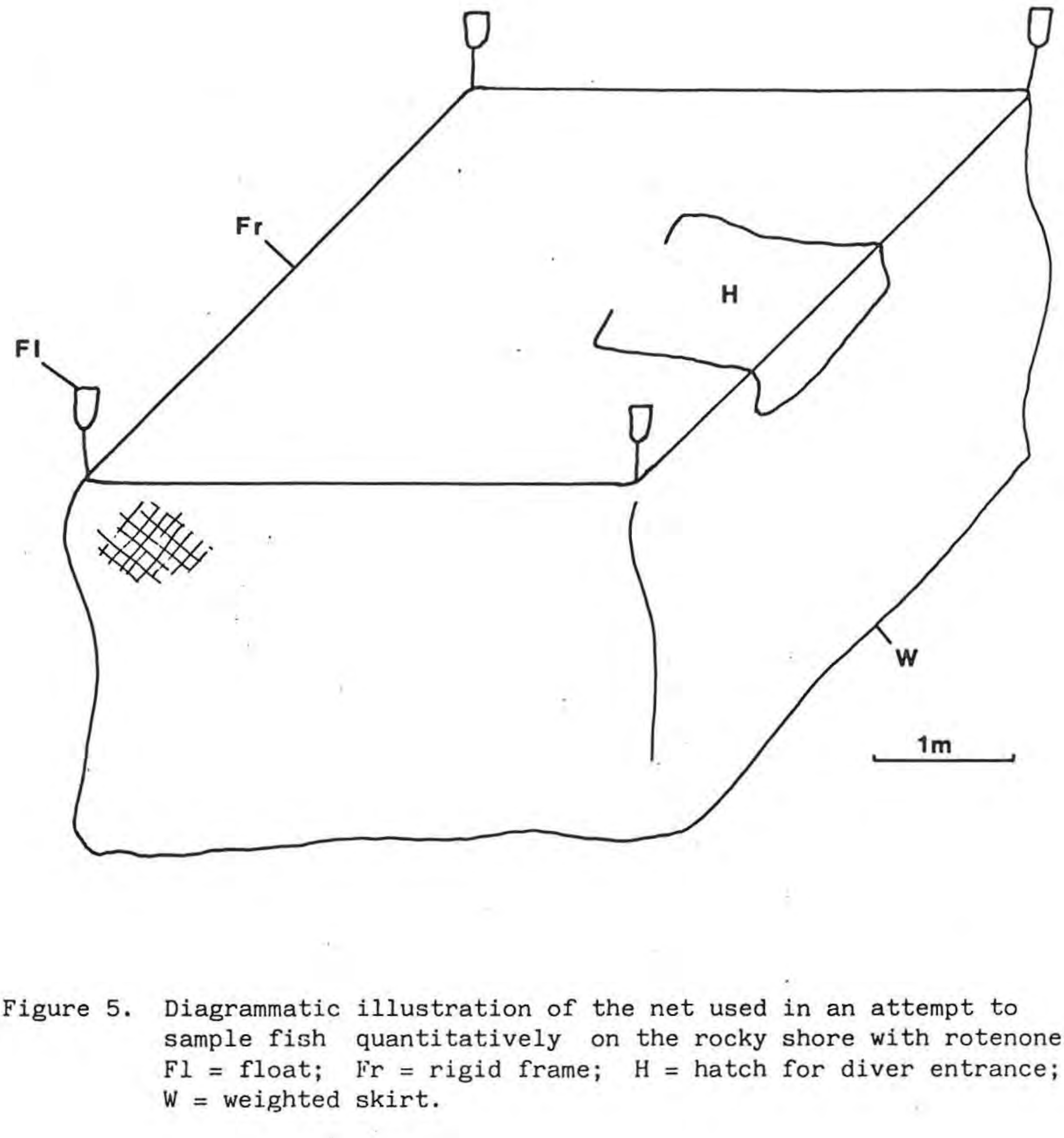

Figure 5. Diagrammatic illustration of the net used in an attempt to sample fish quantitatively on the rocky shore with rotenone. Fl = float; Fr = rigid frame; H = hatch for diver entrance; W = weighted skirt.

reefs (Belk, 1975; Clarke, 1977; Sale & Sharp, in prep.), is that of underwater counts made in strip transects. The basic technique is to lay two parallel lines a known distance apart and of known length. Fish between the lines are counted by a diver swimming along the transect (Figure 7). Several variations on this technique were used to suit conditions at Monkey Bay.

i) $50m^2$ transects, each 2 x 25m (Figure 6) were laid along contours at the following depths, 1-2m; 2-4m; 4-6m; 9-11m and 19-21m. At each site and depth three different transects were counted. In the case of the two common interspecifically territorial species ('<u>Pseudotropheus</u> orange cheek' and '<u>P</u>. aggressive') six different transects were counted at each depth between 1-11m on Thumbi East.

ii) Species with low densities were counted in $200m^2$ transects. These transects consisted of a 50m line which was laid along the selected depth contour. A diver counted fish within two metres of the line, on one side at a time, while gauging distance with a two metre pole held in front of him. Censuses were made at the same depths as the $50m^2$ transects. Three transects were counted at each depth.

iii) The steep slope and irregular nature of the rocky shore made it impossible to lay transects in the extreme shallows, hence all fish in water shallower than one metre were counted along two lengths of shore on Thumbi East. The area within these transects ($262m^2$ and $186m^2$) was calculated by measuring the lengths of the rock bands and their widths at four metre intervals. Counts were made three times in rough and three times in calm weather over a number of days.

iii) To count the dense shoals of juvenile fish in the extreme shallows, fixed transects, each 1,5 x 3m, were laid on large horizontal or slightly sloping rock at 0,5m; 1,5m, 2m; 3m; 6m and 10m depth. Each transect

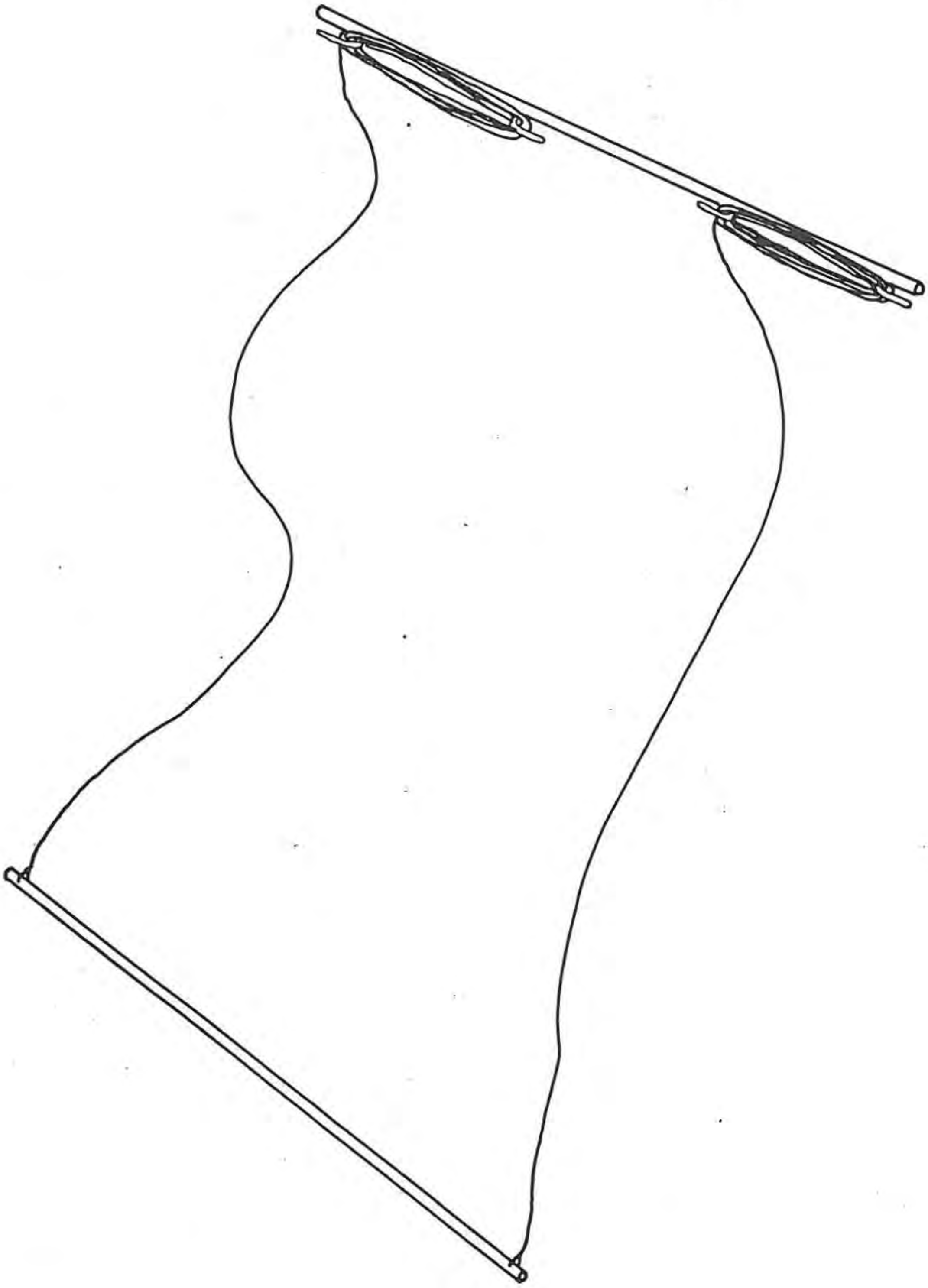

Figure 6. Diagrammatic illustration of one of the 50 $m^2$ transects used during the fish distribution survey. The poles are each two metres long and are connected by two 25 m lengths of rope. See also Figure 7.

Figure 7. A SCUBA diver counting fish in a transect laid on a typical section of broken rock near Monkey Bay.

Figure 8. An adult male Pseudotropheus zebra showing a colour coded floy tag in position.

in water 3m and shallower was counted four times in calm and four times in rough weather over a number of days. The 8 and 10m transects were counted a total of four times each.

When laying the 50 and 200m$^2$ transects it was essential to choose areas of low rock relief (a) because large boulders lift the transect lines too high above the bottom for accurate counts and (b) to limit the depth range within each transect to three metres or less. The fish densities recorded are therefore representative of areas of broken rock and small open rock (3m maximum diameter), and do not include larger boulders. In contrast, the 1,5 x 3m fixed transects were laid on large open rock slabs, the habitat zone most commonly occupied by the juvenile fish they were designed to count. Horizontal slabs were chosen to limit the depth range of the transects to a few centimetres so that accurate comparisons of fish densities over small depth changes could be made.

When counting transects over broken rock it is inevitable that some fish in cracks and below rocks will be overlooked. The resultant error is probably negligible, however, since the species involved feed almost continuously from exposed rock and are easily visible. Nocturnal species and fry which remain concealed during the day were not counted. All counts were made between March and June 1979. Unless stated otherwise, the student's t-test was used for statistical analyses.

## Stomach content analyses

Fish for stomach content analyses were captured at Harbour Island and Thumbi East (Figure 3). Concentrated formalin (20-40%) was injected into the body cavity immediately after capture to stop digestion and kill the fish.

Fish were collected at selected depths between one and 20m, and those from the shallows were sampled at quarterly intervals from September 1978 to October 1979. With two exceptions there were no significant differences between the samples from different depths or between the quarterly samples. Consequently these samples were combined for each species. The two common territorial species '*Pseudotropheus* orange cheek' and '*Pseudotropheus* aggressive' were an exception to this rule, since they were collected in larger numbers and showed marked differences in diet with depth.

A variety of techniques for stomach content analyses are available. Christensen (1976) groups these into eight categories. Seven of these require that the organisms present in the stomachs be either counted or separated for gravimetric or volumetric analyses. Since the stomach contents of the epilithic algal grazing fish are predominantly micro-organisms, none of these methods were practical with the equipment available. The eighth technique is the points method modified from Hynes (1950) whereby the relative frequency of food items is estimated by inspection. This technique was most suitable for the present study. The procedure used was to spread the stomach contents under a coverslip and scan them with a compound microscope. An estimation of the percentage cover of each food category was then made while scanning across the microscope field. This provides a relative measure of food usage by comparing the abundance of the different food categories.

All estimates (over 2000) were made by the author so that the technique was standardized. While the shortcomings of this technique are realised it is felt that it is sufficiently reliable to use the results for the predictions made in this thesis.

Intestines from a minimum of five individuals of each species studied at Monkey Bay were subsampled at intervals along their length. It was found that intestinal contents were generally reduced to a fine-grained amorphous mass which was unsuitable for analysis. An exception to this was the outer sheaths of calothrix strands and diatom frustules, which were not digested.

## Fish tagging

Individuals of '*Pseudotropheus* aggressive' larger than 60mm SL and '*Pseudotropheus* orange cheek' larger than 50mm SL were tagged for underwater identification with bead tags sewn through the musculature anterior to the dorsal fin, or Floy tags inserted with a tagging gun below the posterior end of the dorsal fin (Figure 8). All tags were colour coded. Tagging was conducted within two 10 x 16m grids (one at each work site) marked out with submerged, coded floats at two metre intervals. The positions of tagged fish relative to these floats were recorded approximately weekly. Unfortunately tag retention was poor and complete disappearance of many tagged individuals suggested that they may be subject to increased predation or disease as a result of tagging.

Individuals of '*P*. aggressive' of less than 60mm SL were marked for recognition by clipping a small wedge out of their caudal fin. This frequently used method (reviewed by Konstantinov, 1977 ), did not impair swimming. In fact many individuals in the field have large portions of their fins removed by the scale-biter *Genychromis mento* Trewavas (Fryer *et al*., 1955). Fin clipped fish could be recognized for a maximum of 10-14 days after marking, hence their exact position was recorded for nine consecutive days on a map of the marking site. The area within which each fish was sited was calculated from these maps by joining the outer most points of sighting. Fish marked by this technique were not as visible in the field as those tagged with beads or Floy tags. It is unlikely that any individuals which moved far from the tagging site were located. Fortunately most tagged individuals were found at the same site day after day which facilitated recognition.

### Territory size

To obtain data on territory size it was necessary to establish the position of territory boundaries. This was done by observing the movements of the territory owner, the limits of the algal garden and the topography of the rock (territories were often sited within a crevice and did not extend beyond its lip). Ten to fifteen minutes of observation was sufficient to determine territory boundaries with an acceptable degree of accuracy.

Two measures of territory size were recorded:-

1. Total area of rock included within the territory.

This measure was only taken for '*P*. aggressive' since their territories are small, easy to plot and frequently occur in simple 'V' crevices. Territories which were sited in such a crevice and at the required depth were selected and the positions of their boundaries were ascertained. Territories in simple crevices were chosen because they have only two facets, one on either side of the crevice, thus making them easy to measure. Territories were measured by sketching each facet onto an underwater slate and taking its dimensions at several points. From these data accurate scaled down drawings were made from which the area of rock within the territories could be determined.

2. Horizontal area covered by the territory.

Several sections of the research required maps of portions of the rocky shore onto which territory boundaries could be plotted. These maps were prepared by laying a 2 x 2m grid of nylon line over the area to be mapped. The rocks within the grid were then sketched on an underwater slate with a 10 x 10cm scale. This map was later traced onto paper forming a master copy from which several working copies were taken for underwater use when sandwiched between two sheets of perspex. The same map could be re-used thus saving time and reducing inaccuracies caused by transference of maps to slates. The horizontal area of territories was measured by plotting territories onto these maps. Similar maps were used during removal experiments, during tagging and to determine the proportion of available space occupied by territories.

## Diel rhythm

In order to quantify the extent of aggression shown by territorial '*P.* orange cheek' and '*P.* aggressive', activity counts were made at the two work sites during winter and summer. For the purpose of this study daylight hours were divided into five periods: 0500-0800h, 0800-1000h, 1100-1400h, 1400-1630h and 1630-1800h. In each of these periods 10 fish were observed for five minutes each. The territories of all fish observed were marked with numbered buoys to ensure that the same fish were used in subsequent readings at a particular site. The activities recorded were: number of feeding pecks, number of conspecific chases and number of interspecific chases. All fish observed were larger than 75mm SL.

## Relative aggression

Myberg & Thresher (1974) and Moran & Sale (1977) have determined the distance from the territory centre at which a interspecifically territorial fish attacks intruders of various species by artificially introducing intruders in bottles. From these data the relative aggression with which an intruder species is attacked can be obtained. This technique was attempted for '_P_. orange cheek', since it too attacks some intruder species more aggressively than others. The experiment failed because the responses of the territorial fish were inadequate. An an alternative the positions of natural encounters were plotted on maps of eight '_P_. orange cheek' territories and the average distance of attack was obtained for each intruder species. The distance was taken from the feeding boundary instead of the territory centre because the territories are seldom circular. This distance of attack may be negative where the majority of chases commence when the intruder has already entered the feeding territory. A total of 706 aggressive encounters were observed during this study and a one tailed Wilcoxons signed ranks test (Sokal & Rohlf, 1969) was used to test the significance of differences between intruder species.

The technique used here has the advantage over the 'bottle method' in that only natural encounters are observed. There are, however, disadvantages of the method. For instance, different fish approach the territory by different routes which may affect the distance at which they are first observed by the territorial occupant. Furthermore, one species (_Pseudotropheus auratus_ Boulenger) appears to be an 'Aufwuchs robber' which deliberately approaches the territory in a manner which minimises detection so that it may feed within the territory (see page 51 ). Unfortunately there was no practical way to circumvent these problems.

## Removal experiments

Individual removals: Individual fish of a number of categories (Table 2) were removed from their territories by adopting the following procedure: a territory site between one and four metres depth was mapped and marked with a numbered buoy. The occupant was then removed and the territory site monitored for a replacement after 15 minutes, 1 hour, 6 hours, 1 day, 1 week and 1 month. A fish was said to be in possession of a territory site if it was feeding in the site and exhibited at least some interspecific aggression in the first two minutes of observation. Although this does not constitute fully developed territorial behaviour it was chosen as the criterion for possession of a territory because it is considered to be the minimum requirement indicating potential for complete territorial defence.

'*Pseudotropheus* sky blue' proved to be extremely difficult to catch because they hid among the rocks when approached by divers. It was impractical therefore to do controlled experiments as described above for this species. Instead removals were made whenever possible and the territory was observed for approximately two weeks to see if it had been re-occupied.

Mass removals: '*P*. orange cheek' and '*P*. aggressive' were sufficiently numerous for these experiments. Mass removal experiments were conducted in quadrates (each 6 x 6m) mapped out as described on page 18. Three types of removal were conducted with two replicates each. All quadrates were situated between three and five metres depth on Thumbi East.

The three types of mass removal are:

Table 2

The categories of territorial fish on which individual removal experiments were conducted. 20 fish in each category were removed.

1. '*P*. orange cheek' males among broken rock on Thumbi East.
2. '*P*. orange cheek' males among broken rock at the Chisali site.
3. '*P*. broad mouth' males at the Chisali site.
4. '*P*.aggressive' > 75mm SL among broken rock on Thumbi East.
5. '*P*. aggressive' > 75mm SL among broken rock at the Chisali site.
6. '*P*. aggressive' < 75mm SL on open rock on Thumbi East.
7. '*P*. sky blue' adult males on Thumbi East.

a) Single mass removals (unbiased): All territorial 'P. orange cheek' and 'P. aggressive' which could be caught were removed from the quadrates during a single catching session. Replacements were monitored after 1 day, 1 week and then at monthly intervals for six months.

b) Repetitive mass removals of 'P. orange cheek'. All territorial 'P. orange cheek' were removed from the quadrates along with their conspecific replacements until no more recolonization took place during the 24 hours after the last removal (6 days). Subsequent replacements by any species were monitored after 1 day, 1 week and at monthly intervals for six months.

c) Repetitive mass removals of 'P. aggressive' as for (b) above except the removed species was 'P. aggressive'. Removal of this species lasted for five consecutive days.

Monitoring of quadrates involved a systematic coverage of the quadrate to determine which vacated site had been re-occupied and by whom. For these experiments a fish was said to occupy a site if it was holding a territory at least half of which fell into the area previously occupied by the original owner. In the two instances where fish expanded their original territories to include part of a vacated territory, these territories were said to be half occupied.

Estimation of calothrix composition.

Certain areas of rocky shore were seen to have characteristric calothrix compositions.

To quantify these differences, estimates of percentage calothrix composition were made from 1-20m on the categories of rock face listed in Table 3. The same technique used for estimating percentage composition was used as for stomach content analyses, i.e. relative proportions were estimated by inspection. In this instance the estimates were simplified by the presence of only three categories; calothrix 1, calothrix 2 and uncolonised rock. Estimates were made within a 20cm wire ring placed in the centre of the rock face. The first 20 faces encountered by a diver swimming at the required depth and which fell into the category being monitored were analysed in this way.

The survey was conducted on Thumbi East in May when rocks shallower than one metre had been covered by water for approximately 2-4 months (as a result of increased lake level).

### Exclusion chambers

In order to determine the effect of exclusion of grazing fish on the standing crop and species composition of the Aufwuchs, fish exclusion chambers were bolted to the rock at Thumbi East. Each of the circular chambers was 20cm in diameter and constructed of a ring of 20mm diameter rubber tubing covered on the upper side with fine monofilament nylon net (Figure 35). The bolts securing these chambers were inserted into holes drilled in the rock with a star drill and hammer and were held in place with quick hardening epoxy putty.

Sets of six chambers were placed on each of the following categories of undefended rock faces:

## Table 3

The categories of rock face upon which calothrix distribution surveys were conducted. In each instances 20 faces were sampled at 1, 5, 10 and 20m depth (when present).

1. Undefended vertical faces among broken rock on Thumbi East.
2. Vertical faces within '_P_. orange cheek' territories on Thumbi East.
3. Vertical faces within '_P_. aggressive' territories on Thumbi East.
4. Small rocks within '_P_. sky blue' territories on Thumbi East.
5. Horizontal faces within '_P_. broad mouth' territories at the Chisali site.

1-3m depth, horizontal open rock.

1-3m depth, vertical rock.

18-20m depth, horizontal open rock.

The percentage calothrix composition within these chambers was estimated at approximately monthly intervals for 5 to 8 months and notes were taken on the length of the calothrix and the amount of sediment or loose Aufwuchs present. During each reading a 20cm ring was laid adjacent to each exclusion chamber and the calothrix composition within this was estimated as a control. After 103 days the chambers on the shallow water horizontal sites were removed but observations continued on the unprotected site to monitor reverse trends.

## Aufwuchs standing crop

Calothrix is firmly attached to the rock and it was not feasible to remove it quantitatively in the field. Suitable rocks were therefore returned to the laboratory where the Aufwuchs was dried *in situ* on the rock at 60°C. The dry Aufwuchs is brittle and can easily be brushed off. To minimize loss of dry material, Aufwuchs was removed in a box with openings only for the operator's hands. The area cleared of Aufwuchs was measured and the collected material dried to a constant weight at 105°C then weighed and ashed for five hours at 500°C. The ash-free dry weight per square metre was then calculated. Rocks for calothrix dry weight analysis were collected on a quarterly basis from the following zones on Thumbi East between October 1978 and October 1979:

1-2m depth among broken rock (undefended).

1-2m depth from '*P*. aggressive' territories.

5-7m depth among broken rock (undefended).

5-7m depth from '*P*. aggressive' territories.

In addition, in April 1979 collections were made from 1m, 5m and 10m depth among broken rock at the Chisali site, from 0,5m to 20m depth on Thumbi East (where at 0,5m rocks were collected both among broken rock and from open rock by prizing off flakes with a crowbar), and from '*P*. orange cheek' and '*P*. sky blue' territories on Thumbi East. A minimum of 10 rocks were collected per sample.

## CHAPTER 7

## ECOLOGICAL NOTES ON GUILD SPECIES

To provide the background necessary for an appreciation of the territorial cichlid communities studied at Monkey Bay, a brief account of life history, feeding, distribution and behaviour of the 16 common species is given here. Some of the investigations are a repeat of Fryer's (1959) work at Nkata Bay. This was necessary partly because many of the species dealt with here do not occur where Fryer worked and partly because the underwater research techniques used in the present study enabled more detailed studies to be made. It was therefore possible to gain a great deal of new information as reported below.

Root's (1967) definition of a guild (see introduction) groups species regardless of their taxonomic status. Thus the guild under study here includes all fish species with a diet of predominantly epilithic algae which are resident on the rocky shores near Monkey Bay. Of the nineteen species which meet these criteria, two are cyprinids and the remainder are cichlids. Three species, Melanochromis melanopterus Trewavas, Pseudotropheus microstoma and an undescribed Pseudotropheus species are uncommon and not important to this thesis; they are therefore excluded from the annotated list.

### Family Cyprinidae

### Genus Barbus Cuvier & Cloquet

### Barbus johnsoni Boulenger (Figure 9)*

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* For ease of reference all tables and figures pertaining to the annotated list of species have been arranged at the end of this section.

## Feeding.

It was found that this, the largest guild member, feeds by striking the rock surface with its rigid, cartilaginous lower lip (Figure 9) while swimming forwards and simultaneously jerking its head sideways. Since this process takes place without a pause in swimming, B. johnsoni is able to feed from rocks at the water surface, even when a heavy swell is running. This may allow it access to food not available to other species. The food taken by this mechanism is almost entirely calothrix 2 (Fryer, 1959; and present study, Figure 8).

## Distribution, behaviour and life cycle.

The life cycle of this species remains obscure. Fryer (1959) reports that 'ripe' members of both sexes were caught between February and April at the mouth of Crocodile Creek, a small river flowing into Nkata Bay. He suggests, on the basis of this and other evidence, that they ascend rivers to spawn during the rainy season. The present study can add no more information to the breeding biology of this species except that shoals of small cyprinids (50-80mm SL) presumed to be juvenile B. johnsoni were frequently seen schooling a few centimetres below the water surface in inshore waters. They were apparently feeding on plankton. Specimens of medium size (80-150mm SL) feed individually or in pairs from rocks in the extreme shallows while larger fish form schools of up to 50 individuals which feed principally from horizontal rocks between 0,5 and 5m depth. Large schools of adults were also noted by Fryer (1959). Since it was not possible to count the schools of juvenile or adults with the small transects used, the data on the distribution of this species presented in Figure 19 only includes the

80-150mm SL size range. The true depth distribution of all size ranges is therefore probably broader than depicted in the Figure.

Genus Labeo Cuvier & Cloquet

Labeo cylindricus Peters (Figure 9)

Feeding.

This species feeds by scraping algae from horizontal rocks with its fleshy lips and it invariably leaves a bare patch of rock where it feeds (Fryer, 1959; personal observation). During the present study this species was only seen to feed on horizontal rocks with visible sediment cover. It takes predominantly loose Aufwuchs (Figure 18).

Distribution.

Fryer (1959) states that L. cylindricus is 'the commonest and most important non-cichlid on the rocky shore'. While this is true of the sheltered Chisali site near Monkey Bay, B. johnsoni is apparently more abundant on exposed shores (Figure 19). This conclusion is tentative since it is difficult to obtain accurate counts of these two species, because of their low numbers, high mobility and schooling habits.

Behaviour and life history.

Adults were occasionally seen chasing conspecifics which suggests that they may be intraspecifically territorial. They seldom venture more than a few centimetres above the rock surface.

## Family Cichlidae

### Genus Cyrtocara Boulenger

In a recent revision of the genus Haplochromis, Greenwood (1979) has restricted the use of this generic name to five species, all of which are members of the Lakes Victoria, Edward, George and Kivu species flock. Greenwood suggests that, as a temporary measure until the Malawi species are revised, the 'Haplochromis' of Lake Malawi should be referred to as Cyrtocara. Only one species of this genus is a member of the epilithic algae grazing guild at Monkey Bay.

### Cyrtocara taeniolatus Trewavas (Figure 9).

Feeding.

The mouth of this species is relatively small and narrow but otherwise unspecialized (Figure 9), and the teeth are small and sparsely distributed. Food is collected from the rock by a series of pecks. C. taeniolatus feeds principally on loose Aufwuchs but high proportions of chironomids were also found in the diet (Figure 18). Occasionally almost the entire C. taeniolatus population moves off the bottom to feed in midwater (0,2-2m up). This phenomenon was frequently but not always associated with phytoplankton blooms.

Distribution.

This species, which is by far the most abundant of the non-Mbuna cichlids on the rocky shore at Monkey Bay, has a broad depth distribution and reaches high densities between 1 and 10m depth (Figure 19).

Behaviour and life history.

For the majority of the year C. taeniolatus is unaggressive. During the breeding season (June to November, Ribbink & Marsh, pers.comm.) males do defend territories. These territories, from which all intruder fish are chased, are usually situated on the tops and sides of rocks with a diameter of 1-3m (approximate size only).

### The Mbuna

Life History.

All Mbuna studied to date are maternal mouth brooders which lay between 11 and 120 large yolky eggs per spawning (B.A. Marsh, pers.comm.). The fry take 22-30 days to develop (data for Pseudotropheus auratus (Boulenger), Labeotropheus fuelleborni Ahl and L. trewavasae Fryer from Fryer & Iles, 1972). No instances of Mbuna guarding their young subsequent to release are known, and it is therefore assumed that they are released into narrow cracks and patches of small rock where they remain relatively safe until large enough to emerge. The mature males of many species are territorial throughout the year. This territoriality is usually directed intraspecifically. As far as can be a ascertained courtship and spawning take place within the territory of the male.

### Genus Melanochromis

### Melanochromis vermivorous Trewavas (Figure 10).

Feeding.

This small species has a broad mouth relative to its size (Table 4, Figure 10). It feeds with discrete pecks from the rock surface and takes principally loose Aufwuchs (Figure 18). M. vermivorous is opportunistic and may feed entirely on phytoplankton during blooms of *Anabaena*.

### Distribution.

Although not abundant at Monkey Bay, this species occurs at both work sites and at all depths on Thumbi East (Figure 20). They are most common in the extreme shallows of the exposed Thumbi East site, particularly in calm weather (Table 5).

### Behaviour.

At Monkey Bay this is a skulking species which is frequently seen feeding deep down among the rocks where it shows no territorial behaviour. On small islands away from the mainland, however, it is often far more abundant and females feed predominantly on phytoplankton while swimming in large shoals 1-2m above the bottom. On Chinyamwezi, Chinyankwazi, Mitande Rocks, Maleri and Mbenje Islands the males vigorously defend interspecific territories.

### Genus *Pseudotropheus* Regan.

This genus embraces at least 40 species varying considerably in body form, mouth form and behavioural patterns. With the exception of *Pseudotropheus zebra* (Boulenger), all members of this genus at Monkey Bay feed by pecking algae from the rock surface.

### *Pseudotropheus auratus* (Boulenger) (Figure 10).

The *P. auratus* recorded at Nkata Bay by Fryer (1959) has since been placed in *Melanochromis parallelis* (Ribbink *et al.*, in press).

Feeding.

The most common items in the diet of this elongate species is calothrix 2 (Figure 18). Individuals have also been found with high proportions of loose Aufwuchs and benthic invertebrates in their stomachs. During phytoplankton blooms they may feed on plankton in the shallows.

Distribution.

This species has a wide vertical distribution with two peaks of abundance on Thumbi East, one in the extreme shallows and one at 10m (Figure 20).

Behaviour.

P. auratus usually occurs individually but groups of 10 or more juveniles and females have been observed swimming in a shoal. The reason for this behaviour is not known. Adult males are frequently seen chasing conspecifics and it is assumed that they are intraspecifically territorial. Isolated instances of individuals exhibiting interspecific aggression on large vertical rock faces have been recorded at Monkey Bay. In addition, on one occasion when a 'P. aggressive' territory was vacated, a large P. auratus male moved into the territory and defended part of it intermittently for at least 45 minutes. In yet another case when an 'Aufwuchs garden', which was artificially developed in an exclusion chamber, was exposed by the removal of the chamber, the garden was defended by a large male P. auratus (see Figure 36). These observations indicate a potential for territoriality in this species. Although this territoriality was not strongly manifest at the two work sites studied it is possibly more fully developed elsewhere (Ribbink, pers.comm.) and deserves further study.

Individuals were frequently seen feeding just within the territory boundaries of interspecifically territorial fish. When they were observed by the territory defender they were aggressively chased. It is suspected that this species is an 'Aufwuchs robber' which gains access to territories by means of stealth or rapid approach, thus enabling individuals to feed for a short while before being chased away. Similar behaviour has been reported for marine fish and birds. For instance, Belk (1975) reports that Pomacentrus albofasciatus is a threat to the algal food source present in Pomacentrus lividus territories. This fish was often observed 'sneaking' quick bites of the lush algal growth guarded by P. lividus. Similarly, among humming birds, Eugenes fulgens feeds extensively off plants defended by Colobri thalassinus when the latter is quiescent at dawn and dusk (Colwell, 1973). While P. auratus is obviously by no means dependant upon the algae within the territories of other fishes, this may be an important supplement to its diet.

## The complex of species resembling Pseudotropheus tropheops Regan

This complex comprises a group of species which, because of the taxonomic difficulties mentioned on page 5 , have not yet been adequately classified. These species are grouped merely to emphasise similarities in the basic morphology and not to establish any formal systematic classification.

The external morphological features which characterize the group are a downward angled mouth, combined with a sharply inclined snout and enlarged unicuspid lateral teeth (Figures 11 & 12). Within the framework of these characteristics the species may differ considerably in coloration, morphology and ecology. Territoriality is common in the males and may be inter- or ~~n~~traspecific. At Monkey Bay this group is represented by four distinct species, Pseudotropheus microstoma and three undescribed species which, for the purpose of this dissertation shall be referred to as 'Pseudotropheus orange cheek', 'P. broad mouth' and 'P. dark'.

'Pseudotropheus orange cheek' (Figures 11 & 23)

'P. orange cheek' has a narrow pointed mouth, relative to most other members of the 'tropheops' group. This is particularly noticeable in the juveniles. Males of this sexually dimorphic species are brown with 6-7 slightly darker vertical bars and yellow opercular and gular regions which fade dorsally and posteriorly. The dorsal fin has yellow lappets and the anal fin has one to three orange egg dummies. Female coloration is variable but they are usually grey/brown with vertical bars discernible on the body; they have no yellow in the gular region. The dorsal fin has dark horizontal stripes and slightly yellow lappets. Juveniles may be light grey with slightly darker bars or have the female coloration.

Feeding.

Diet consists principally of calothrix 2 (Figure 16) which is nipped from the rock while the fish is orientated at approximately 45° to the rock surface.

Distribution.

Depth distributions of territorial males, females and juveniles differ markedly from one another on Thumbi East (Figure 20). This may be because non-territorial fish are partially excluded by territorial males from the depths at which they (the territorial males) are most common.

Behaviour.

Adult males and occasionally females defend interspecific territories. These territories do not develop noticeable algal gardens but do have a slightly higher standing crop of algae within the territories than on surrounding rock (see Chapter 8)

Pseudotropheus 'broad mouth' (Figure 11).

This member of the 'tropheops' group has a broad mouth and a very steeply inclined snout (Figure 11). Males have a similar coloration to 'P. orange cheek' males but differ by having more distinct barring and the orange in the gular region extends up to the dorsal fin. In females and juveniles the ground colour is light grey with seven slightly darker vertical bars. Their most striking characteristic is two horizontal rows of black spots which run the length of the body. The dorsal fin has a dark horizontal bar and light orange lappets.

Feeding.

Their diet includes the highest proportion of calothrix taken by any Monkey Bay Mbuna (Figure 18). The remainder of the stomach contents consisted of loose Aufwuchs.

Distribution.

This species is far more abundant at the Chisali site than on Thumbi East (Figure 20). It has also been recorded over rocks that occur among sand, but does not occur below 7m depth.

Behaviour.

Adult males and occasionally females hold interspecific territories.

'Pseudotropheus dark' (Figure 12).

This is an elongate, broad mouthed, 'tropheops' species with sexually dimorphic coloration. Males have a bronze/yellow ground colour on the head darkening to chocolate brown on the tail. The dorsal and caudal fins have prominent white and yellow lappets and there are two blue interorbital bars. Females and juveniles usually have yellow/white ground coloration but yellow individuals also occur. The dorsal fin has a dark horizontal bar and white and yellow lappets. The posterior portion of the dorsal fin and the entire caudal fin are covered in faint white dots; the anal fin is yellow.

Feeding.

Their principal food is loose Aufwuchs (Figure 18) which is pecked from rocks which have a visible sediment covering. Very little calothrix is taken. Occasionally benthic copepods, which live amongst the surface sediment, have been found in high concentrations in stomachs, suggesting that this species may have some mechanism for separating them from the sediment.

Distribution.

On the exposed Thumbi East site this species is confined to water deeper than 5m, but on protected shores such as Chisali, with higher sediment levels, it is also found in the shallows (Figure 20). Their range extends into the zone where rocks occur among sand.

Behaviour.

Adult males hold intraspecifically defended territories in hollows with high sediment coverage. Females may form small shoals (5-10 individuals) which feed over large open rocks with visible sediment.

## The complex of species resembling *Pseudotropheus fuscus* Trewavas.

Once again, by grouping these species under this heading, I do not imply any formal systematic classification, but only wish to stress basic similarities in their ecology and morphology. A complete taxonomic study may find that their true affinities lie elsewhere.

Members of this complex are characterised by broad, rounded to square mouths, relatively rigid jaws and closely spaced teeth. Males, females and large juveniles commonly defend interspecific territories. At Monkey Bay this group is represented by two species both of which are undescribed. They are therefore referred to as '*Pseudotropheus* aggressive' and '*Pseudotropheus* sky blue'.

### '*Pseudotropheus* aggressive' (Figures 12 & 24).

'*P.* aggressive' is an elongate fish with rigid, rounded jaws and closely set teeth which are never completely covered by the lips. Both sexes of this species are almost completely black or dark brown, but, in some, particularly males, the black is split into 5 or 6 vertical bars with blue in between. The dorsal fin is dark with blue stripes between the spines. Males and females have one or two egg dummies on the anal fin which has a blue leading edge.

Feeding.

Diet changes with age, with non-territorial juveniles taking more phytoplankton and less calothrix than territorial adults (Figure 17). This trend may be correlated with the defence of an algal garden by the adults (see below). In one instance a small fish was ingested. Considering the high standing crop of algae present in the territories of this species and in particular the length of calothrix strands (which are often considerably longer than in surrounding areas), it is surprising that the proportion of calothrix ingested by territorial fish is not higher. This may indicate a low growth rate for the particular calothrix species or community involved (calothrix 1), in which case the calothrix probably serves principally as a substrate for the growth of epilithic algae and other loose Aufwuchs. Examination of calothrix strands taken from territories shows an abundance of loose Aufwuchs. In contrast, the interspecifically territorial '_P_. orange cheek' feed almost entirely on calothrix, but of a different species (calothrix 2). This could be a result of slightly different methods of feeding (see page 119) but may also indicate a higher productivity for calothrix 2 relative to calothrix 1.

Distribution.

This species is abundant from 1 - 18m but does not occur in the extreme shallows or below 18m on Thumbi East (Figure 20). It is considerably more abundant on Thumbi East than at Chisali.

### Behaviour.

Both males and females larger than 60-65mm SL hold interspecifically defended territories. Territories of large individuals often contain thick gardens of calothrix 1 and associated algae. More will be said on the subject of their territoriality in Chapter 8.

### '<u>Pseudotropheus</u> sky blue' (Figure 13).

This undescribed species is a deep-bodied fish with a broad, rounded mouth and closely spaced teeth. Mature males are sky blue with a yellow/gold patch in the gular region. A dark interorbital bar and 6-7 vertical bars may be discernible. The dorsal fin is blue with a dark spot posteriorly while the anal fin is dark with 1-3 egg dummies. The caudal fin is blue with dark rays. Females and juveniles are brown with 6-7 vertical bars and a dark horizontal bar running the length of the body.

### Feeding.

Diet includes loose Aufwuchs, calothrix and benthic invertebrates (Figure 18). As was suggested for '<u>P</u>. aggressive', the small proportion of calothrix taken probably indicates that the long strands of calothrix defended by this species serve principally as a substrate for the growth of loose Aufwuchs.

### Distribution.

Near Monkey Bay this species is confined to the shallows of exposed shores (Figure 20) where they are commonly associated with small rocks. They are also found at Thumbi West and all the Maleri Islands where their habitat and feeding requirements are apparently identical with the Monkey Bay population (Ribbink <u>et al</u>., 1982).

Behaviour.

Males, females and large juveniles (>5,5mm SL) hold interspecifically defended territories. These territories may contain thick gardens of calothrix 1 and associated loose Aufwuchs.

## Pseudotropheus zebra (Boulenger) (Figure 13).

The P. zebra taxon at Nkata Bay which Fryer (1959) studied and considered to be one polymorphic species, has recently been shown to comprise at least two species (Holtzberg, 1978) and there may be several more (Ribbink *et al.*, in prep.). At Monkey Bay, however, only one form, the blue/black striped species, is recognised.

Feeding.

Females, immature males and non-territorial males form shoals and spend most of their time feeding on phytoplankton 1-3 metres above the bottom, but descend at intervals to feed from the rock. Since fish used for stomach content analyses were caught near the bottom, it is possible that a disproportionate number of the fish feeding from the rocks were caught for analysis, hence underestimating the proportion of phytoplankton eaten (Figure 20). In contrast, territorial males feed almost entirely on loose Aufwuchs which is brushed from the rock surface with a series of rapid 'kissing movements' (Fryer, 1959). These are executed with the mouth pressed to the rock surface and the body at right angles to it. The jaws are relatively flexible compared to other Pseudotropheus species, thus facilitating the collection of loose Aufwuchs by allowing the tooth band to mould to the shape of the rock surface (Fryer, 1959).

Distribution.

They are most abundant in deep water and do not venture into the extreme shallows of the exposed Thumbi East shore (Figure 21).

Behaviour.

Mature males may hold small territories (0,47 ± 0,039m$^2$) from which conspecifics are excluded. These territories always appear to contain a hole which serves as a shelter or spawning site.

Genus Petrotilapia Trewavas (Figure 14).

Although Petrotilapia was originally considered to be a monospecific genus, it has recently been shown (Marsh et al., 1981) that there are three species at Monkey Bay, and possibly an additional fourteen species elsewhere in the lake. For the purpose of this thesis no attempt is made to distinguish between these species as they have not as yet been formally described.

Feeding.

These species are characterised by their many elongate tricuspid teeth which are arranged in multiple rows to form brushes on both jaws. The manner of feeding is the same as that used by P. zebra and the diet consists of loose Aufwuchs and invertebrates (Figure 18). Small individuals may take phytoplankton when it is plentiful.

Distribution.

Although the genus as a whole is most abundant in the shallows (Figure 21) each species has a different depth distribution (Marsh, 1981). In calm weather large numbers of females and juveniles

feed in the extreme shallows. The majority of these are forced into deeper water when the surface waters are turbulent (Tables 5).

Behaviour.

Males hold large territories (up to 40m$^2$) which are defended principally against conspecifics. These territories overlap those of other Petrotilapia species and all other Mbuna species (Marsh, 1981).

By virtue of their large size, adult males are able to enter and feed in the territories of the four interspecifically territorial species, and make full use of this ability (Marsh, 1981). Females seldom feed in these territories as individuals, but may form large feeding schools (often more than 100 individuals) which descend on a territory, swamping the aggressive action of the owner. This shoaling behaviour ceases for short periods of the year (possibly due to breeding activity) and has only been observed on exposed shores near Monkey Bay and on Thumbi West.

Similar behaviour has been recorded among many coral reef fish (Barlow, 1974; Vine, 1974; Belk, 1975; Brawley & Adey, 1977; Robertson et al., 1979) where it is considered to be a mechanism for circumventing the territoriality of competitors and to gain access to defended areas. Schooling in Petrotilapia probably serves a similar function. Other possible functions which schooling may serve include defence from predators (Neill & Cullen,1974; Pitcher,1973; Seghers,1974), the mechanical advantages gained by fishes swimming in schools (Belyayev & Zuyev,1969) and facilitation of reproductive activities and migration (Shaw, 1970). None of these advantages are applicable to Petrotilapia schooling because they are relatively large fish and in little danger from predators, at least diurnally. They spend most of their time feeding and when they do swim as a school it is slowly and in a long, drawn out line thus making it unlikely that they gain any mechanical advantage. Finally, no reproductive behaviour was observed apart from occasional, apparently unsuccessful, courtship attempts by males whose territories were entered.

Genus Labeotropheus Ahl.

The two species which belong to this genus, L. fuelleborni and L. trewavasi, differ principally in their body depth/length ratio. Only the deep bodied species, L. fuelleborni, occurs at Monkey Bay.

L. fuelleborni Ahl (Figure 14).

Feeding

The mouth of this species is ventrally situated and the jaws are broad and square with closely set teeth forming opposing knives (Fryer, 1959) (Figure 14). Feeding involves a series of nibbles, executed while the fish moves slowly forwards with the mouth pressed to the rock surface and the body at an angle of 30 to 40° from it. Diet is predominantly loose Aufwuchs and calothrix 2 (Figure 18), which confirms the findings of Fryer (1959) at Nkhata Bay.

Distribution.

L. fuelleborni is predominantly an extreme shallow and shallow water species (Figure 21), but has been recorded down to 15 metres on Thumbi East. Juveniles form mixed feeding shoals with 'P. orange cheek' juveniles in the extreme shallows (Figure 22).

Behaviour.

Males hold territories from which conspecifics and, very occasionally, other species are chased. By virtue of their large size these males may feed in the territories of small '*P*. aggressive' individuals but are excluded from those of other interspecifically territorial fish. Non-territorial males and possibly territorial males occasionally join *Petrotilapia* species feeding schools and thus gain access to the territories which the schools enter.

Genus *Labidochromis* Trewavas.

Only one member of this genus, *L. vellicans*, occurs at Monkey Bay. This is not the same species which Fryer (1959) called *Labidochromis vellicans* at Nkhata Bay; the latter is now being re-described by Dr D. Lewis.

*L. vellicans* Trewavas (Figure 15).

Feeding.

This small species has a very narrow mouth and elongate unicuspid teeth which are arranged to form a pincer-like feeding structure. Fryer (1959) found that both *Labidochromis* species at Nkhata Bay, the undescribed species and *L. caerullius*, feed almost entirely on benthic invertebrates and commented that the pincer-like feeding structure was admirably suited to plucking these from the Aufwuchs mat. In contrast, *L. vellicans*, which has an almost identical feeding structure to the Nkhata Bay species, rarely ingested invertebrates at any time of the year at Monkey Bay. Instead the principal food item was calothrix 2 (Figure 18*).

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* Analysis of stomach contents of *L. caerulius* and the undescribed *Labidochromis* collected during a field trip to Nkhata Bay in May 1978 confirmed that *D. caerulius* is an invertivore but revealed that the undescribed species is herbivorous at this time of year with a diet almost identical to *L. vellicans* i.e. principally calothrix 2 (Ribbink *et al.*, in prep.).

Distribution.

This species is most common in the shallows of exposed shores (Figure 21) where it mixes with the shoals of juvenile 'Pseudotropheus orange cheek' and Labidochromis fuelleborni.

Behaviour.

Individuals are frequently seen swimming in pairs. One pair was caught and proved to be a male and female. As far as can be ascertained they are non-territorial.

## DISCUSSION

The aim of this discussion is to present an overall picture of resource subdivision among the guild members at Monkey Bay. Particular attention is directed at possible mechanisms of resource subdivision acting within the guild.

### Feeding, opportunistic or specialized?

The feeding habits of this guild are best described as 'opportunistic'. The major food resource is Aufwuchs, and, although there is an annual fluctuation in abundance (see ' The Food Resource'), this resource can be relied upon to be present at all times. Whether it is present in sufficient quantities to be considered superabundant is discussed in the final chapter. As was mentioned previously, the seasonal variations in stomach content compositions are small, which suggests that, as far as the utilization of the Aufwuchs food resource is concerned, the guild members are not opportunistic but have a distinct feeding niche. It is when a transient food supply is available that their opportunistic nature becomes evident. This has been demonstrated on several occasions.

The most common transient food supply is phytoplankton, of which dense blooms may occur at Monkey Bay in winter. During these blooms many guild species feed in the water column, and stomach content analyses of these fish confirm that they are feeding on phytoplankton. The distance above the bottom at which the fish feed varies with the species. Shoals of Pseudotropheus zebra commonly feed up to 4m from the bottom where they congregate in large loosely cohesive shoals which may number several hundred fish. These shoals are not stationary but move through the water column as they feed. In contrast, *C. taeniolatus* adults do not shoal as they feed on phytoplankton but hover more or less stationary 1-2m above the bottom. Juveniles of this species may, however, form small shoals (5-15 individuals) which congregate 10-20cm above high rocks while feeding on phytoplankton. The remaining species which may feed directly on phytoplankton but seldom move more than a metre from the rock include: *M. vermivorous*, *Pseudotropheus auratus*, '*P. aggressive*', juvenile *Petrotilapia* species and *L. vellicans*. But content analyses of fish caught when phytoplankton blooms are not present suggest that *Pseudotropheus zebra* and possibly *M. vermivorous* are the only guild members which feed on phytoplankton under these conditions.

Further evidence of the opportunistic nature of feeding is found when extra food is artificially supplied. For instance, occasionally a mouthbrooding female swam into the catch net and released her brood during the ensuing struggle. The released eggs or fry were always rapidly snapped up by other fish in the vicinity. Similarly when a territorial fish is removed a mass of fish descend and graze on the undefended algal mat (Chapter 8).

### Food Resource Subdivision

Returning to the utilization of the Aufwuchs resource, the present study revealed very little food subdivision (as evident from stomach content analyses), other than that found by Fryer (1959) for the Nkhata Bay species. When one considers the nature of the Aufwuchs food resource it is not surprising that so little specialization in diet has occurred since the various components of the Aufwuchs are associated in such a way that it is inevitable that in collecting one component (e.g. calothrix) elements of others will also be taken (e.g. loose Aufwuchs). The possibility remains that the food resource is subdivided by other mechanisms such as microhabitat, zonation within the habitat or territoriality. These are considered below.

Subdivision by microhabitat

Consider first those species which feed predominantly on Loose Aufwuchs. These may be divided into those which brush their food from the rock (L. cylindricus, Pseudotropheus zebra and Petrotilapia species) and those which peck it from the rock (C. taeniolatus, M. vermivorous, 'Pseudotropheus dark', 'P. agressive','P. sky blue'). Those which brush are assumed to have the ability to collect loose Aufwuchs from between calothrix strands. This is particularly likely for the Petrotilapia species because of their long, flexible teeth; on the other hand it is unlikely that peckers can collect loose Aufwuchs from between calothrix strands without taking the calothrix itself since their teeth are short and immobile. The latter are therefore expected to be feeding on that loose Aufwuchs and sediment lying free on top of the rock and the calothrix. If this is occuring it could well result in a degree of ecological segregation between these two groups of species.

Among the calothrix feeders it is apparent that mouth width may play an important role in resource subdivision. For example, consider the juveniles of 'Pseudotropheus orange cheek' and L. fuelleborni which feed side by side in dense shoals in the extreme shallows. Both feed principally on loose Aufwuchs and calothrix 2 (Figure 16 & 18 but the relative proportions taken are different. However, their methods of feeding differ. 'P. orange cheek' has a narrow mouth (Table 4) with which it apparently pecks its food from small interstices on the rock surface, L. fuelleborni, on the other hand, has a very broad mouth(Table 4) which will prevent access to narrow interstices. They therefore feed from exposed convex faces between the interstices thereby effecting resource subdivision.

This theory was tested by comparing the number of feeding 'P. orange cheek' and L. fuelleborni on very smooth (few interstices) and very rough (many interstices) rock. Two horizontal rock slabs, one rough and one smooth, were selected and their texture was quantified with the aid of plastic templates (see Figure 25 for a diagram and explanation and Table 6 for results). A 1,5 x 3,0m quadrate was then laid on each face and the number of 'P. orange cheek' and L. fuelleborni within the quadrates was counted six times each over a period of one hour. The results (Table 7) show that slightly fewer L. fuelleborni occurred on the rough rock relative to the smooth rock and hardly any 'P. orange cheek' fed on the smooth rock while large numbers utilized the rough rock. Both differences are statistically significant ($P > 0{,}01$). This suggests that 'P. orange cheek' is dependant on interstices for its food whilst L. fuelleborni may feed from convex and other exposed surfaces.

## Subdivision by Zonation

Further food subdivision may occur by the guild species feeding in different habitat zones. Although Fryer (1959) was aware of differences in depth distributions of the fish at Nkhata Bay, he was unable to quantify their distribution as was done here using SCUBA. Three environmental parameters were found to influence the habitat utilization of the epilithic algal grazing species: wave action, water depth (and associated sediment changes) and rock size. These are considered below.

Censuses of fish feeding in the extreme shallows were made during rough and calm weather to examine each species' ability to tolerate wave action (Table 5). Only one species, Barbus johnsoni, was equally common in calm and rough weather. B. johnsoni has an underslung mouth and feeds by scraping its jaw with its cartilaginous lower lip while swimming swiftly forwards. Due to this ability to feed while swimming, B. johnsoni is able to move up with the waves and even feed above the calm water level of the lake. In contrast, L. vellicans, which has a similar diet to B. johnsoni is almost entirely excluded from the extreme shallows during rough weather yet is relatively common during calm weather. 'P. orange cheek' and L. fuelleborni fall between these two extremes for, although they are not excluded from the extreme shallows during rough weather, their distributions are displaced downwards (Figure 22). The morphological feature which results in this difference between L. vellicans and the latter two species is thought to be the angle at which the body is orientated while feeding. 'P. orange cheek' and L. fuelleborni have downward angled mouths and feed with the body between 30-45° from the rock. During rough weather they move with the swell and are able to feed during a lull because the body is almost in the feeding position at all times and hence can be rapidly brought into the feeding stance to make use of even short lulls in the turbulence. Furthermore the low body angle at which these species feed allows them to hold their position against a moderate current by swimming, even when feeding. This is not possible for L. vellicans which feed in an almost vertical position. That the downward angled mouths of

'P. orange cheek' and L. fuelleborni are adaptations to turbulent conditions and not a result of some other selection pressure is suggested by the presence of the same adaptation in the acanthurid Acanthurus achilles. Jones (1968) reports that this common surge zone fish has a more steeply inclined mouth than acanthurids from deeper water.

As might be expected the majority of species have their peak densities in the shallows or extreme shallows, hence there is little ecological segregation by depth. However, two species, P. zebra and 'P. dark', have peak densities in water 10m or deeper on Thumbi East. This may afford them ecological segregation from the three Petrotilapia species and L. fuelleborni which have similar diets and broad mouths but occur principally in the shallows.

It is interesting to compare the depth distributions on the exposed Thumbi East site and the sheltered Chisali site. The kite diagram for a given species is often similar for both shores except that where on Thumbi East they are spread over 20m, at Chisali they are compressed into 10m (Figures 19-21). That this concertina affect is merely a result of the narrow width of the rock band at Chisali is unlikely. A more practical theory is that fish abundance is related, not to depth, but to sediment levels. As mentioned in Chapter 3, sediment increases with depth and high sediment levels are reached at a shallower depth on Chisali than on Thumbi East.

Apart from the concertina affect, some species are relatively more abundant at one site than the other. For example, 'P. sky blue' is only found on Thumbi East while 'P. broad mouth' is most abundant at Chisali. These distributions are probably also a result of different sediment levels resulting from different exposures of the shores to wind. Some segregation by this means is also apparent between the three Petrotilapia species (Marsh, 1981).

The localisation of the territories of '*Pseudotropheus* sky blue' to areas of small rock (see Chapter 8) suggests that rock size may also affect species distribution. This possibility was not followed up for the non-territorial species.

## Subdivision by Territoriality

A great variety of behaviour patterns of potential importance to ecological segregation have been reported in the annotated list. Of obvious significance among these are schooling (*B. johnsoni*, *Pseudotropheus zebra*, and *Petrotilapia* species) and territorial behaviour. Only the interspecifically defended territories of '*Pseudotropheus* orange cheek', '*P.* broad mouth', '*P.* aggressive' and '*P.* sky blue' may result in interspecific resource subdivision. One other species, *C. taeniolatus*, defends interspecific territories but this behaviour is restricted principally to the breeding season and may serve a breeding function only.

Among the remaining species, males of the following are known to defend intraspecific territories: *Pseudotropheus zebra*, '*P.* dark, *Petrotilapia* (3 species) and *L. fuelleborni*. Other possible territorial species are *Pseudotropheus auratus* and *L. cylindricus*. Whereas interspecific territories are non-overlapping, intraspecific territories may overlap with territories of other intraspecifically territorial species but not with those of conspecifics or interspecifically territorial species (Figure 26). The territories of male *Petrotilapia* are an exception to this since they overlap the territories of '*P.* orange cheek' and '*P.* aggressive' in which they feed.

It is evident from the above discussion that as an alternative to diet specialization, the members of the Monkey Bay epilithic algal grazing guild may achieve ecological segregation by the three categories of resource subdivision listed in the literature review i.e. by microhabitat utilization, zonation within the rocky shore habitat and by territoriality. There is no way of telling if the segregation resulting from these alone is sufficient for the continued coexistence of these fish. There may be other means of resource subdivision which have been overlooked and as yet our understanding of ecological communities is such that we are not even sure if ecological segregation is necessary for coexistence (for instance, see Roughgarden, 1974 and Sale, 1977). Nonetheless, these observations are important in that they present a realistic alternative to Fryer's superabundance hypothesis (Fryer, 1959) for explaining how the epilithic algae grazing fish coexist. Furthermore, the study provides support for the suggestion made by Smith & Tyler (1973) that how and where a fish feeds may be more important than on what it feeds.

## Table 4

Morphological measurements of the members of the epilithic algae grazing guild at Monkey Bay.

* These measures estimated only.

| Species | Max.SL Female (mm) | Max.SL Male (mm) | Max. mouth Width (mm) | Mouth width/SL |
|---|---|---|---|---|
| *Barbus johnsoni* | 250* | 250* | 16,8 | 0,0818 |
| *Labeo cylindricus* | 190* | 190* | 21,5 | 0,1065 |
| *Cyrtocara taeniolatus* | 90 | 102 | 8,4 | 0,0834 |
| *Melanochromis vermivorous* | 69 | 74 | 8,7 | 0,1121 |
| *Pseudotropheus auratus* | 80 | 80 | 7,8 | 0,0986 |
| *Pseudotropheus zebra* | 81 | 91 | 10,5 | 0,1113 |
| '*Pseudotropheus* orange cheek' | 95 | 105 | 11,2 | 0,0937 |
| '*Pseudotropheus* broad mouth' | 84 | 91 | 10,9 | 0,1205 |
| '*Pseudotropheus* dark' | 88 | 91 | 9,2 | 0,1055 |
| '*Pseudotropheus* aggressive' | 84 | 100 | 11,0 | 0,1139 |
| '*Pseudotropheus* sky blue' | 72 | 82 | 10,5 | 0,1244 |
| *Petrotilapia* species | 118 | 129 | 18,2 | 0,1384 |
| *Labeotropheus fuelleborni* | 87 | 100 | 11,9 | 0,1389 |
| *Labidochromis vellicans* | 60 | 67 | 5,7 | 0,0808 |

Table 5

Density of fish in the extreme shallows (<1m) on Thumbi East in calm and rough weather. Each estimate is calculated from the mean of 6 counts, 3 in each of two transects. No. Indiv. gives the total number of individuals of that species counted in all 6 censuses. For data on '*Pseudotropheus* orange cheek' and *Labeotropheus fuelleborni* see Figure 22.

| Species | Number (100m$^2$ ± 1 SE) | | |
|---|---|---|---|
| | Calm | Rough | No. Indiv. |
| *Barbus johnsoni* | 47,2 ± 3,6 | 94 ± 5,6 | 472 |
| *Cyrtocara taeniolatus* | 17,2 ± 4,8 | 14 ± 3,2 | 114 |
| *Melanochromis vermivorous* | 23,2 ± 5,2 | 6,8 ± 0,8 | 101 |
| *Pseudotropheus auratus* | 30,8 ± 4,4 | 5,2 ± 0,8 | 121 |
| *Petrotilapia* species | 84 ±13,2 | 22,8 ± 5,6 | 375 |
| *Labidochromis vellicans* | 68 ± 7,6 | 9,2 ± 1,6 | 266 |

## Table 6

Mean number of interstices (± 1 S.E.) per 30 cm:A, into which a template the shape and size of a 50-60 mm SL *Labeotropheus fuelleborni* mouth would not fit and, B, into which a template the shape and size of a 50-60 mm SL '*Pseudotropheus* orange cheek' would not fit. Counts were made along ten randomly placed 30 cm transects on both the rough and the smooth rock used in the experiment described on page 67. For a diagrammatic illustration of the templates used see Figure 25.

| | Rough Rock | Smooth Rock |
|---|---|---|
| A | 29,4 ± 1,6 | 3,4 ± 0,6 |
| B | 5,5 ± 0,76 | 0,3 ± 0,16 |

## Table 7

Mean number of individuals per 100 $m^2$ (± 1 S.E.) feeding on rough and smooth rock in 1,3 - 1,6 m of water. These data were calculated from 6 replicate counts in each of two 3 x 1,5 m quadrates, one quadrate on each rock type.

| | Rough Rock | Smooth Rock |
|---|---|---|
| *Labeotropheus fuelleborni* | 93 ± 12 | 138 ± 17 |
| '*Pseudotropheus* orange cheek' | 493 ± 25 | 27 ± 7,5 |

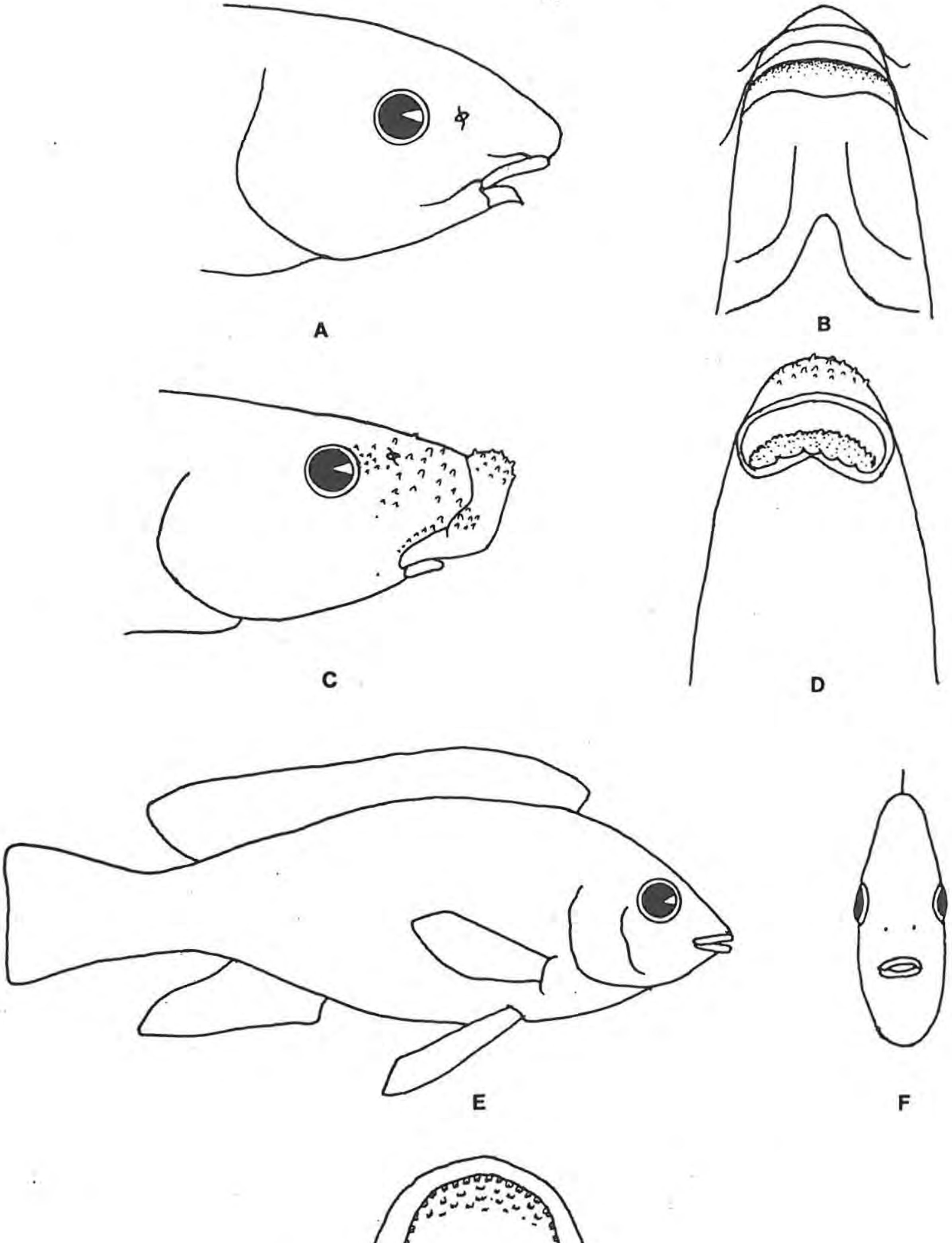


Figure 9. Diagrammatic illustrations to show lateral (A) and ventral (B) views of the head of Barbus johnsoni, lateral (C) and ventral (D) views of the head of Labeo cylindricus; lateral (E) and frontal (F) views and upper jaw and teeth (G) of Cyrtocara taeniolatus.

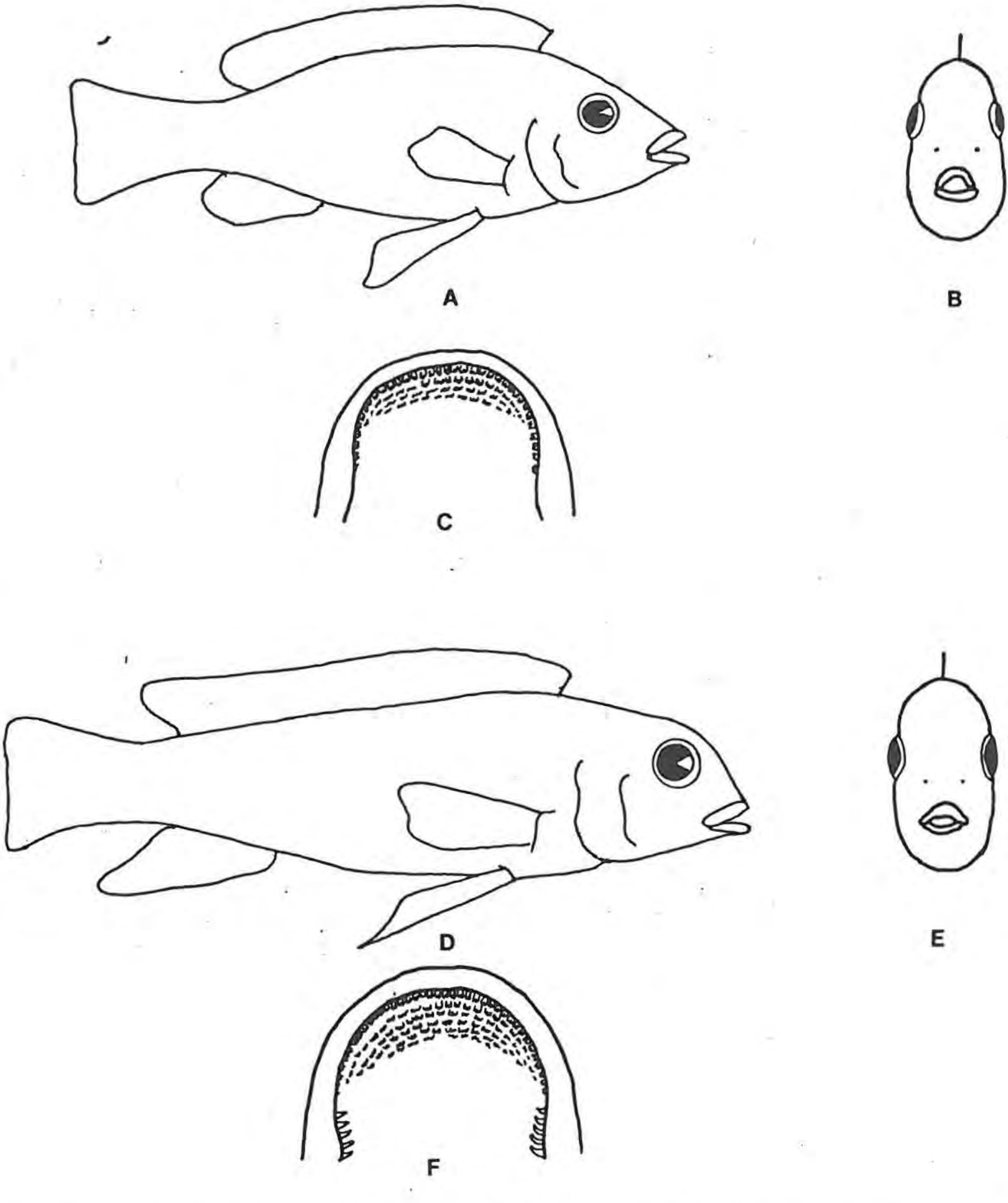


Figure 10. Diagrammatic illustration to show lateral (A) and frontal (B) views and upper jaw and teeth (C) of *Melanochromis vermivorous* and lateral (D) and frontal (E) views and upper jaw and teeth (F) of *Pseudotropheus auratus*.

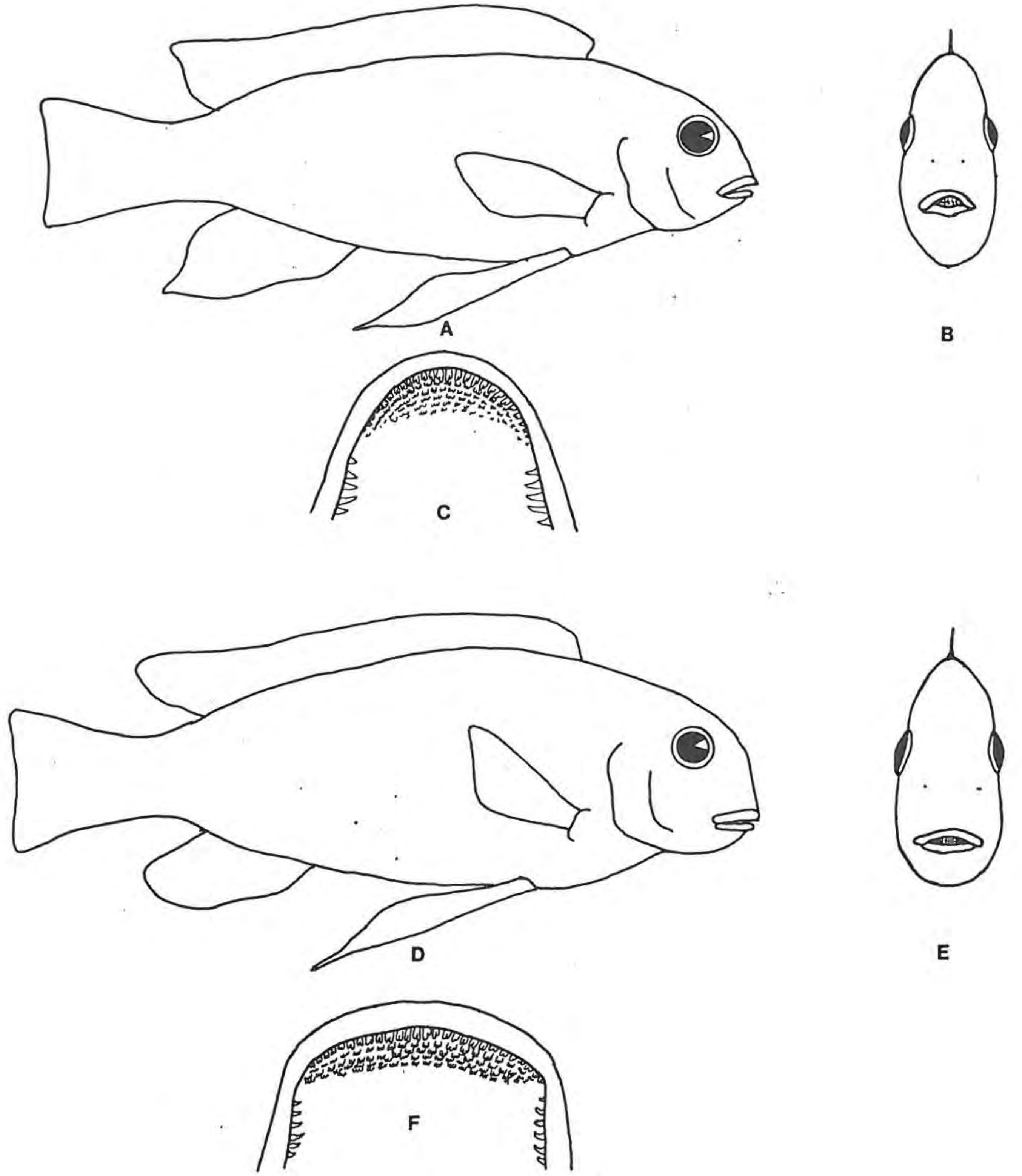


Figure 11. Diagrammatic illustrations to show lateral (A) and frontal (B) views and upper jaw and teeth (C) '*Pseudotropheus* orange cheek' and lateral (D) and frontal (E) views and upper jaw and teeth (F) of '*Pseudotropheus* broad mouth'.

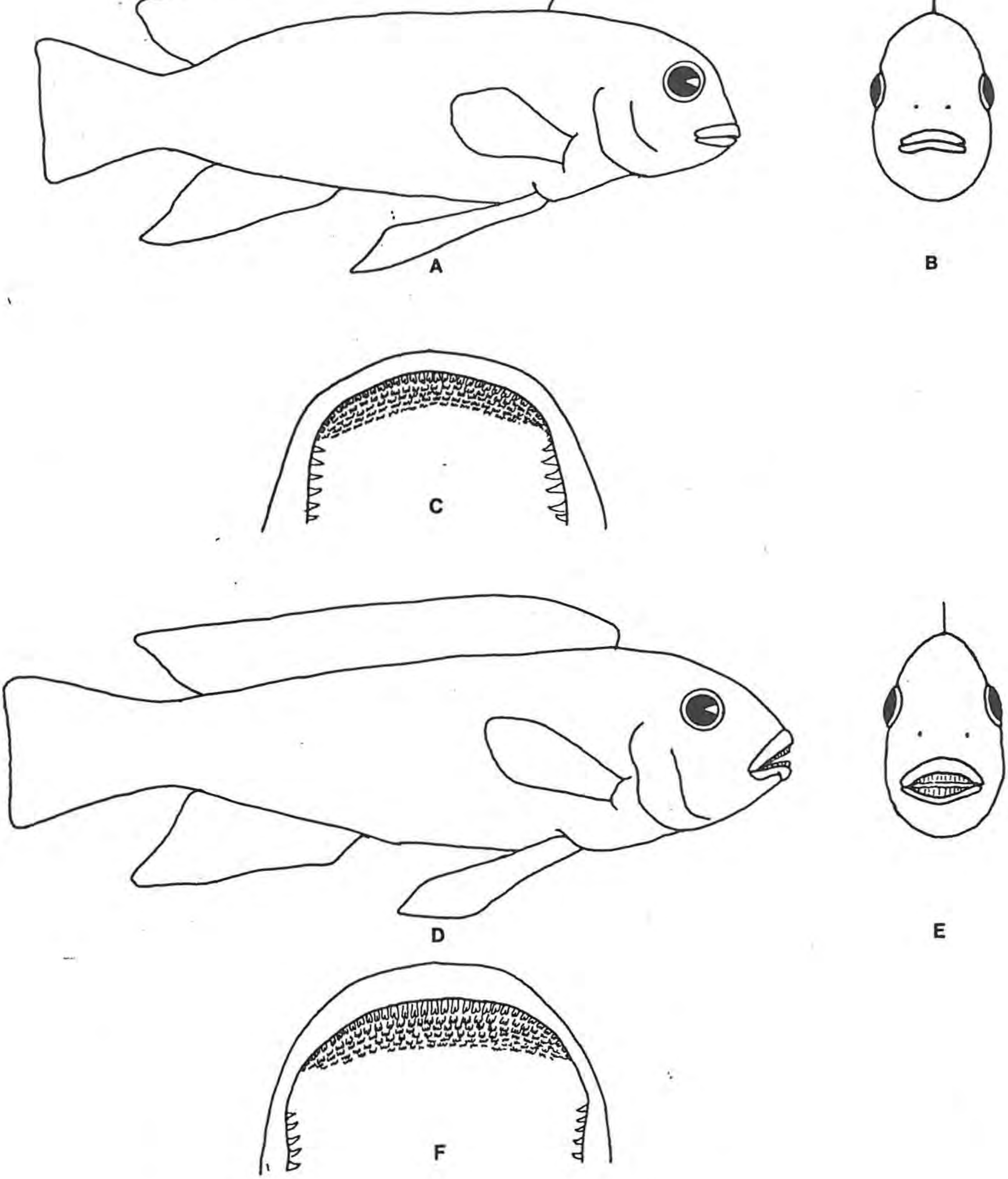


Figure 12. Diagrammatic illustrations to show lateral (A) and frontal (B) views and upper jaw and teeth (C) of '<u>Pseudotropheus</u> dark' and lateral (D) and frontal (E) views and upper jaw and teeth (F) of '<u>Pseudotropheus</u> aggressive'

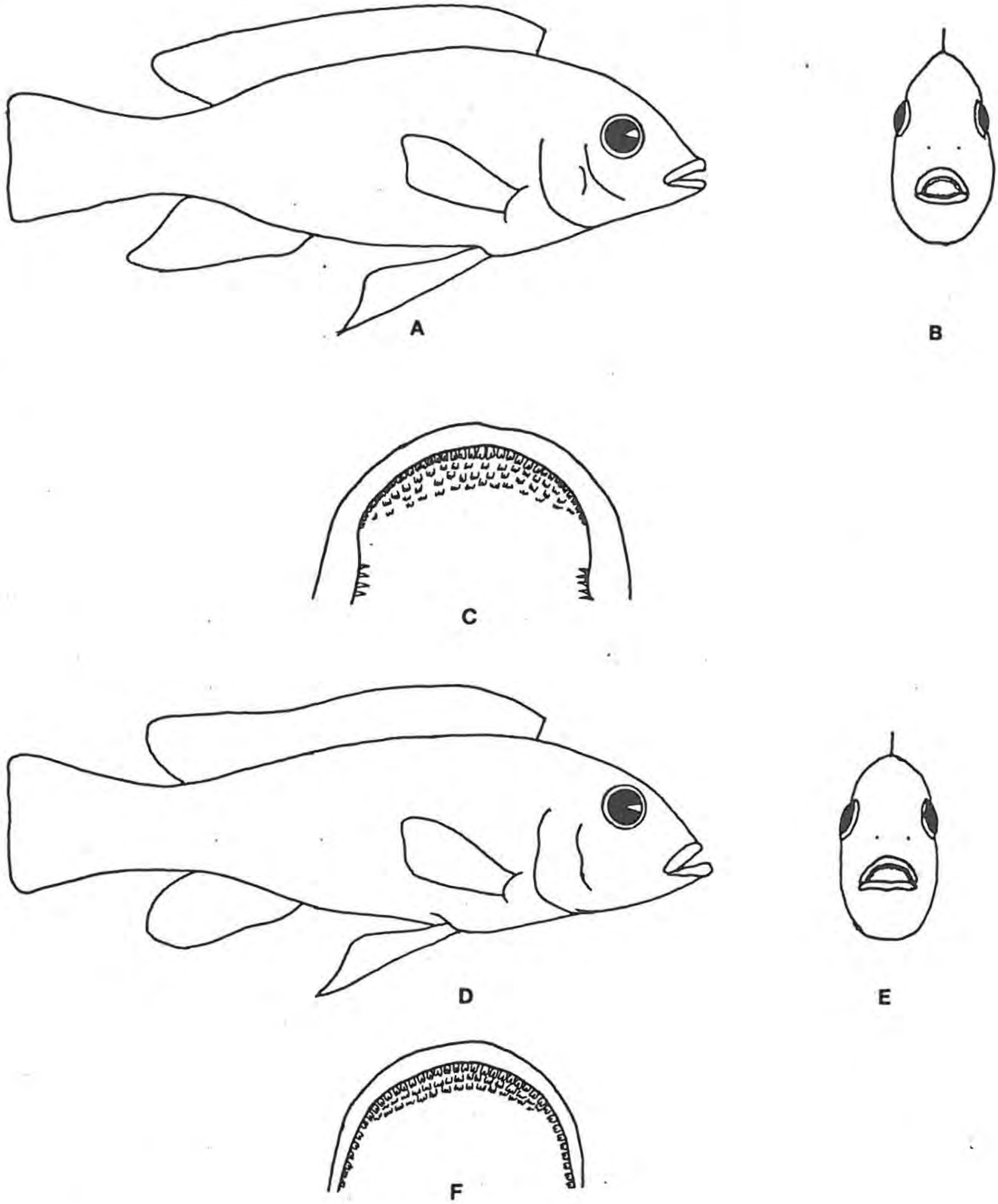


Figure 13. Diagrammatic illustrations to show lateral (A) and frontal (B) views and upper jaw and teeth (C) of 'Pseudotropheus sky blue' and lateral (D) and frontal (E) views of upper jaw and teeth(F) of Pseudotropheus zebra.

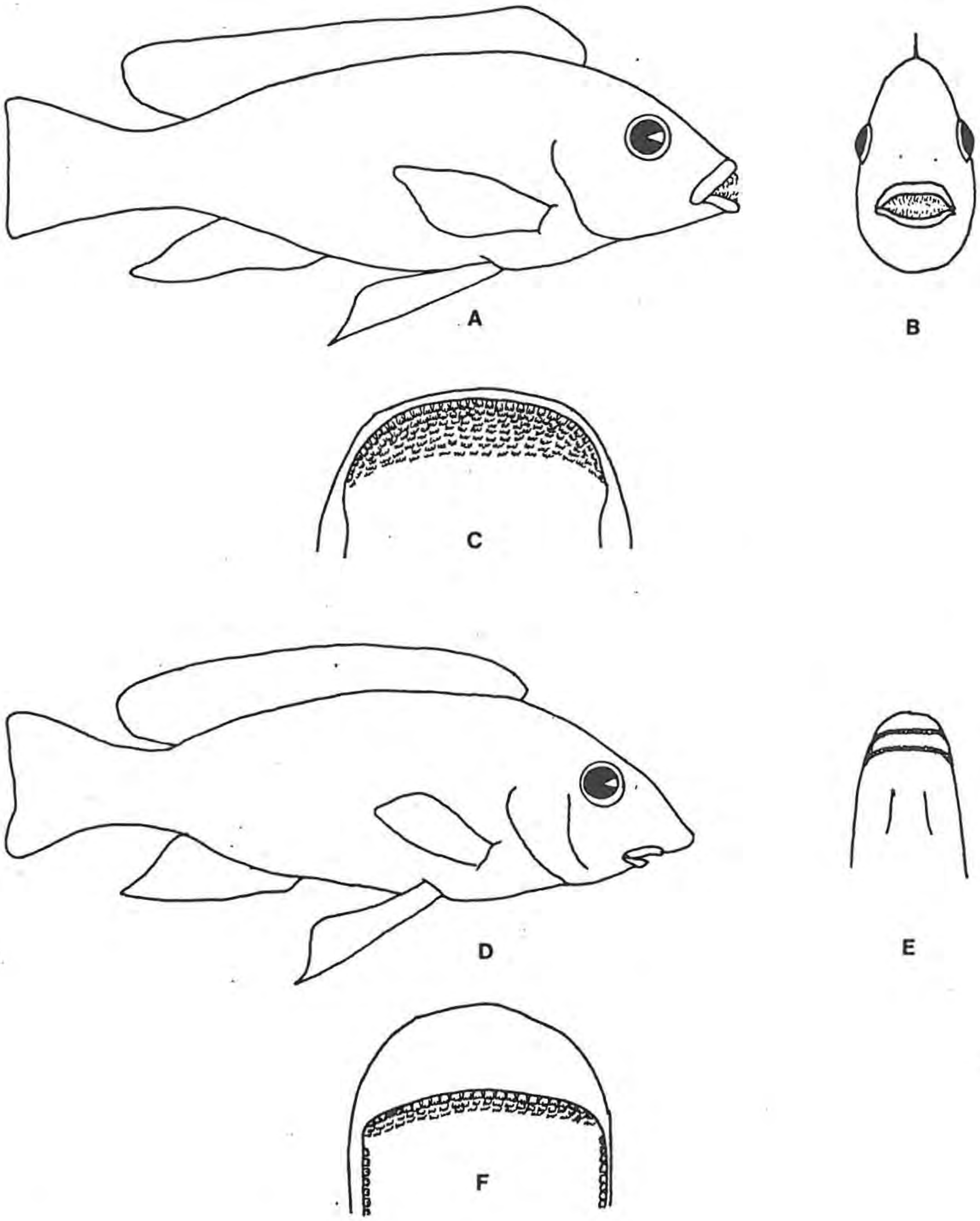


Figure 14. Diagrammatic illustrations to show lateral (A) and frontal (B) views and upper jaw and teeth (C) of a typical Petrotilapia specie and lateral (D) and frontal (E) views and upper jaw and teeth (F) of *Labeotropheus fuelleborni*.

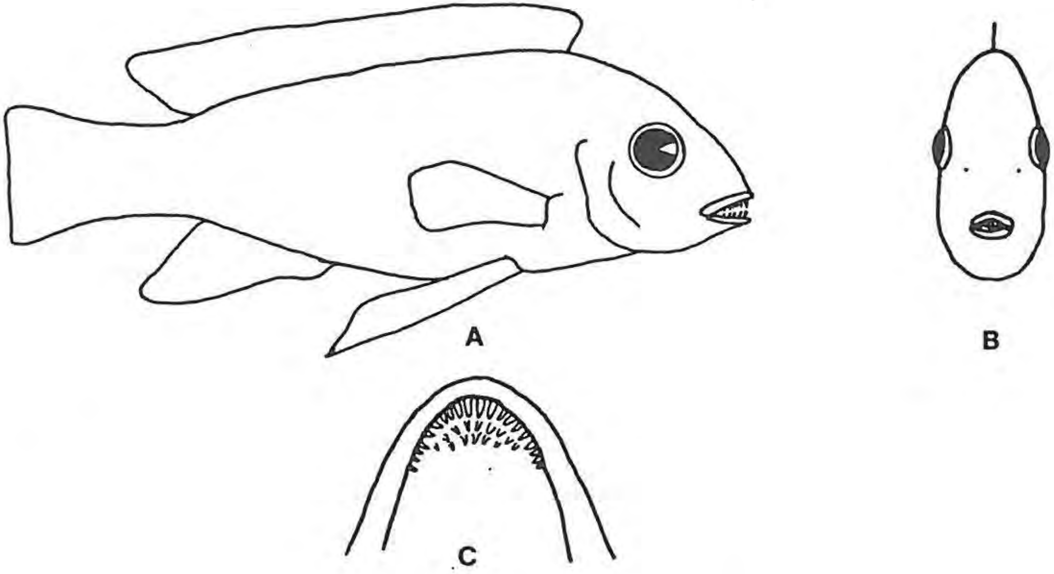


Figure 15. Diagrammatic illustration to show lateral (A) and frontal (B) views and upper jaw and teeth (C) of Labidochromis vellicans.

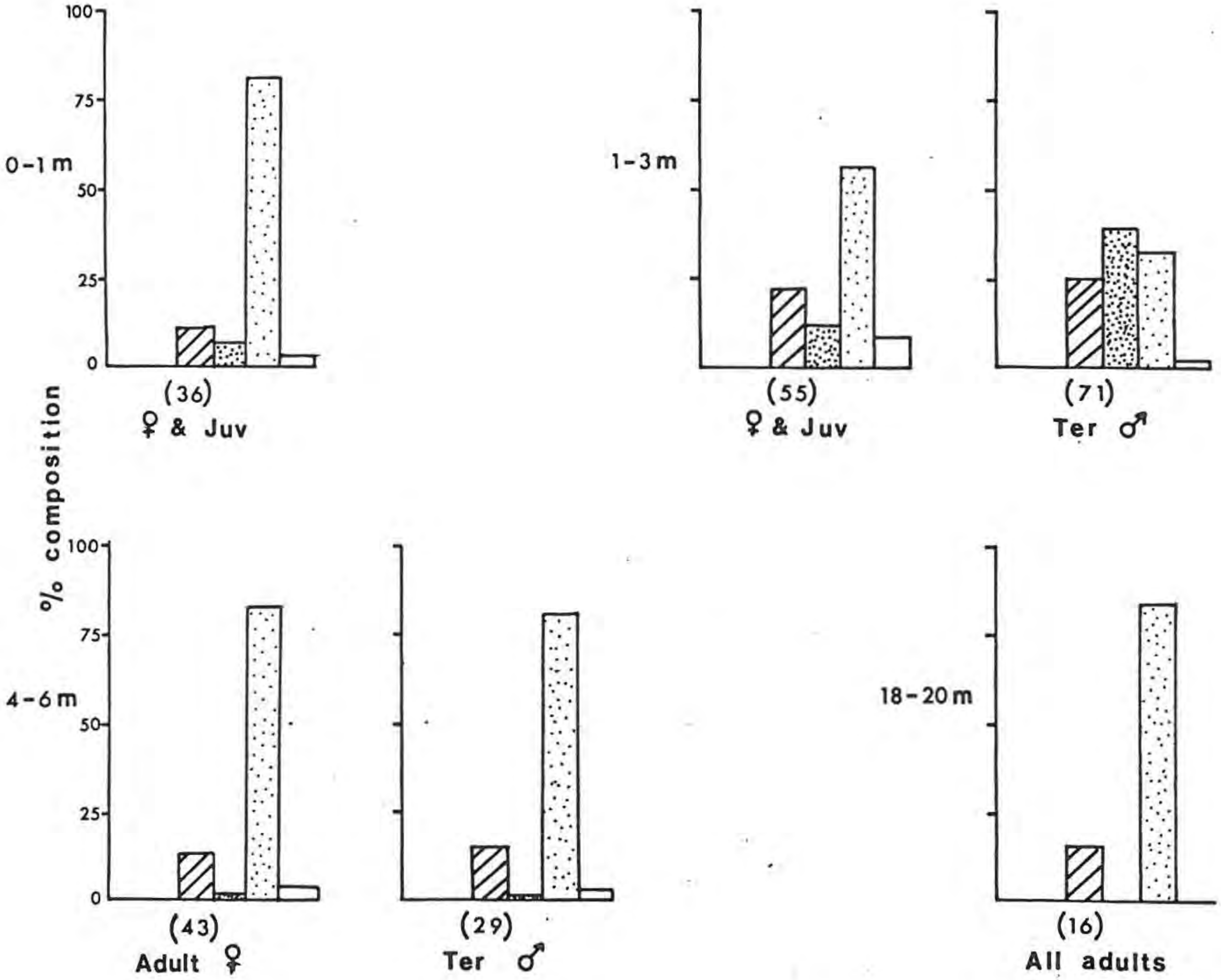


Figure 16. Composition of stomach contents of 'P. orange cheek' at different depths ▨ = loose aufwuchs; ▒ = calothrix$_1$; ░ = calothrix 2; □ = benthic invertebrates. SL = Standard Length. 'n' is given in brackets.

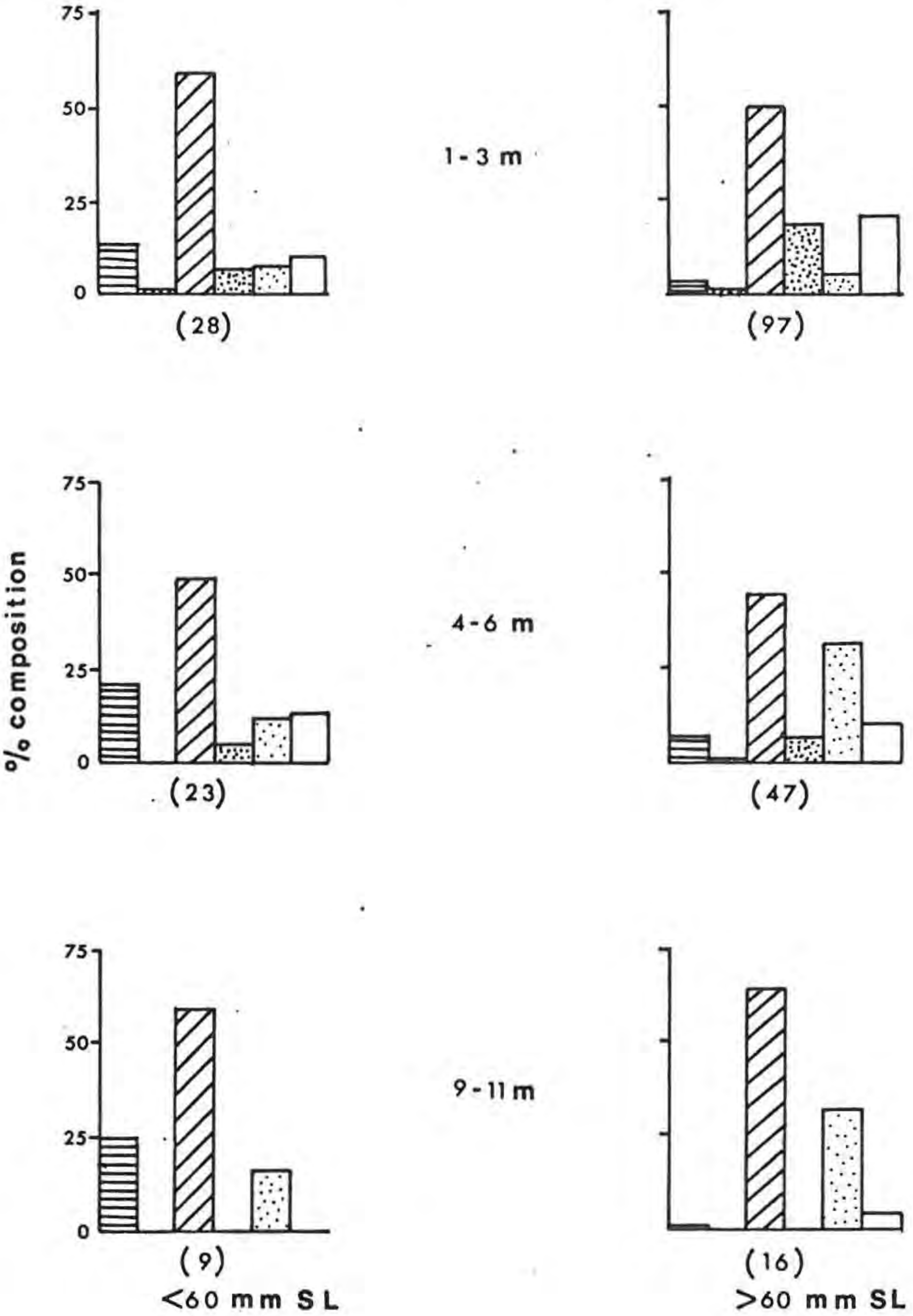


Figure 17. Composition of the stomach contents of 'P. aggressive' for different size classes and at different depths. ▤ = phytoplankton; ▥ = zooplankton; ▨ = loose aufwuchs; ▦ = calothrix 1; ⬚ = calothrix 2; □ = benthic invertebrates; SL = Standard Length. 'n' is given in brackets. Only 'P. aggressive' >60 mm SL are territorial.

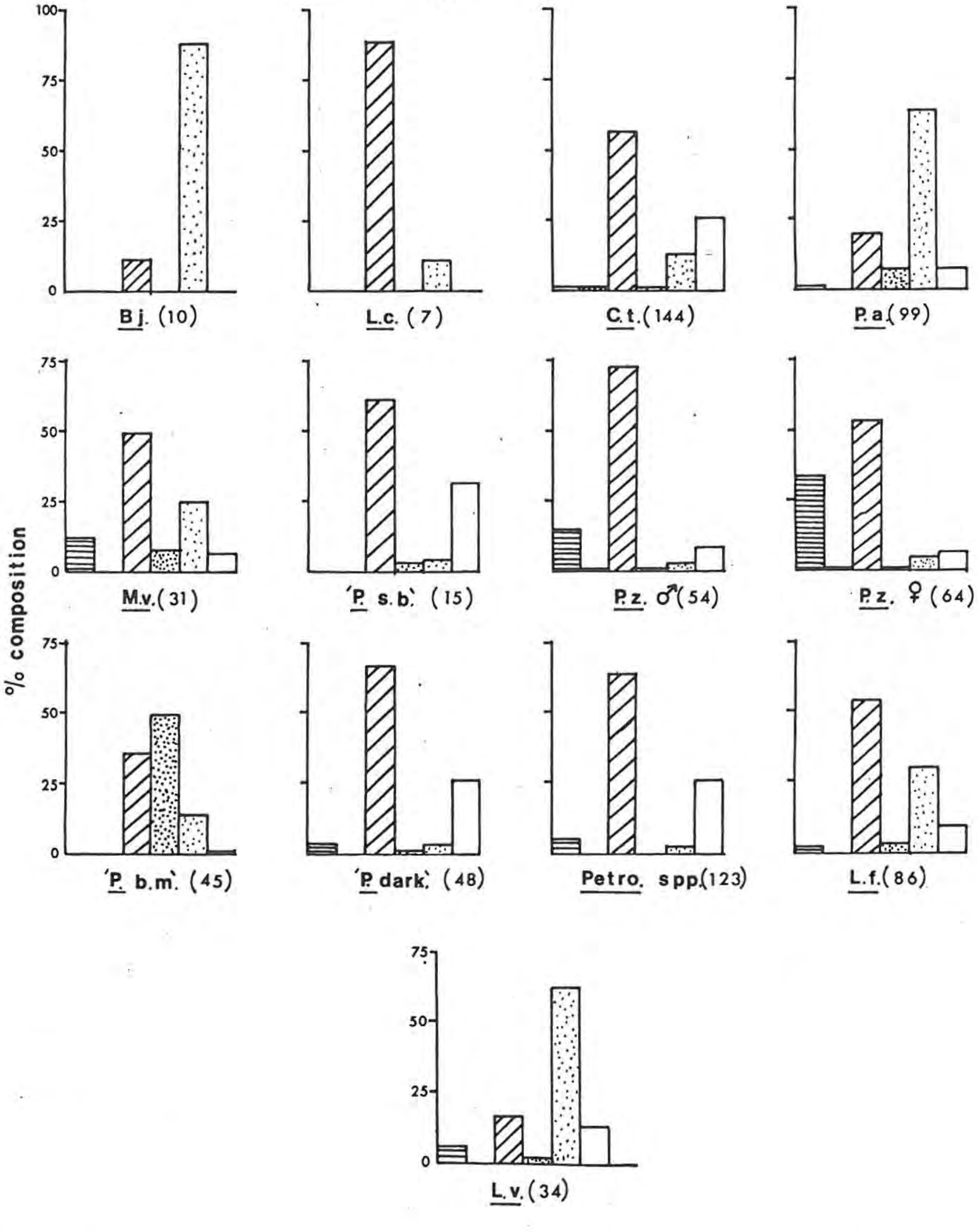


Figure 18. Composition of the stomach contents of the epilithic algae grazing species at Monkey Bay. Samples from all depths and sites are combined. ▤ = phytoplankton; ▥ = zooplankton; ▨ = loose Aufwuchs; ▒ = calothrix 1; ░ = calothrix 2; □ = benthic invertebrates. B.j = *Barbus johnsoni*; L.c = *Labeo cylindricus*; 'P. s b' = 'P. sky blue'; P.z. = *P. zebra*; 'P. b m' = 'P. broad mouth'; Petro. spp. = combined data from the three *Petrotilapia* species; L.f. = *Labeotropheus fuelleborni*; L.v. = *Labidochromis vellicans*. 'n' is given in brackets.

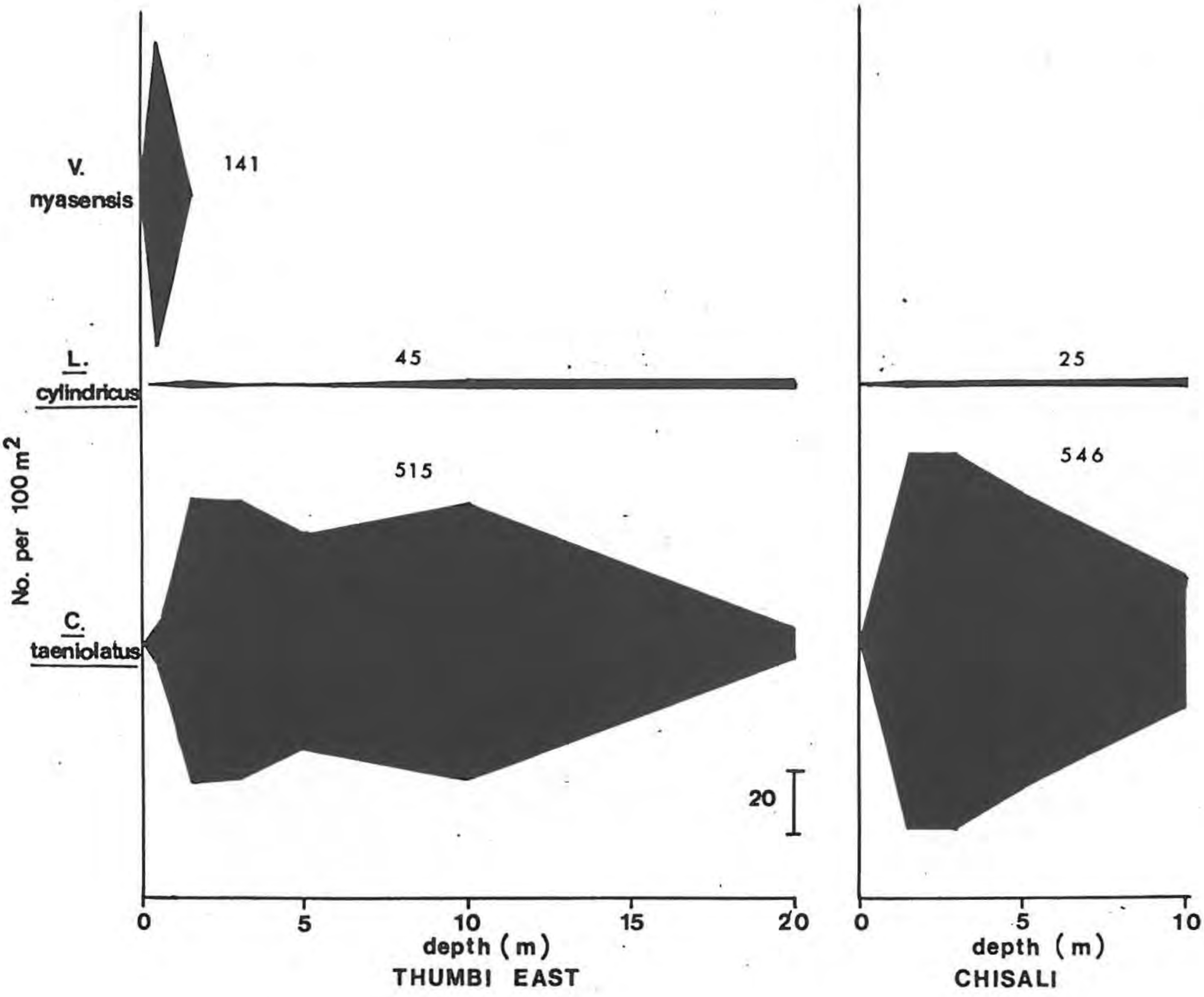


Figure 19. Depth distributions of the cyprinids, Barbus johnsoni and Labeo cylindricus and the cichlid, Cyrtocara taeniolatus, at the two work sites near Monkey Bay. The number adjacent to each diagram is the total number of individuals of that species counted at that site. All counts in 0,5m of water at Thumbi East were made in rough weather.

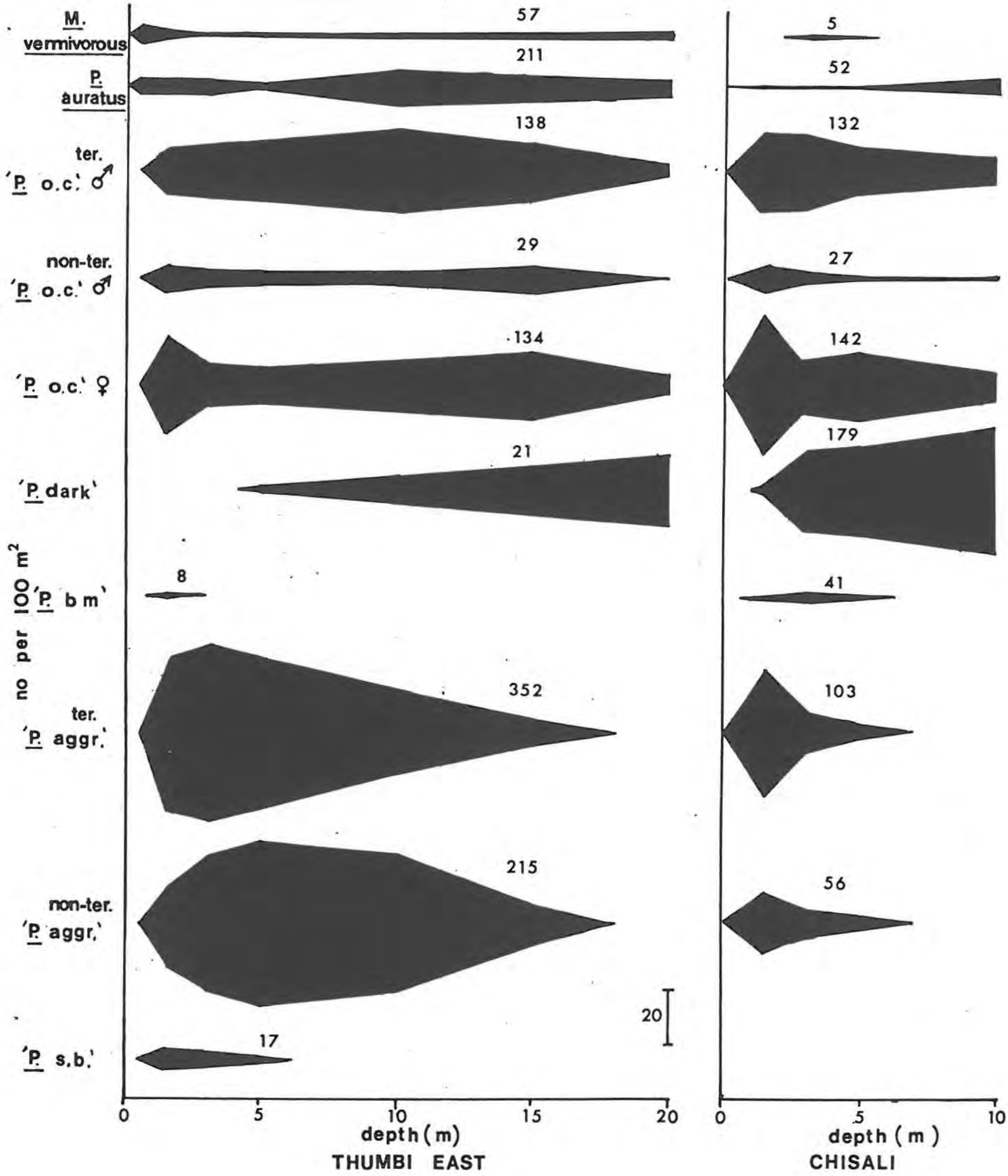


Figure 20. Depth distribution of Melanochromis vermivorous and some Pseudotropheus species on the two work sites near Monkey Bay. The abbreviation 'ter' = territorial. The number adjacent to each diagram is the total number of individuals of that species counted in transects at that site. All counts in 0,5m of water at Thumbi East were made in rough weather. Details on the distribution of juvenile 'P. orange cheek' are given in Figure 22. 'P. o c' = 'P. orange cheek'; 'P. b m' = 'P. broad mouth'; 'P aggr' = 'P. aggressive'; 'P. s b' = 'P. sky blue'.

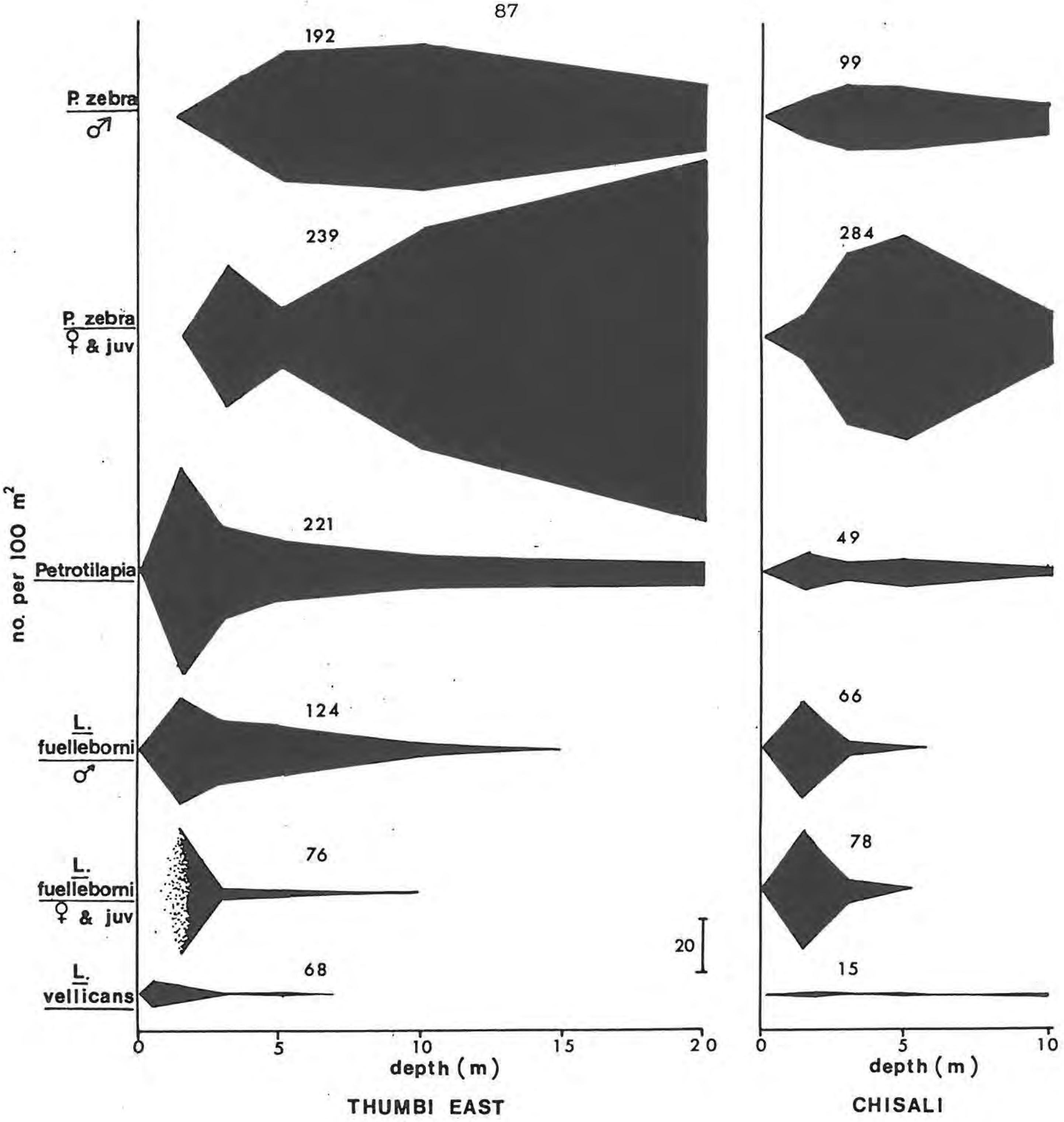


Figure 21. Depth distributions of Pseudotropheus zebra, Petrotilapia species, Labeotropheus fuelleborni and Labidochromis vellicans on the two work sites near Monkey Bay. The number adjacent to each diagram is the total number of individuals of that species counted in transects at that site. All counts in 0,5m of water on Thumbi East were made in rough weather. Details of the distribution of L. fuelleborni females and juveniles in the shallows are given in Figure 22.

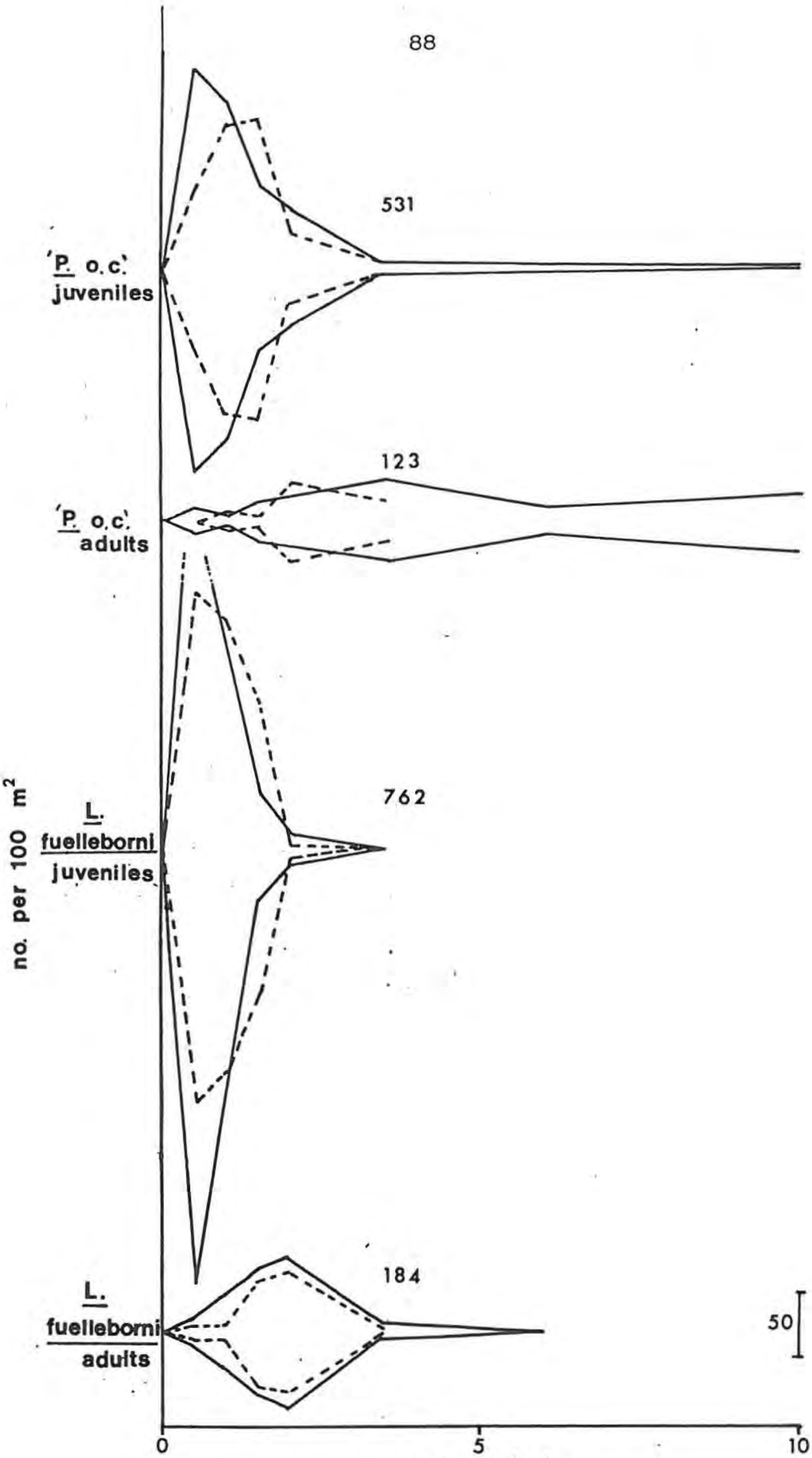


Figure 22. Depth distributions of non-territorial '<u>P</u>. orange cheek' and <u>Labeotropheus</u> <u>fuelleborni</u> on horizontal open rock on Thumbi East during calm (solid line) and rough (broken line) weather. The number adjacent to each diagram is the total number of individuals of that species counted in transects at that site. '<u>P</u>. o c' = '<u>Pseudotropheus</u> orange cheek'.

Figure 23. An adult male '<u>Pseudotropheus</u> orange cheek'

Figure 24. A territorial adult male '<u>Pseudotropheus</u> aggressive'. Note the thick mat of calothrix 1 in the territory below the fish.

Figure 25. Templates used to quantify rock coarseness (see text page 67).

A. Template cut to the shape and size of a 50-60 mm SL *L. fuelleborni* mouth.

B. Template cut to the shape and size of a 50-60 mm SL '*P*. orange cheek' mouth.

These templates were used to quantify rock texture by counting, along ten 30 cm transects, the number of interstices into which each of the templates would not fit i.e. in which the individuals they represented could not feed.

Figure 26. Territories in an undisturbed 6 x 6m quadrate at 3-5m depth on Thumbi East. In A) ▧ = '*P.* orange cheek'; ▩ = '*P.* aggressive' > 75mm SL; ⬚ = '*P.* aggressive' < 75mm SL; □ = '*P.* sky blue'. In B) *Pseudotropheus zebra* males territories are outlined with a solid line and *Labeotropheus fuelleborni* territories with dotted line. A & B represent the same quadrate and were both mapped between 15/4/79 and 26/4/79.

Boundaries of *L. fuelleborni* territories are based on the movements of the territorial fish. These fish did not feed in the interspecifically defended territories which lie within their territories.

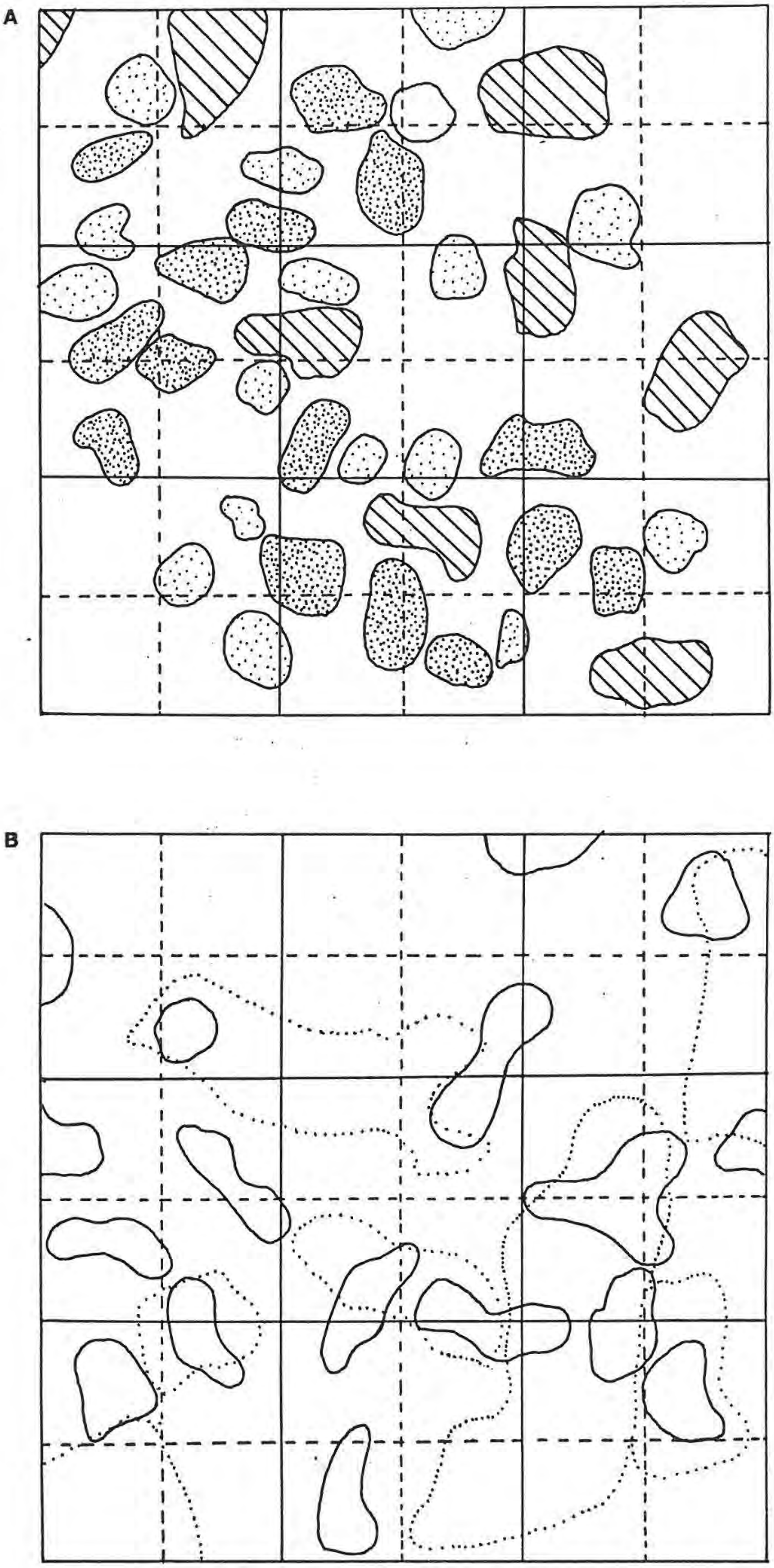


Figure 26.

# CHAPTER 8

## TERRITORIALITY

In this section an overall picture of interspecific territoriality in two Mbuna species, '*P*. orange cheek' and '*P*. aggressive' is given and the function and evolution of territoriality in these fishes is discussed. Brief notes on the interspecifically territorial '*P*. broad mouth' and '*P*. sky blue' are also presented.

Details of the ethological aspects of territoriality are omitted since these have little bearing on the ecological problem and have been adequately described for other cichlids with similar behaviour (e.g. Baerends & Baerends-van Roon, 1950, and reviewed by Fryer & Iles, 1972). However, since Baerends & Baerends-van Roon do not describe interspecific aggression, brief notes on this form of territorial behaviour in the Mbuna are given below.

The vast majority of interspecific encounters observed in this study involved a simple chase-flee interaction between the defendant and the intruder. Intruders are normally chased off before they begin feeding and chasing is the most common behavioural activity. Some intruders tend to feed just inside the territory boundary. When chased, they flee a short distance but return immediately to continue feeding. This sequence was seen most frequently between male *P. zebra* and territorial '*P*. orange cheek'. One *P. zebra* individual was chased 13 times from a single territory in 25 minutes of observation.

Although attacks of conspecific intruders may, infrequently, involve the whole sequence of aggressive behavioural interactions described for *Tilapia natalensis* (= *Oreochromis mossambicus* (Peters)) by Baerends & Baerends-van Roon,(1950) i.e. lateral display - circling - butting -

chasing, this sequence was seldom observed during interspecific attacks. '*P*. aggressive' were, however, seen to show frontal displays to intruding *P. zebra* which occasionaly stood their ground within the territory boundary. Interspecific boundary disputes are rare but were recorded between '*P*. orange cheek' and '*P*. aggressive' on five occasions. These disputes involved frontal displays but not physical contact.

Ecological aspects of territoriality in four Mbuna species are discussed below.

## '*Pseudotropheus* aggressive'

### General.

All individuals of this species, except juveniles smaller than 60-65mm SL, are territorial. Non-territorial juveniles are commonly found in or near crevices which are too small for adults to use, but these crevices may be situated within the territories of adults. Juveniles occupying such cracks are vigorously chased whenever they emerge to feed. These chases account for the majority of instances of intraspecific aggression.

Tagging indicates that the range of movement of non-territorial fish is very restricted. The mean area within which tagged individuals smaller than 60mm SL were sighted over nine days was $0,16m^2 \pm 0,02m^2$ ($n = 21$). Similarly, of the 34 large individuals ($>$60mm SL) sighted two or more times after tagging, only one (a female of 74mm SL) changed its territory. Despite the small range of movement over short time spans, several facts suggest that these fish may progress through a series of territories during their lives.

i) Random collections of '*P*. aggressive' at different depths and habitat zones reveal that the proportion of large males is highest among broken rock in shallow water (1-3m) while females and small males predominate in deeper water and over open rock (Figure 27). Furthermore, whilst large individuals amongst broken rock usually have territory sites in crevices, the territories of small individuals in the same habitat zone are often found on the tops and sides of rocks (Chapter 9, Table 15). These trends can only result from territory shifts as fish grow.

ii) The potential for territory change is indicated by the rapid replacement of removed individuals (Chapter 9, Figure 40). The new tenant was often an adult which previously occupied a territory up to three metres away. The old territory site can sometimes be recognized by the behaviour of the fish which may initially attempt to defend both territories simultaneously by moving from one to the other.

iii) Finally, observations of territories under undisturbed conditions reveal that as many as 50% of the territory sites held by '*P.* aggressive' smaller than 75mm SL may be vacated within the space of a month (Table 8). It is highly unlikely that this is entirely due to mortality and some territory changes must therefore occur. The territories of larger fish are far more stable as the maximum loss recorded for one month was approximately 8%. These figures represent the minimum number of losses because if a vacated territory was immediately re-occupied by a conspecific of similar size, the change would not be noticed.

## Table 8

Monthly territory changes within two undisturbed 6 x 6 m quadrates in 3-5m of water on Thumbi East. The numbers in brackets indicate the number of territories taken over by conspecifics of a different size class. There was no interchange of territories between species.

| | No. Initially Present | Apr/May | May/Jun | Jun/Jul | Jul/Aug | Aug/Sept | Sept/Oct | Oct/Nov |
|---|---|---|---|---|---|---|---|---|
| Total number '_P_. aggressive'>75 mm SL. | 26 | 26 | 26 | 27 | 27 | 26 | 26 | 28 |
| Total number of territories lost by '_P_. aggressive'>75 mm SL. | - | 1(1) | 1 | - | 1 | 2(2) | 2(1) | - |
| Total number of territories gained by '_P_. aggressive' >75 mm SL. | | 1(1) | 1 | 1(1) | 1(1) | 1(1) | 2(1) | 2(2) |
| Total number '_P_. aggressive' <75 mm SL. | 27 | 23 | 19 | 18 | 19 | 20 | 20 | 22 |
| Total number of territories lost by '_P_. aggressive'<75 mm SL. | - | 9(2) | 5 | 3(1) | 4(1) | 3(1) | 5(1) | 11(2) |
| Total number of territories gained by '_P_. aggressive'<75 mm SL. | - | 5(1) | 1 | 1 | 5 | 4(2) | 5(1) | 13 |
| Total number 'P. orange cheek' | 15 | 15 | 14 | 16 | 17 | 16 | 16 | 17 |
| Total number of territories lost by '_P_. orange cheek' | - | - | 2 | - | - | 2 | - | - |
| Total number of territories gained by '_P_. orange cheek' | - | - | 1 | 2 | 1 | 1 | - | 1 |

The pattern of territory succession apparent from the above is initial colonization of open rock by small individuals. These territories are unstable relative to those held by large fish and may be occupied for no more than a few days or weeks. As the fish grow they form territories in crevices with males occupying most sites in the shallows. At this stage territories stabilize and fish larger than 75mm SL may possibly retain a single site until death. It was not possible to follow the progress of individuals from territory to territory because of the short time which Floy and bead tags remained in position. The one tagged fish which did change its territory was a female of 74mm SL which moved from an open rock to a crevice site.

### Territory size

The size of territories increases with the size of the tenant and the depth at which they are located (Table 9). This may be predicted because all the tenants' food requirements are met within the territory. Consequently a larger fish with larger food requirements will require a bigger territory. Similarly, where Aufwuchs productivity, is low a large territory is needed to produce sufficient food. It is safe to assume that the high sediment levels and low light levels of deep water sites will reduce Aufwuchs productivity, territories in deep water are therefore predicted to be larger than those in the shallows.

The (assumed) higher productivity of the shallows probably makes this the most suitable zone for territories. This might explain the presence of the largest fish in these sites (Figure 27) and the rapid drop off of numbers of territorial fish below 5m on Thumbi East (Figure 20).

## Table 9

Territory sizes amongst broken rock on Thumbi East. * Actual rock surface area incorporated within the territory ** horizontal area covered as calculated from mapped quadrates.

| | Territory Size ($m^2$ ± 1 SE) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Depth | '*P.* orange cheek' | n | '*P.* agressive' >75 mm SL | n | '*P.* aggressive' <75 mm SL | n | '*P.* sky blue' | n |
| 4-6 m | 0,49 ± 0,024** | 44 | 0,28 ± 0,008** | 117 | 0,17 ± 0,013** | 27 | 0,36 ± 0,023** | 22 |
| | | | 0,67 ± 0,27* | 20 | | | | |
| 9-11 m | 0,66 ± 0,088** | 13 | 0,82 ± 0,034* | 20 | | | | |
| 19-21 m | 1,04 ± 0,054** | 5 | | | | | | |

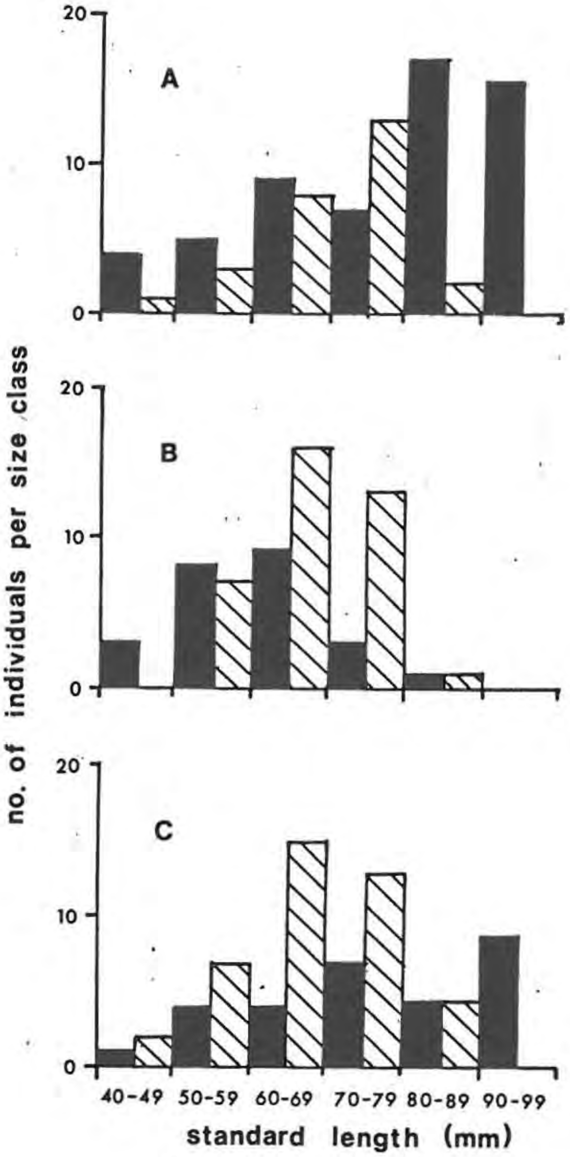


Figure 27. Size distribution of '<u>P</u>. aggressive' in random collections made on Thumbi East in three habitat zones: - A) broken rock at 1-3m depth; B) open rock at 1-3m depth and C) broken rock at 5-7m depth. ■ = males; ▨ = females.

Interspecific aggression.

The importance of territories for the continued survival of 'P. aggressive' can be gauged from the amount of time and energy spent in their defence. Large 'P. aggressive' individuals (>75mm SL) consistently exclude all other benthic algae grazing fish from their territories. Aggressive interactions with piscivores and omnivores are, however, rare. This is partly because of the relatively low densities of these species compared to herbivores and partly because they are often ignored when they enter the territory.

Activity counts on Thumbi East show that large 'P. aggressive' may chase more than fourteen intruders in a five minute period (Figure 28). Both aggressive behaviour and feeding activity reach a peak in the late afternoon. It is not known if the increased aggression is due to the presence of more intruders or increased aggression in the territorial fish (Rasa, 1971).

Lack (1939) has stressed that for territorial behaviour to be adaptive it must exclude intruders. The efficiency with which a territory is defended depends upon:

a) the vigilance and aggression of the owner,

b) the number and nature of the intruders and,

c) the size and situation of the territory.

For 'P. aggressive' these factors are all favourable for territorial defence.

a) As can be seen from the activity counts (Figure 28), 'P. aggressive' are almost continually vigilant during daylight hours. They are also highly aggressive and were often seen to chase off fish several times larger than themselves.

Figure 28. Diurnal activity rhythms:- A) '*P*. aggressive' at Chisali; B) '*P*. aggressive' at Thumbi East; C) '*P*. orange cheek' at Thumbi East. ● = number of feeding pecks (scale 0-100); ○ = number of conspecific attacks (scale 0-10); + = number of interspecific attacks (scale 0-10). Vertical lines indicate 2 SE. 10 fish were observed in each set of readings except the summer counts on Thumbi East where n = 20.

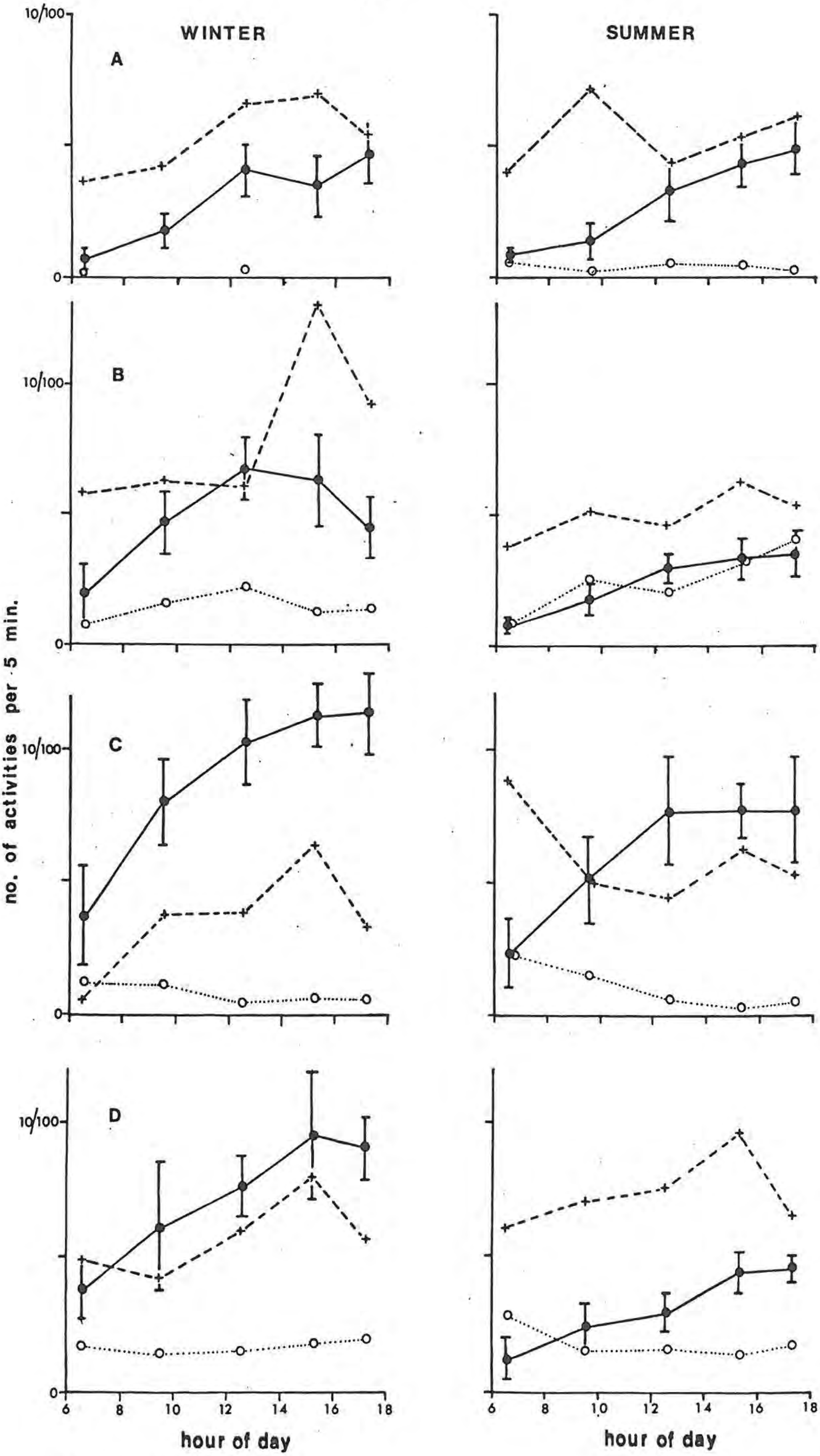

WINTER
SUMMER
A
B
C
D
10/100
0
no. of activities per 5 min.
6
8
10
12
14
16
18
hour of day

Figure 28.

b) Large '<u>P</u>. aggressive' appear to be capable of excluding all guild members except adult male <u>Petrotilapia</u> species and schooling female <u>Petrotilapia</u> species.

c) Territories are small and often situated in a crevice. Both these factors reduce the boundary length which has to be patrolled and hence facilitate territory defence. The advantage of having a territory in a crevice is reflected in the number of chases made. '<u>P</u>. aggressive' individuals with territories on open rock chase on average 10,5 intruders per 5 minutes (n = 10) between 14.00hrs and 16.00hrs on Thumbi East in winter. Similar sized individuals with territories in crevices execute, on average, only 6,5 chases per 5 minutes at the same time of day and year (n = 10).

The efficiency and effect of territorial behaviour in '<u>P</u>. aggressive' was shown by counting the number of fish feeding in 30 x 30cm quadrates within territories before and after removal of the owners (Table 10). No fish, apart from the owner, fed within the quadrates before removal, but two hours after removal many fish of a variety of species had congregated at densities considerably greater than on previously undefended rock.

The only herbivorous fish seen to feed unmolested within '<u>P</u>. aggressive' territories were adult <u>Petrotilapia</u> males. Many aggressive encounters were, however, observed in which <u>Petrotilapia</u>, when attacked by '<u>P</u>. aggressive', retaliated and chased the '<u>P.</u> aggressive' from its own territory. Female <u>Petrotilapia</u> also have access to '<u>P</u>. aggressive' territories by means of their schooling behaviour (see page 60 ).

## Table 10

Comparison of the number of fish feeding in 30 x 30 cm quadrates within '*Pseudotropheus* orange cheek' and '*Pseudotropheus* aggressive' territories before and after removal of the owner and on undefended rock.

A: Total number of fish seen to feed in all eight quadrates over a 10 minute period before the removal of the owner.

B: Total number of fish seen to feed in all eight quadrates over a 10 minute period after removal of the owner.

C: Mean number of feeding pecks per 10 minutes per quadrate before removal.

D: Mean number of feeding pecks per 10 minutes per quadrate after removal.

| Species | '*Pseudotropheus* orange cheek' Territory | | | | '*Pseudotropheus* aggressive' Territory | | | | Undefended | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | A | B | C | D | A | C |
| *Cyrtocara taeniolatus* | 8 | 6 | 20,7 | 5,12 | 0 | 10 | 0 | 22 | 13 | 8,4 |
| *Pseudotropheus auratus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3,4 | 0 | 0 |
| *Pseudotropheus zebra* | 3 | 12 | 9,4 | 126, 5 | 0 | 6 | 0 | 31,6 | 2 | 11 |
| '*Pseudotropheus* orange cheek' | 0 | 8 | 11,9 | 60 | 0 | 12 | 0 | 30,9 | 3 | 2,5 |
| '*Pseudotropheus* dark' | 0 | 2 | 0 | 40,2 | 0 | 3 | 0 | 12,4 | 2 | 1 |
| '*Pseudotropheus* aggressive' | 1 | 2 | 0,24 | 4 | 0 | 5 | 7,7 | 7,4 | 0 | 0 |
| *Petrotilapia* species | 0 | 2 | 0 | 14,25 | 0 | 4 | 0 | 57,2 | 2 | 2,25 |
| *Labeotropheus fuelleborni* | 0 | 3 | 0 | 4,0 | 0 | 6 | 0 | 44,7 | 1 | 1, 4 |

## 'Pseudotropheus orange cheek'

### General.

Most territorial fish of this species are mature males, but mature females may also hold territories. The depth distributions of these territorial fish and the schooling habit of the juveniles has already been mentioned in Chapter 6. Tagging shows that the range of movement is smallest in the large fish, irrespective of their sex or territorial status (Figure 29).

Random catches made on Thumbi East revealed that territorial males were slightly larger in the shallows (1-3m) than at 10m (94 ± 2,4mm SL cf 87,4 ± 1,4mm SL, n = 20) which suggests that territorial fish progress from territories in deep water to those in the shallows. It is possible that a faster growth rate in the shallows could account for the difference, but no attempt was made to age fish to check this possibility.

As for 'P. aggressive', removed territorial fish were rapidly replaced (Chapter 9, Figure 40). It was not possible to ascertain whether the replacements were territorial fish which had changed sites, or previously non-territorial fish.

### Territory sites.

The same trend of increasing territory size with depth which was found for 'P. aggressive' is apparent in 'P. orange cheek' (Table 9). Once again this probably relates to decreasing Aufwuchs productivity in deeper water. No attempt was made to correlate territory size and fish size for this species since only large adults are territorial.

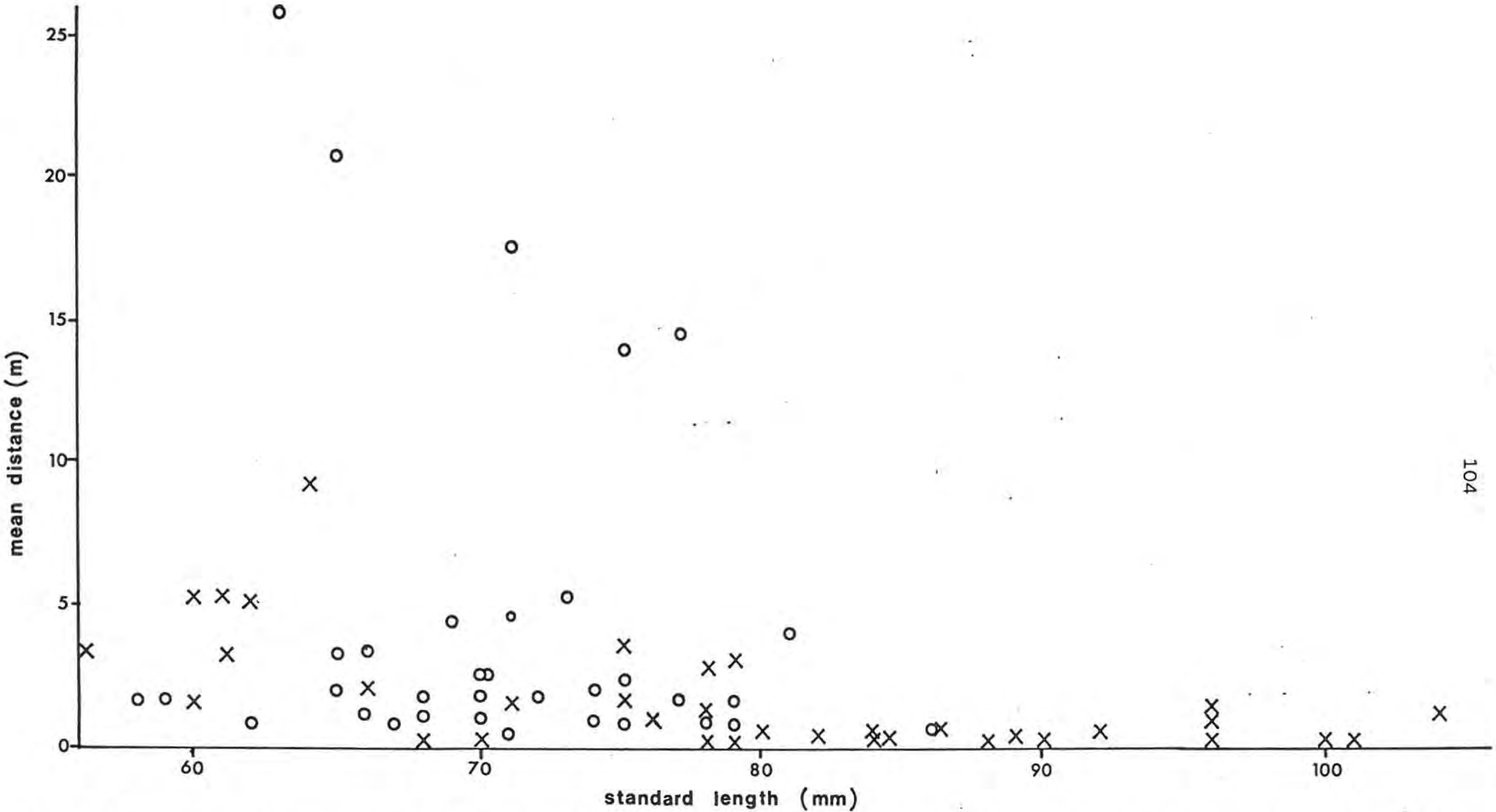


Figure 29. Mean distance between the points at which '<u>P.</u> orange cheek' individuals were sighted. X = males; 0 = females. Mean distance was calculated by measuring the distance from each point of sighting to all other points and taking the average.

Interspecific aggression.

'P. orange cheek' concentrates its interspecific aggression on benthic herbivores and rarely attacks omnivores and piscivores. The territories of this species are larger than those of 'P. aggressive' and are often situated such that the tenant cannot simultaneously feed and view its entire territory. Regular patrols preclude excessive feeding by other individuals within the territory.

Territorial males attack some species of intruders far more aggressively (vigorously) than others. A possible explanation for this is discussed later.

'Pseudotropheus sky blue'

In this species males, females and large juveniles (>50mm SL) hold interspecifically defended territories which are invariably associated with small rocks (Chapter 9, Table 16). Non-territorial juveniles are also confined to patches of small rock. All benthic herbivores may be attacked by this species if they enter their territories but there are insufficient observations to comment on the aggression shown to piscivores and omnivores.

Territory size ranges between 0,22 to 0,62m$^2$ in mature males (mean: 0,36 ± 0,023m$^2$, n = 22). Where territories are held over accumulations of small rocks between large boulders, the territory boundaries are often formed by these boulders. This results in territories with irregular outlines and individuals have even been seen defending two separate rock patches connected by a tunnel under the intervening boulder. Under these conditions it is common to find a large male moving over and defending the entire patch of small rocks whilst conspecific females and juveniles and, on a few occasions, small '*P*. aggressive', defend territories in the outlying portions of the patch, yet within the male's territory. Individuals which share the male's territory are presumably subordinate to him since they dart away as soon as he approaches. Their presence may, however, be an advantage if they perform the majority of the territorial defence and the '*P*. sky blue' merely moves in to feed.

### '*Pseudotropheus* broad mouth'

The territorial individuals of this species are predominantly adult males and occasionally adult females. Their territories are normally situated in the vicinity of a narrow crack or depression on open rock and are defended against all guild members but apparently not against piscivores. There are insufficient data available to comment on the aggression shown to omnivores.

## EFFECT OF TERRITORIALITY ON AUFWUCHS

Records of herbivore populations affecting the species composition and standing crop of benthic algae are common in ecological literature (Randall, 1961; Paine & Vadas, 1969; Earle,1972b; Lubchenco, 1978). Of particular relevance to this discussion are several studies on territorial coral reef fish which may maintain an algal mat within their territories which is both thicker and of different species composition to surrounding areas (Vine, 1974; Belk, 1975 ; Brawley & Adey, 1977; Robertson *et al*., 1979).

The presence of thick mats of calothrix 1 and associated algae within '_P_. aggressive' territories indicates that the behaviour of this species may have similar effects. A study was initiated to quantify the differences in defended and undefended Aufwuchs mats and to determine whether they result from the aggression of the territory owner or selection of territory sites with calothrix 1 gardens. This study was centred principally on '_P_. aggressive' but the other three interspecifically territorial species are also considered.

Standing crop.

'_P_. aggressive'

In all but the 1-2m samples taken in October 1978 and 1979, the standing crop of Aufwuchs in '_P_. aggressive' territories is significantly higher ($p < 0,01$) than in surrounding areas (Figure 30 & 31). Three facts indicate that this is a result of territorial aggression of '_P_. aggressive' lowering the grazing pressure within their territories:

1) No difference, apart from the presence or absence of a territorial fish, was detected between the sites at which 'defended' and 'undefended' rocks were collected.
2) When territory owners are removed, increased grazing (Table 10) results in a marked visual depletion of the Aufwuchs garden.
3) Exclusion experiments show that a lowering of the grazing pressure can result in a dramatic increase in the Aufwuchs standing crop (see below).

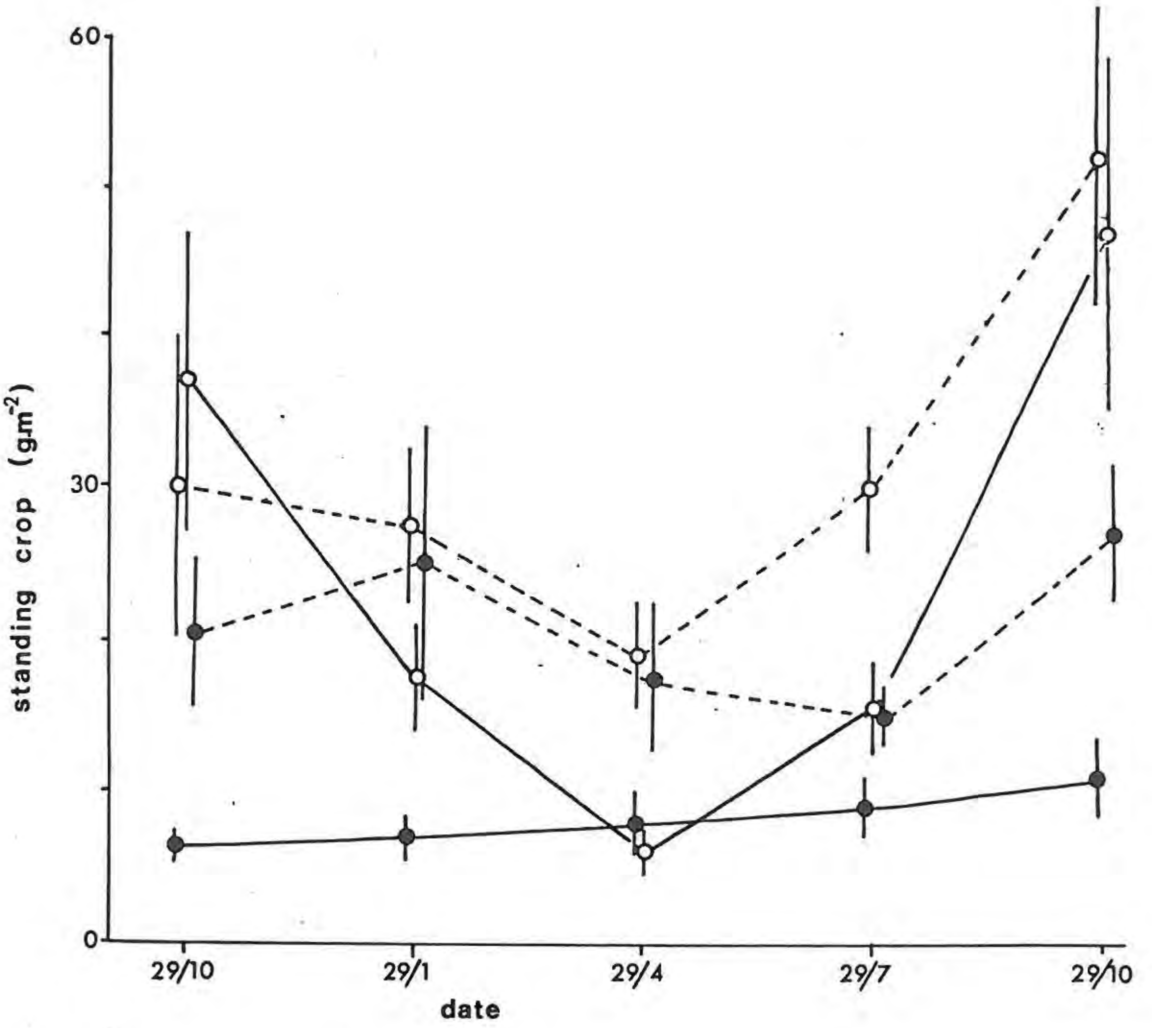


Figure 30. Standing crop (ash free dry weight) of Aufwuchs on rocks collected at Thumbi East. ○ = 1-2m depth; ● = 4-6m depth; —= undefended amongst broken rock;---= in '*P*. aggressive' territories. Vertical lines indicate 2 S.E.

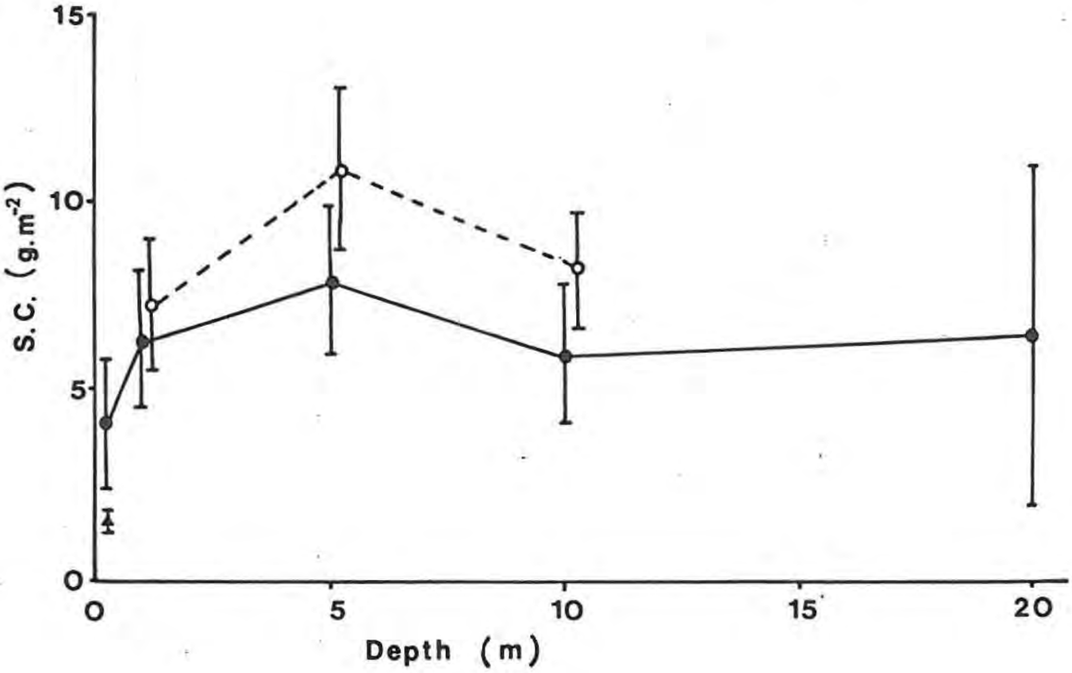


Figure 31. Standing crop (S.C.) of epilithic algae (ash free dry weight) on Thumbi East (closed circles and triangle) and at Chisali (open circles) in April 1979. Circles = among broken rock, triangle = on open rock. Vertical lines indicate 2 S.E.

'P. orange cheek' and 'P. sky blue'

Estimates of standing crop in 'P. orange cheek' and 'P. sky blue' territories made in April (Table 11) show that they too have a significantly higher standing crop ($P < 0{,}05$ and 0,001 respectively) than in surrounding areas. It is suspected that these high standing crops are also a result of territorial defence. The standing crop estimate in 'P. orange cheek' territories would probably be higher if it were possible to sample the vertical faces within their territories since these often appear to be the focus of territorial defence. The present estimates are based on rocks collected at the base of these faces.

It was not possible to sample 'P. broad mouth' territories because they are sited predominantly on open rock and hence contain no loose rocks suitable for standing crop analysis.

Calothrix composition.

Several factors such as grazing pressure, depth, rock slope, light levels, sedimentation etc. have potential to effect calothrix composition. The relative importance of these factors cannot be determined from calothrix distribution data alone. Nevertheless, the high proportion of calothrix 1 on rock faces in 'P. aggressive' territories, compared with undefended rock faces (Figure 32), suggests that reduced grazing pressure, which results from their territorial behaviour, may favour the growth of calothrix 1.

## Table 11

Standing crop of aufwuchs (gm$^{-2}$ ± 1 SE) on 29.4.1979. T.E. = Thumbi East site; B.R. = undefended amongst broken rock; O.R. = undefended on large open rocks; '*P*. orange cheek' = within '*P*. orange cheek' territories; '*P*. sky blue' within '*P*.sky blue' territories.

| Depth. | T.E. B.R. | T.E. O.R. | Chisali B.R. | T.E. '*P*.orange cheek' | T.E. '*P*. sky blue' |
|---|---|---|---|---|---|
| 0.5 m | 4,13 ± 0,85 | 1,76 ± 0,24 | - | - | - |
| 1,5 m | 6,36 ± 0,85 | - | 7,17 ± 0,89 | - | 1,52 ± 0.99 |
| 5,0 m | 7,94 ± 0,98 | - | 10,84 ± 2,12 | 13,05 ± 1,86 | 14,97 ± 1,8 |
| 10,0 m | 5,91 ± 0,94 | - | 8,09 ± 0,94 | - | - |
| 20,0 m | 6,37 ± 2,24 | - | - | - | - |

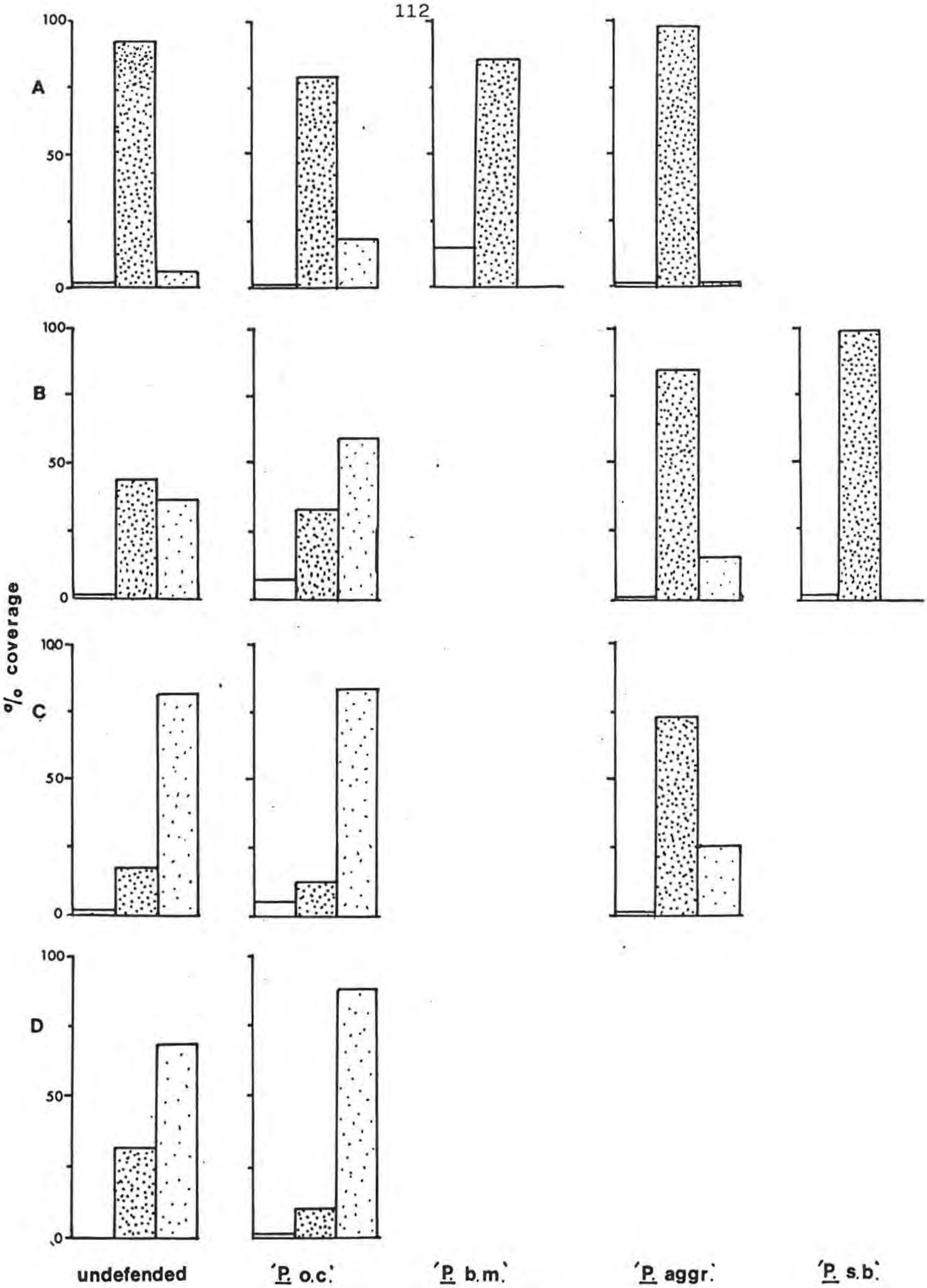


Figure 32. Estimates of the percentage coverage of calothrix in May 1979 □ = bare rock; ▦ = calothrix 1; ⬚ = calothrix 2. A = 1m; B = 5m; C = 10m and D = 20m depth. Undefended = coverage on undefended vertical faces among broken rock on Thumbi East. 'P.o c', 'P.s b' and 'P. aggr.' = coverage on vertical faces within territories of 'P. orange cheek', 'P. sky blue' and 'P. aggressive' on Thumbi East; 'P. b m' = coverage on horizontal faces in territories of 'P. broad mouth' at the Chisali site. n = 20.

To test this hypothesis, exclusion chambers were laid to simulate the reduced grazing pressure brought about by territoriality. Changes in Aufwuchs abundance and calothrix composition within these chambers were rapid: within 21 days tufts of calothrix 1 in the shallow water horizontal chambers were 15-20mm long while those in the controls remained 2-3mm in length. Simultaneously, a large build up of loose Aufwuchs completely covered the calothrix 2, which had not increased in length. Similar, but less rapid increases in Aufwuchs abundance occurred in the shallow water vertical chambers. In the 20m chambers, however, the Aufwuchs was completely covered with sediment (fish faeces and fine detritus) and only a slight increase (2-3mm) in the lengths of some tufts of calothrix 1 was noticeable after 107 days.

Considerable changes in calothrix composition were also apparent. In the shallow water chambers calothrix 1 rapidly became dominant, replacing the calothrix 2 (Figures 33, 34, 35 & 36). Coverage of calothrix 2 in the shallow, horizontal chambers decreased more rapidly than the increase in calothrix 1. This indicates that calothrix 2 was not actively excluded by calothrix 1, but was 'smothered' by the rapid build up of loose Aufwuchs. It also suggests that calothrix 2 may be more resistant to grazing pressure. After 72 days the calothrix 1 in the vertical chambers started to die off, leaving exposed rock; the reason for this is not known. In contrast to the shallow chambers, very little change in calothrix composition occurred in the 20m chambers (Figure 36).

Controls also show changes in calothrix composition which, in the shallows, may be related to season or changing lake levels. These changes were not as dramatic as those recorded in the experimental chambers.

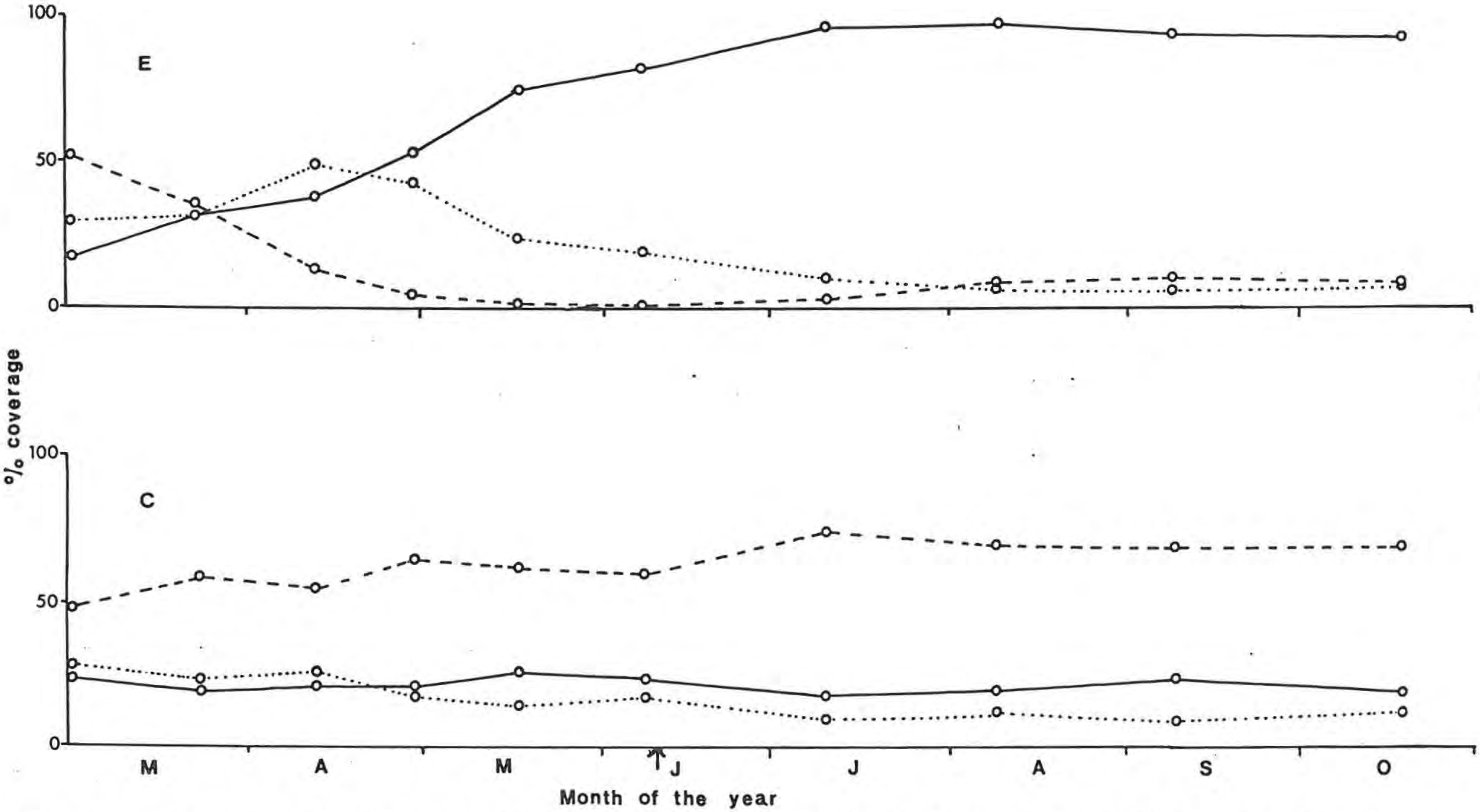


Figure 33. Changes in calothrix composition within exclusion chambers situated on undefended, horizontal, open rock on Thumbi East. E = experimental; C = control; —— = calothrix 1; - - - = calothrix 2; ······ = bare rock. The chambers were laid on 2.3.79. The arrow indicates the point at which the exclusion chambers were removed.

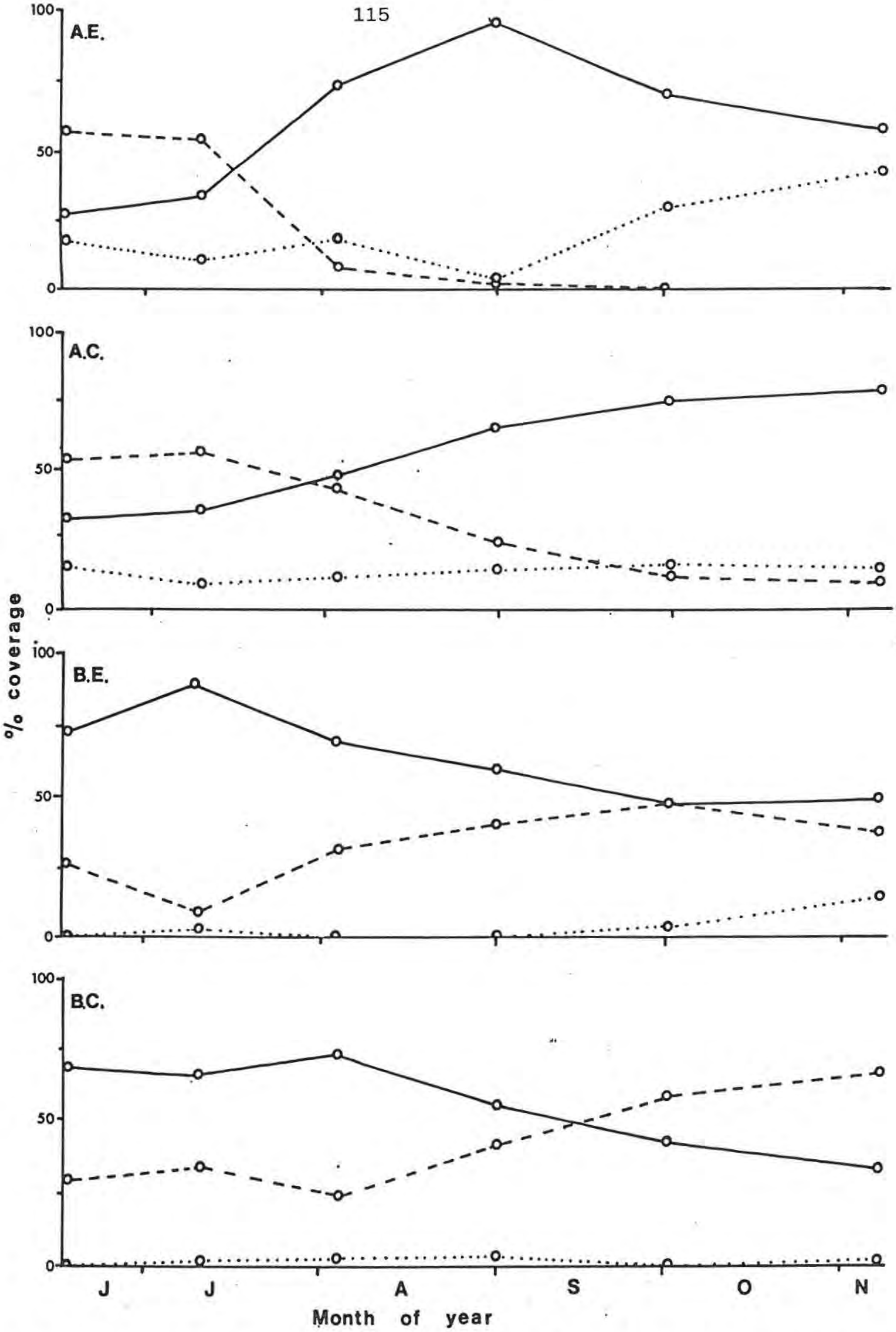


Figure 34. Changes in calothrix composition within exclusion chambers situated on: AE & AC = vertical rock at 1-3m depth on Thumbi East and BE & BC = horizontal rock at 20m depth on Thumbi East. AE & BE = experimental, AC & BC = controls; —— = calothrix 1; - - - = calothrix 2; ······ = bare rock. Chambers were laid on 16.6.79.

Figure 35. An exclusion chamber in position on horizontal open rock in 1,5 m of water on Thumbi East.

Figure 36. A patch of calothrix formed within an exclusion chamber (see above) one month after the chamber was installed. The black and yellow striped fish hovering over the patch is an adult male Pseudotropheus auratus which temporarily defended the patch following the removal of the chamber.

The above results show that complete removal of grazing pressure from the rocks in the shallows results in the development of calothrix 1 gardens similar to those in 'P. aggressive' territories. This supports the suggestion that the territory gardens are a result of reduced grazing pressure brought about by the territorial behaviour of the occupant. The proximate factor bringing about the dominance of calothrix 1 is more likely the increase in sediment and loose aufwuchs than the reduction in grazing pressure itself.

It is unlikely that every 'P. aggressive' individual has to cultivate its own garden from the beginning since vacated territories are rapidly re-occupied by conspecifics. The new owners also take over the associated gardens. Similarly the constant occupancy of many territory sites in areas monitored over a seven month period (Figure 37) indicates that once a garden is established it may be defended for many months, perhaps years. Finally the artificially developed gardens within shallow water horizontal chambers showed little sign of returning to their original species composition following the re-instatement of grazing (removal of chamber) (Figure 33). This suggests that the territory gardens will retain their species composition even if left undefended for several months between owners.

### '*Pseudotropheus* sky blue'

Territories of this species often contain thick mats of calothrix 1 similar to those of 'P. aggressive' territories. These are also assumed to result from reduced grazing pressure caused by territorial aggression.

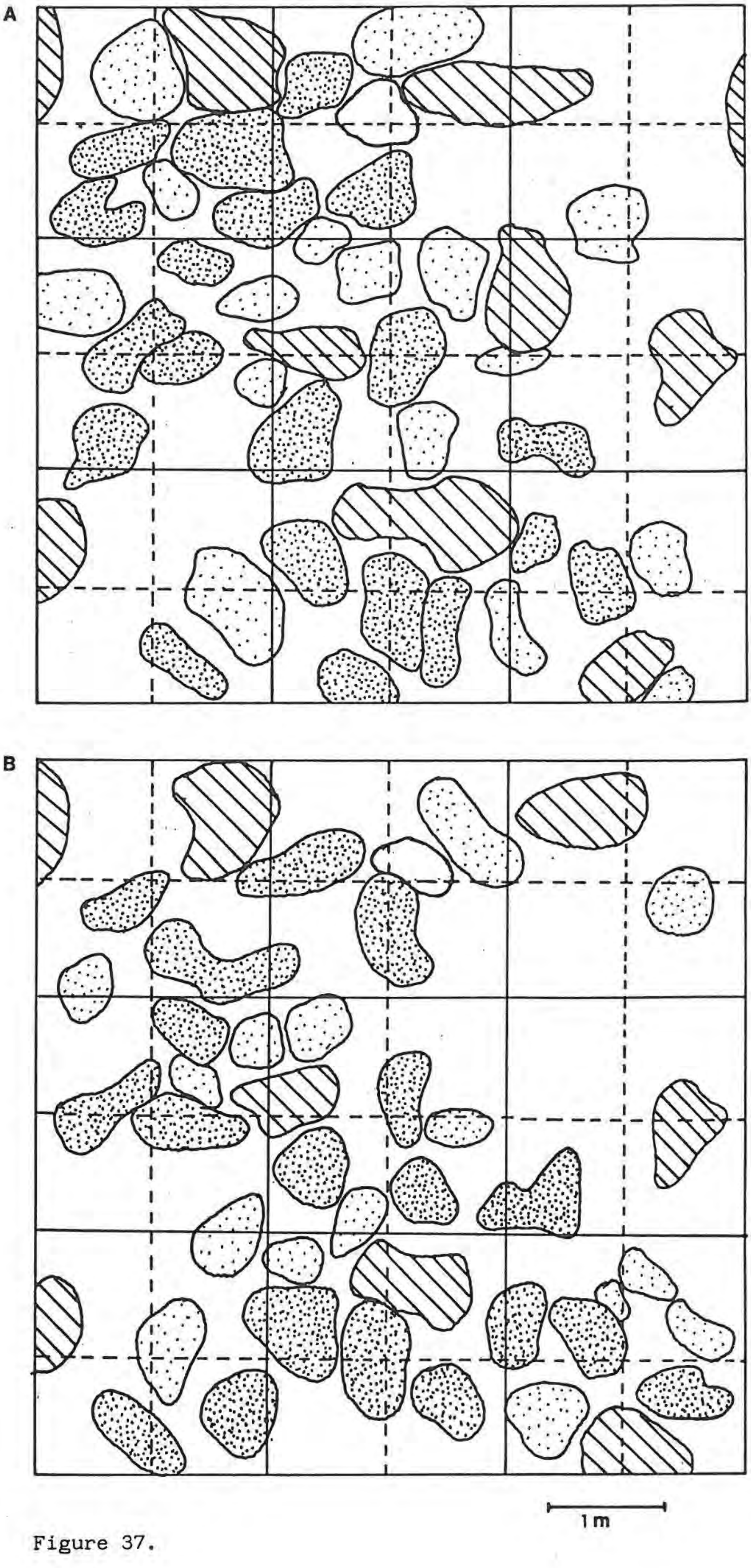


Figure 37.

'Pseudotropheus broad mouth'

A comparison cannot be made between this and the other species since estimates of calothrix composition within its territories were made at Chisali. There were no obvious calothrix gardens.

'Pseudotropheus orange cheek'

Unlike the other territorial species, 'P. orange cheek' has a higher proportion of calothrix 2 within its territories relative to similar (vertical) undefended faces (Figure 32). This difference could be due to a different form of territorial defence resulting in different grazing regimes (pressures) within the territories. 'P. aggressive' and 'P. sky blue' consistently exclude all guild members, apart from Petrotilapia sp. from their territories. Whereas 'P. orange cheek' often allow P. zebra and C. taeniolatus to feed undisturbed in their territories for short periods. The diet of the latter species is predominantly loose Aufwuchs. Calothrix 2 is apparently smothered by large quantities of loose Aufwuchs and it is therefore possible that by selectively removing loose Aufwuchs P. zebra and C. taeniolatus promote the growth of calothrix 2. Since 'P. orange cheek' eat principally calothrix 2 it is tempting to speculate that the low aggression shown to these species is in adaptive characteristic which increases the supply of this resource within their territories.

Another possible explanation for the abundance of calothrix 2 is that the presence of 'P. orange cheek' encourages its growth because it grazes in a different way to 'P. aggressive' and 'P. sky blue'. It was often observed that when 'P. orange cheek' feed in areas of thick calothrix 1, they pluck the tufts away at their base leaving patches virtually devoid of calothrix . This was not recorded in 'P. aggressive' or 'P. sky blue' territories, suggesting that these species remove only the uppermost portions of the calothrix strands. Indeed, as commented on earlier, these species take a surprisingly low proportion of calothrix and may merely be using its strands as a substrate from which to collect loose Aufwuchs. The complete removal of calothrix 1 tufts by 'P. orange cheek' may give calothrix 2 an opportunity to colonise the rock in 'P. orange cheek' territories.

## Discussion on the adaptive function of interspecific territoriality

It must be emphasised that much of the discussion which follows is speculative but has been included because of its value in pointing the way for future research.

That territorial marine fish may chase some species more aggressively than others has been reported by several authors (Myrberg & Thresher, 1974; Ebersole, 1977; Moran & Sale, 1977). These authors have based predictions of territory function on the correlation between the relative aggression directed at a species and its similarity in resource use to the territorial species. The assumption they make is that if aggression is directly proportional to overlap in the use of a particular resource, e.g. food or space, then the territory serves principally to preserve that resource. For instance, if aggression is proportional to the potential of the intruder to raid the nest for eggs, then nest defence is indicated as a function of territoriality.

A similar study on the relative aggression of '*P*. orange cheek' showed that the distance of attack also varies from the intruder species to another (Table 12). Many of these differences are statistically significant (see Appendix 1). The high Aufwuchs standing crop within the territories of the Mbuna studied here, combined with the consistent exclusion of other herbivorous fish from the territories, suggests that defence of a food supply is a function of territoriality. To test this, the correlation between diet overlap and relative overlap was determined using Pianka's (1973) formula:-

$$O_{kj} = \left( \sum_{i}^{m} P_{ij} \; P_{ik} \right) / \left( \sum_{i}^{m} P_{ij}{}^{2} \sum P_{ik}{}^{2} \right)^{\frac{1}{2}}$$

$O_{kj}$ = overlap between species k and j

$P_{ij}$ = proportion of the i'th resource used by the j'th species

$P_{ik}$ = proportion of the i'th resource and used by the k'th species.

There is a general positive correlation between diet overlap and relative aggression (Figure 38). Two species, '*Pseudotropheus* dark' and *P.auratus*, do not fit the correlation, and are discussed below.

'*Pseudotropheus* dark'

'*P*. dark' and '*P*. orange cheek' are morphologically similar and apparently closely related. It is suggested that the high level of aggression shown to '*P*. dark' by '*P*. orange cheek' is a result of this similarity and has no bearing on the function of territoriality, i.e. it is probably a case of mistaken identity as suggested for birds (Murray, 1971). Although emphasis is laid here on visual recognition it is also possible that sound cues are important. However, although sound production in fish may be associated with territorial behaviour (Winn, 1964), these sounds apparently function either to attract mates (Tavolga, 1958; Gray & Winn, 1961) or to warn off intruders (Winn *et al*., 1964).

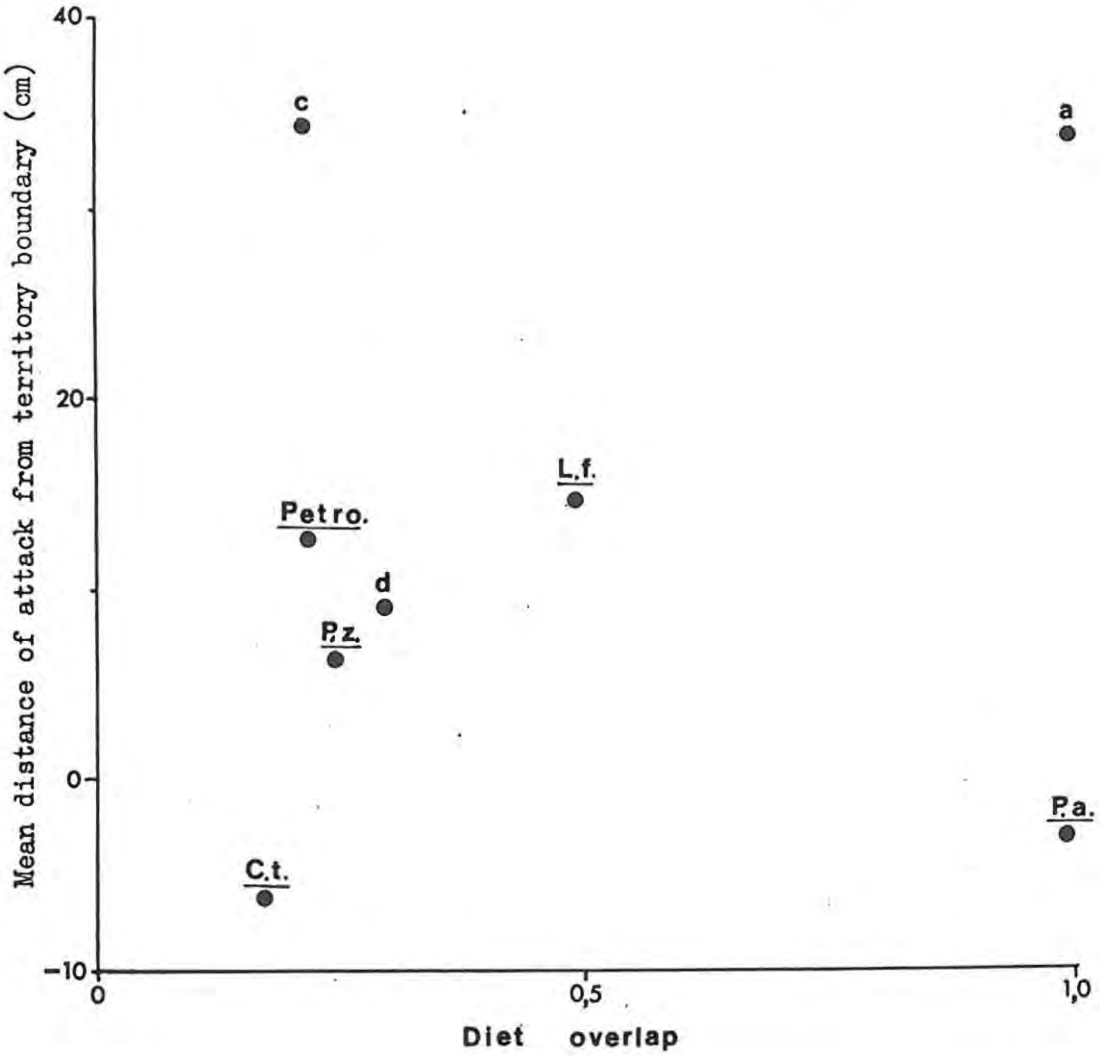


Figure 38. Correlation between diet overlap with 'P. orange cheek' and the relative aggression shown to intruder species. Relative aggression is represented by the mean distance of attack from territory boundary. a = '*P*. orange cheek'; c = '*P*. dark'; d = '*P*. aggressive'; *P.z* = *P. zebra*; P.a = *P. auratus*; *Petro.* = combined data from all *Petrotilapia* species; *L.f* = *L. fuelleborni*; *C.t.* = *C. taeniolatus.*

### *P. auratus*

The distance from the territory centre at which an individual is attacked depends on both the aggression shown to that species and the point at which the individual was first sighted. It is not possible to distinguish between these two when using natural encounters to determine the relative aggression as was done here. Thus if a species is an 'Aufwuchs robber' which, by means of stealth or rapid approach, is able to feed in occupied territories, it will appear to be less aggressively chased, i.e. nearer to the territory centre, than predicted from diet overlap alone. If this species consistently seeks out territories to feed in it will be chased more frequently than expected from its numerical density on the rocky shores. This is the case for *P. auratus* which is thought to be an 'Aufwuchs robber' (Chapter 7, page 51) and is chased three to four times more often than predicted from this density (Table 12). It is therefore suggested that the apparent low aggression shown to *P. auratus* is a reflection of its feeding behaviour.

If '*P.* dark' and *P. auratus* are ommited from the relative aggression/diet correlation then the product moment correlation co-efficient (r) for the remaining six species is 0,9008, which is significant at the 1% level. It is concluded that the relative aggression of '*P.* orange cheek' to intruder species supports the suggestion that the principal function of territoriality in this species is the defence of a food supply.

Table 12

Results of the relative aggression experiments on territorial male '*P*. orange cheek' (column 1) and related data. *n . Ind*. gives the total number of aggressive interactions from which the mean distance of attack was calculated. A total of 8 territorial '*P*. orange cheek' were observed for this study. * Negative numbers are mean distances which fall within the territory boundary.

| Intruder Species | *n* *Ind*. | Mean Distance of Intruder from feeding boundary when chase commences*(cm)* | Indices of Food Overlap with '*P*.orange cheek' (Pianka's,1973, formula). | Proportion of chases found / Prop.of chases expected from RelativeFrequency. |
|---|---|---|---|---|
| '*Pseudotropheus* dark' | 15 | 34,2 | 0,2133 | 3,2 |
| '*Pseudotropheus* orange cheek' | 128 | 33,8 | 1,0000 | 1,7 |
| *Labeotropheus fuelleborni* | 133 | 14,9 | 0, 489 | 1,9 |
| *Petrotilapia* species | 46 | 12,8 | 0,2121 | 0,6 |
| '*Pseudotropheus* aggressive' | 81 | 9,3 | 0,2933 | 0,4 |
| *Pseudotropheus zebra* | 109 | 6,2 | 0,2396 | 0,5 |
| *Pseudotropheus auratus* | 49 | -3,0 | 0,9964 | 3,4 |
| *Cyrtocara taeniolatus* | 337 | -6,2 | 0,1727 | 1,4 |

It is not possible to use the above approach to determine the adaptive function of territoriality in the other three interspecifically territorial species since no difference in aggression to different intruders was detectible. However, when all possible functions of interspecific territoriality are considered only one, the defence of a food supply, can be applied to these Mbuna. Ebersole (1977) lists four possible hypotheses for interspecific territoriality in coral reef fish. They are that territoriality

a) is a non-adaptive error in species identification,

b) functions to protect a nest or eggs,

c) functions to preserve a refuge, and

d) functions to protect food resources from competitors. The applicability of these to the Mbuna is considered below.

a) a non-adaptive error.

As has been argued for coral reef fish (see Chapter 2), it is unlikely that interspecific territoriality among the Mbuna is an error because fish with a large range of size, colour and body forms are attacked.

b) defence of a nest or eggs.

None of the Mbuna studied defend a conspicuous nest and, since they are maternal mouthbrooders, it is also not necessary to defend the eggs by territoriality.

c) defence of a refuge.

The majority of '_P_. broad mouth' and many small '_P_. aggressive' defend territories which are sited on open rock and therefore do not contain any shelter. Furthermore, fish possessing territories with a shelter hole often flee from the territory and shelter elsewhere when chased by a diver, suggesting that the defence of a refuge is not an important function of territoriality in Monkey Bay Mbuna.

d) defence of a food supply.

Since none of the above hypotheses for interspecific territoriality can be applied to these mbuna and no other functions are apparent it is assumed that territoriality is a means of assuring a food supply. This hypothesis is supported by the presence of thick calothrix gardens in many territories. If this hypothesis is accepted, two important questions are raised:

1) Why is interspecific territoriality limited to four out of a possible nineteen epilithic algae grazing species at Monkey Bay?

and

2) Why do male, female and juvenile '_P_. aggressive' and '_P_. sky blue' defend territories whereas principally adult males hold territories in '_P_. orange cheek'?

Unfortunately there are insufficient data available to give a conclusive answer. It is constructive, however, to speculate, but it is necessary to consider first some of the theory behind competition and resource utilization.

Competition may be divided into two categories, exploitation and interference competition (Brian, 1956; Miller, 1967; Case & Gilpin, 1974). These terms may be applied to inter- or intraspecific competition but only interspecific competition is considered here.

Exploitation competition.

This term refers to competition based on the respective abilities of the species involved to use the available resources without direct physical interaction with competitor species. When two species use exactly the same resource (which is in short supply), without physical interference, the species with the highest exploitation efficiency will eventually exclude the other by competitive exclusion (Hardin, 1960). (Obviously complicating factors such as predation or disease could affect the outcome of such a situation). The term 'exploitation efficiency' is defined here as 'a measure of the ability of a species to fulfil its resource requirements at low resource levels without resorting to interspecific aggression'. This measure has relative units of 'proportion of the individuals total resource requirements obtained at a particular resource availability'.

The above mentioned competitive exclusion of one species by another occurs because, as resources diminish, the species with the high exploitation efficiency can continue to feed and reproduce at resource levels which are too low for other species. Normally, however, even very similar species seldom, if ever, use exactly the same resources (Schoener, 1974). Thus, even if there is a large overlap of resource utilization, the species involved invariably have adaptations which give them an advantage over all other competitors under some circumstances.

There will be selective pressure for species competing in this way to increase their exploitation efficiency, i.e., if the limiting resource for which they are competing is food, selection will favour those individuals with the most efficient feeding mechanisms. Furthermore, selection will also favour divergence in the specialisation of the species involved thus resulting in further resource subdivision. It is possible that, as competitively driven evolution proceeds, the respective specializations of the species involved may be perfected to the point that they are no longer in significant competition. Nonetheless the importance of competition in the evolution of these specializations is obvious.

Species that compete by exploitation competition or subdivide resources by competitively evolved specializations shall be referred to as exploitation strategists.

Interference competition.

Interference competition occurs between two species when the one prevents the other from using a resource, or part thereof, by interference. This includes secretion of chemicals (Steinwascher, 1978) and predation on eggs (Park, 1962) but more commonly involves physical aggression or threat, such as interspecific territoriality. It is the latter form of interference competition which concerns us here.

As previously mentioned, interspecific territoriality in which the competitors for a renewable resource (e.g. food) are excluded from a defended area will result in resource partitioning since the occupant of each territory will utilize the resources within its territory whilst non-territorial individuals must use resources outside the territories. Since competitors are excluded there is no selective pressure on territorial species to evolve high exploitation efficiencies for the defended resource. Instead the selective pressure favours a more efficient means of territorial defence.

As a general rule it may be predicted that species which defend feeding territories will have low feeding efficiencies whereas non-territorial species require high feeding efficiencies to survive in the face of competition. Exceptions to this rule might occur when two species with high feeding efficiencies, yet specialized to take the same resource, co-exist. In order to prevent competitive exclusion they may subdivide the space resource by defending mutually exclusive territories but would not need to exclude species with lower feeding efficiencies or different specializations. Apparently this is often the case in birds (Miller, 1971). Another possible exception occurs when species with low feeding efficiencies co-exist with species with high feeding efficiencies, either as fugitive species (McArthur, 1972) or by robbing from territories of other species.

Thus it is expected that, among the epilithic algae grazing guild at Monkey Bay, the interspecifically territorial species should have a low feeding efficiency while intraspecifically territorial and non-territorial species should have high feeding efficiencies. This possibility is examined below.

The only indicators of feeding efficiency available for Lake Malawi fish are: a) mouth form and hence feeding mechanism, b) their ability to feed in areas with a low algal standing crop and c) their size.

a) Fryer (1959) suggests that the ancestral Mbuna was a Melanochromis/ Pseudotropheus-like fish with nipping mouth morphology and that the highly modified mouth forms of the other genera evolved to increase feeding efficiency. Since no other selective pressures are apparent this is assumed to be correct.

b) The standing crop of Aufwuchs in the extreme shallows of Thumbi East is considerably lower than elsewhere on the shore (Figure 31). Species commonly found feeding on these rocks in calm weather (i.e. when they are not excluded by surge) are assumed to have high feeding efficiencies. It does not follow, however, that species which do not feed in this zone have low feeding efficiencies.

c) Finally, since feeding efficiency is defined as the ability of a species to fulfil its energy requirements, a small species with low energy requirements will be more efficient than a large species with a similar ability to obtain food.

These indicators are used below to obtain a relative assessment of the feeding efficiencies of the species listed in Chapter 7.. Four distinct feeding mechanisms can be discerned among the epilithic algae grazing species (see also Fryer, 1959 ).

1. Nibbling

At Monkey Bay two species, Labeotropheus fuelleborni and Labeo cylindricus, feed with a series of nibbling movements which are rapidly executed while the fish moves slowly forwards with its mouth continually pressed to the rock surface.

L. fuelleborni juveniles form dense feeding shoals in the extreme shallows, this together with their highly modified mouth structure (Chapter 7, Figure 14), indicates a high feeding efficiency.

*L. cylindricus* never feeds in the extreme shallows but is commonly seen feeding on horizontal rock with relatively high sediment levels. They often feed, for several minutes at a time, in a restricted area (diameter approximately 30cm) where they leave a conspicuous patch from which most sediment and loose Aufwuchs are removed. They are therefore assumed to be relatively efficient feeders but, since sediment is presumably a low quality food, they may require a very efficient digestive process.

### 2. Brushing

Two groups, the *Petrotilapia* species and the *Pseudotropheus zebra* complex, have long flexible teeth with which loose Aufwuchs is brushed from the rock. This specialization is best developed in *Petrotilapia* (Figure 14) which are also common in the extreme shallows and therefore assumed to have a high feeding efficiency. *P. zebra* on the other hand, does not occur in the extreme shallows. It is suspected that this may be due to its inability to compete with *Petrotilapia*. Nonetheless *P. zebra* does have a specialized feeding mechanism and is therefore assumed to be a relatively efficient feeder.

### 3. Scraping

Only one species, *Barbus johnsoni*, uses this feeding mechanism which involves scraping the rock with its rigid, semi-circular, cartilaginous lower lip while still moving forwards at normal swimming pace. Since medium sized individuals of this species feed almost entirely in the extreme shallows they are assumed to have a high feeding efficiency.

### 4. Pecking

Many species of *Melanochromis*, *Pseudotropheus*, *Labidochromis* and some *Cyrtocara* have rigid jaws with which Aufwuchs is removed by individual nips or pecks. Despite their similarity in feeding mechanism, these species appear to exhibit a wide range of feeding efficiencies.

At Monkey Bay four pecking species, '*P*. orange cheek' (juveniles), *P*. *auratus*, *M*. *vermivorous* and *L*. *vellicans* reach high densities in the extreme shallows and are therefore considered to have high feeding efficiencies. The remaining species in this category of feeders are uncommon in this zone, they are '*P*. broad mouth', '*P*. dark', '*P*. aggressive', '*P*. sky blue' and *C*. *taeniolatus*. The absence from the extreme shallows and lack of morphological specialization in the latter group may indicate low feeding efficiencies. An examination of mouth width shows that those species which feed in the extreme shallows have the narrowest mouths (see Chapter 7, Table 4 for mouth widths).
This correlation is complicated by the increase in mouth width as fish grow. Thus '*P*. orange cheek' have narrow mouths relative to their body length but, because of their large size, adults develop broad mouths. In contrast, *M*. *vermivorous* has a broad mouth relative to its body length, but, because of its small size, its maximum mouth width is narrow.

The high feeding efficiency of the narrow mouthed species is probably due to their ability to pluck calothrix 2 from interstices on the rock surface (three of the four pecking species common in the extreme shallows have high proportion of calothrix 2 in their diets). If this is the case feeding efficiency will decrease as fish size increases, both because the mouth broadens, hence preventing access to many of the narrower interstices, and because energy requirements increase. It would therefore be advantageous for these species to reach maturity at a small size. This does indeed appear to be the case: three of the four pecking species found in the extreme shallows, L. vellicans, M. vermivorous and P. auratus, are the three smallest guild members (Table 2) and although the fourth 'P. orange cheek' may reach 105mm SL, only juveniles are common in the extreme shallows.

Broad mouthed species will be unable to feed in interstices on the rock surface and will therefore have to feed from the broad depression and exposed convex surfaces. These are the same surfaces which the broad mouthed L. fuelleborni, P. zebra and Petrotilapia species will utilize. It is unlikely that the morphologically unspecialized broad mouthed pecking species will be able to feed as efficiently as is possible with the rapidly executed nibbling and brushing mechanisms of these species. Broad mouthed pecking species are therefore considered to be relatively inefficient feeders.

C. taeniolatus has a narrow mouth yet does not feed in the extreme shallows. Furthermore, their teeth are very poorly developed (Figure 9). This may explain why they take very little calothrix which is firmly attached to the rock. It is possible that they use their narrow mouths to collect loose Aufwuchs from interstices which are too narrow for other loose Aufwuchs feeders. Their high abundance on the rocky shore may also be partially explained by the low aggression shown to them by 'P. orange cheek' which allows them to feed within its territories.

There are too many assumptions made in the above discussion to reach any definite conclusions about the feeding efficiencies of particular species.

It is apparent, however, that if the original assumptions with respect to the indicators of feeding efficiency, are correct, then the broad mouthed pecking species probably have the lowest efficiencies. It is predicted therefore that these species will be the most likely ones to defend interspecific territories. On the whole it is true,however, that '*P.* dark' has a broad pecking mouth yet does not defend interspecific territories, and '*P.* orange cheek', which apparently has a high feeding efficiency, defends interspecific territories.

'*P.* dark' is restricted to deep water and sheltered shores where it feeds from rocks which high sediment levels. As a result of its feeding mechanism it will be unable to brush loose Aufwuchs from between the calothrix strands and therefore probably feeds predominantly on sediment and associated live cells and invertebrates. Sediment is presumably a low quality food resource, but one which is in plentiful supply. If '*P.* dark' has physiological adaptations which enable it to digest this resource more efficiently than other species, this will result in a relative increase in feeding efficiency by allowing it to feed at a lower food quality than these species.

The only indicator of digestive ability available is gut length. Several authors have shown that in fish the gut length : body length ratio is greatest in detritivores and decreases down the sequence: herbivores — omnivores — piscivores (Verigina & Medani, 1968; Emery, 1973; Fryer & Iles, 1972; Kruger & Mulder, 1973). Although there is no experimental proof, it is generally implied that a long gut is required to digest foods with low nutrient content and hence represents an increased digestive efficiency. The gut lengths of '*P.* dark' (which is broad mouthed and non-territorial), '*P.* orange cheek' (which is relatively narrow mouthed and territorial) and '*P.* aggressive' (broad mouthed and territorial) were compared (Figure 39).

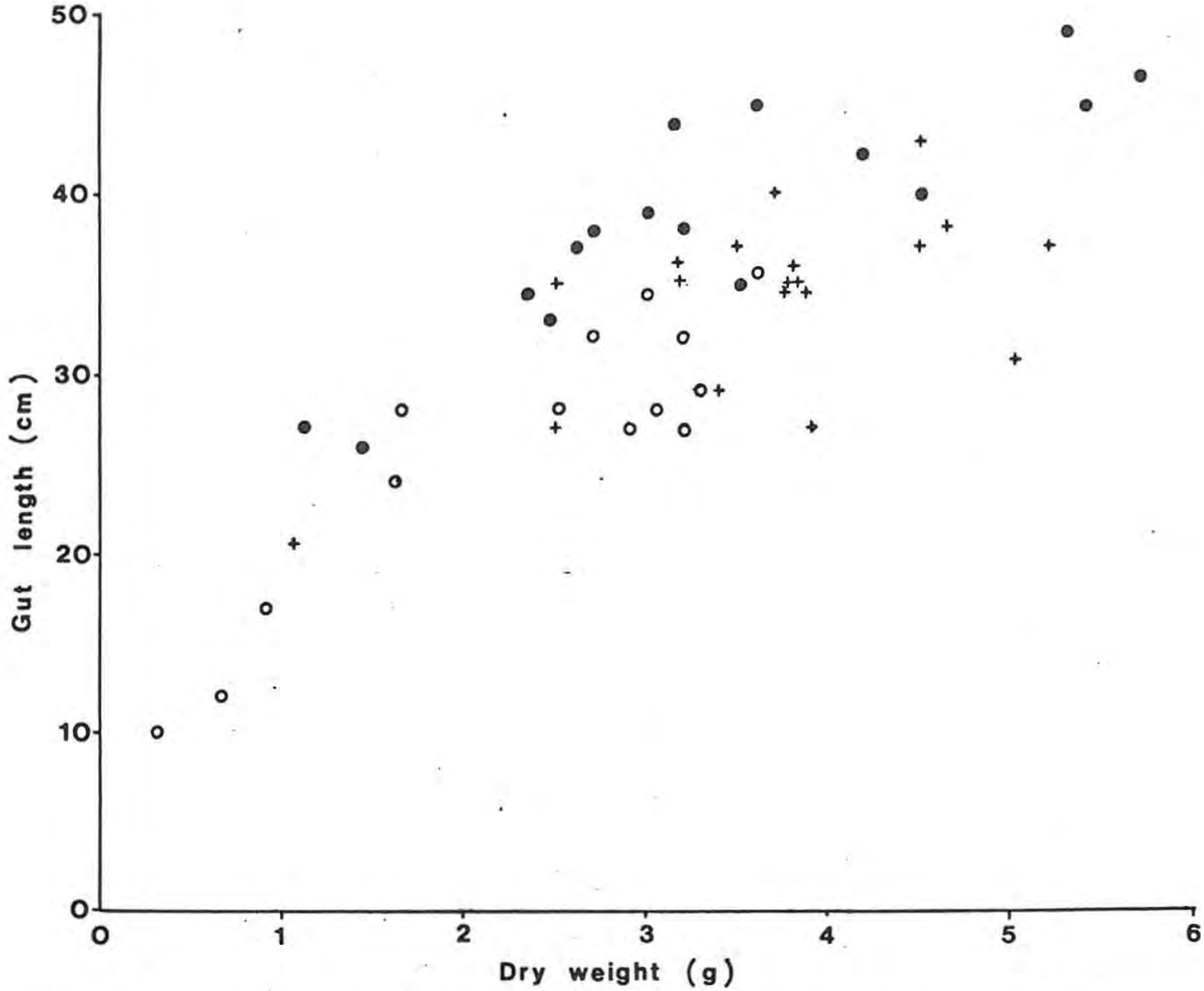


Figure 39. Relationship between gut length and dry body weight in three cichlid species. o = '_P_. orange cheek'; ● = '_P_. dark'; + = '_P_. aggressive'.

The gut length of 'P. dark' is relatively longer than in either of the other species. This therefore supports the hypothesis that the relative feeding efficiency of 'P. dark' is increased by a high digestive efficiency which enables it to feed on the low quality sediment resource and thus coexist with the more morphologically specialized species without defending a territory.

It has already been suggested that the key to 'P. orange cheek's' high feeding efficiency is its narrow mouth, hence efficiency will decrease as they grow and a point may be reached where the efficiency is sufficiently low to necessitate the defence of a feeding territory. Although this may explain why territoriality occurs only in adults, it is not immediately obvious why so few females are territorial. There are two possible explanations for this, either, females are smaller than males and therefore do not need to defend territories, or, there are insufficient territories for both males and females.

Only 8% of the females caught in the shallows of Harbour island were larger than 85mm SL (n = 300). In comparison, the smallest territorial male caught in the shallows of Thumbi East (a similar habitat) was 87mm SL (n = 20). It is possible that males are larger because they hold territories and not visa versa.

Secondly, the rapid replacement of removed, territorial 'P. orange cheek' individuals (Chapter 9, Figure 40) suggests that suitable sites may indeed be in short supply. The presence of non-territorial males within the size range of territorial fish (Table 13) supports this suggestion. Why the available sites are defended predominantly by males is unclear, unless the fact that the females have to leave their territories to spawn and brood their young makes territoriality less profitable for them while for the male a territory is an advantage (possibly essential) in attracting a mate.

Apparently either of the above suggestions could explain why 'P. orange cheek' females do not consistently defend territories.

Table 13. Measurements of the standard length of territorial and non-territorial 'P. orange cheek' males collected randomly at preselected depths on Thumbi East.

| | Depth | n | SL mm ( ± 1 S.E.) |
|---|---|---|---|
| Mature (adult coloration) non-territorial 'P. orange cheek' males | 2-3m | 20 | 80,4 ± 4,12 |
| Territorial 'P. orange cheek' males. | 2-3m | 20 | 94,0 ± 2,38 |
| Territorial 'P. orange cheek' males. | 10m | 19 | 87,4 ± 1,42 |

Finally, since 'P. orange cheek' have relatively broad mouths throughout their lives they are expected to defend territories as juveniles and adults. That this does not occur cannot be attributed to a shortage of territory sites since the majority of individuals hold territories over open rock and, as shall be argued in Chapter 9, these sites appear to be in plentiful supply. Since detailed data on the life history of this species is not available, no suggestion can be made to explain how this situation evolved.

Thus, with the possible exception of '*P.* broad mouth', the answers to the question asked on page 126 are in accordance with the hypothesis that the principal function of interspecific territoriality among the Mbuna of Monkey Bay is to defend a food supply. It is suggested that, although interspecific territoriality in these fish results in food resource subdivision, by space, the actual selective pressure which resulted in the evolution of this behaviour was more likely the need to ensure a food supply of high standing crop for those species or individuals otherwise incapable of competing with the more specialized,non-territorial species.

A further point in favour of this hypothesis is that the pattern in homologous communities throughout Lake Malawi is similar to that reported here for Monkey Bay. For instance, studies of epilithic algae grazing guilds at Nkhata Bay and Likoma island show that, here too, those species with apparently specialized feeding structures and feeding mechanisms (e.g. *Petrotilapia*, *Labeotropheus*, *Labidochromis* and *P. zebra*-like species) are non-territorial or intraspecifically territorial. The interspecifically territorial species, on the other hand, have primitive, broad mouthed, pecking feeding structures. This is true even though the actual species involved are invariably different from site to site.

Unfortunately there is very little data available on marine fish with which to test this hypothesis, since the majority of authors who suggest that these fish are defending a food supply do not consider why this should be necessary for some species but not others. The available data apply to three territorial, herbivorous acanthurids studied by Robertson *et al*. (1979). They found that the three species exhibit a gradient in the intensity of territorial defence and an inverse gradient in feeding efficiency as measured by their ability to feed in areas of low algal standing crop. Thus the largest species, *Acanthurus lineatus*, has the "largest, flattest mouth" and can consequently only feed efficiently on dense stands of algae. This species is highly territorial and defends a small territory from which all other benthic algal grazing species are excluded. These territories contain thick mats of algae. At the other end of the scale is *Zebrasoma scopas*, the smallest of the three species with an elongate rostrum and narrow mouth which impart a high feeding efficiency. As a result this species can feed on a lower standing crop mat of algae than either of the other two species. *Z. scopas* defends a large territory from which a few selected benthic algal grazing species only are excluded. The standing crop of benthic algae within these territories is low. The remaining species, *Acanthurus leucosternon*, falls between the above species in all characteristics. If this progression were taken one step further it may be predicted that a completely non-territorial species will have the highest feeding efficiency of all. In other words these results conform to the hypothesis suggested above for the Mbuna.

'*P*. aggressive' and '*P*. orange cheeck' show a similar progression to that reported by Robertson *et al*. (1979). '*P*. aggressive' is analogous to *A. lineatus* in that it vigorously defends small territories with thick algal mats and has a low feeding efficiency. '*P*. orange cheek' is similar to *A. leucosternon* in that it defends a slightly larger territory, allows some species to feed within the territory and has a standing crop of algae in the territory which is slightly higher than on surrounding rock yet lower than in '*P*. aggressive' territories. '*P*. orange cheek' may also have a slightly higher feeding efficiency than '*P*. aggressive' on account of its relatively narrower mouth.

There is also evidence that the predictions made on the basis of the present study are met in humming bird communities. Wolf & Stiles (1976) report that the territorial *Panterpe insignis* is 'broad niched' i.e. unspecialized, due to its bill size and body weight which allow exploitation of a wide array of flowers. Furthermore, Colwell (1973) concludes that 'Although body size and bill shape are complicating factors .... the humming bird species with the longest bill in any community is likely to be an interstitial species (i.e. non-territorial), since its morphology permits it nearly exclusive access to flowers with long corolla tubes even without resorting to behavioural defence against other species. Species with shorter bills, on the contrary, must defend their nectar resources behaviourally against long billed species."

Finally there is evidence that similar principles to the above may apply to invertebrate territoriality. Stimson (1970 &1973) reports that large individuals of the intertidal limpet, *Lottia gigantica*, defend territories from small *Lottia* and *Acmaca* species. He argues that this is because the latter are able, with their small radulae, to crop the algal film more closely than larger *L. gigantica*. In other words the large limpet has to exclude the smaller on an exploitation basis.

# CHAPTER 9

# SPACE UTILIZATION

An important point to emerge from TERRITORIALITY is that the four territorial Mbuna species studied defend territories from which the other interspecifically territorial species are excluded (i.e. their territories are non-overlapping), yet these territories occur side by side in the same habitat. This raises the question of why one species does not exclude the others by acquiring all the available space. The principal aim of this section is to answer this question.

## Subdivision of the space resource.

The invariable replacement of removed individuals by conspecifics (Figure 40 and Table 14) indicates a strong site specificity among the four interspecifically territorial species. This could be a result of one or more of the five factors considered below.

1. Neighbours holding territories adjacent to a vacated territory may influence which species occupies the site.

If territory owners attack conspecifics further from the territory centre than they attack other species they may prevent the colonization of nearby sites by conspecifics thereby allowing other species an opportunity to colonise these sites. This behaviour occurs in '*P*. orange cheek' (see Chapter 8) and may have a bearing on recolonization by this species. To test this possibility single mass removal experiments were conducted in which all territorial '*P*. orange cheek' and '*P*. aggressive' were removed from two 6 x 5m quadrates, thus removing the influence of neighbours. Sites within these quadrates were still re-occupied by conspecifics (compare a & b of Figure 41) indicating that neighbours do not play an important role in controlling which species re-occupies a particular site.

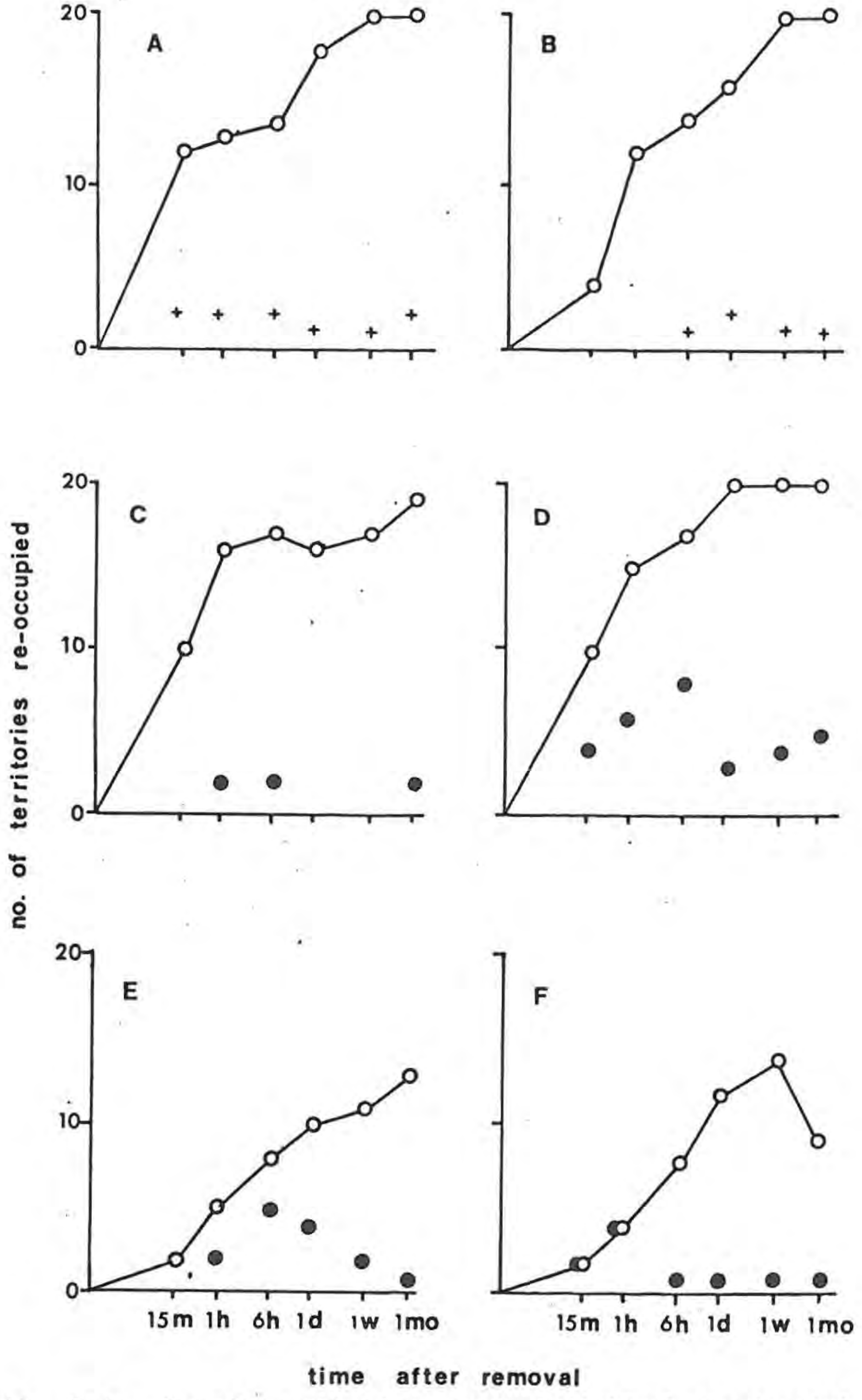


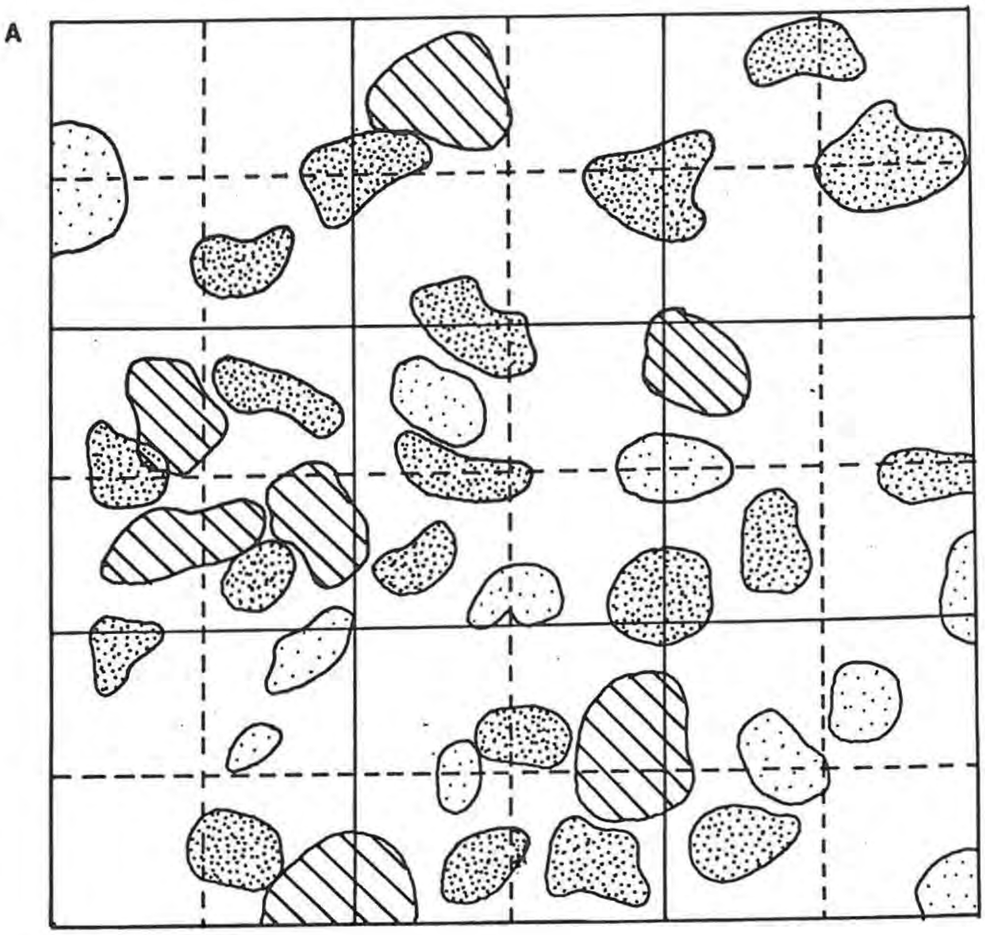
Figure 40. Rate of replacement of removed, individual territorial fish. ○ = total no. of territories re-occupied; + = no. of territories re-occupied by '*P.* aggressive' where the other territories are re-occupied by conspecifics of the removed species; ● = no. of territories re-occupied by '*P.* orange cheek' where all other territories are re-occupied by conspecifics of the removed species. A) '*P.* orange cheek' amongst broken rock on the Thumbi East site; B) '*P.* orange cheek' amongst broken rock at the Chisali site; C) '*P.* aggressive'>75mm SL amongst broken rock on the Thumbi East site; D) '*P.* aggressive'>75mm SL amongst broken rock at the Chisali site; E) '*P.* aggressive'<75mm SL on open rock at the Thumbi East site and F) '*P.* broad mouth' on open rock at the Chisali site. In each experiment 20 fish were removed. The horizontal axis has a 'log' scale. m = minutes; h = hours ; d = days; w = weeks; mo = months.

Table 14

Recolonization of artificially vacated '*P*. sky blue' territories on Thumbi East monitored between 1 week and 1 month after removal of the original owner. A total of 11 territorial fish were removed.

| State of Territory | *n* |
|---|---|
| Vacant | 3 |
| Reoccupied by '*P*. sky blue' adult males | 4 |
| Reoccupied by '*P*. sky blue' adult females | 1 |
| Reoccupied by '*P*. sky blue' juveniles | 1 |
| Reoccupied by '*P*. sky blue' juveniles | 1 |
| Reoccupied by '*P*. aggressive' >75mm SL | 1 |
| Reoccupied by '*P*. aggressive' <75mm SL | 1 |

Figure 41. Territories in a 6 x 6m quadrate at 3–5m depth on Thumbi East. A) before removal, and B) one month after the removal of all territorial fish. ▨ = '*P.* orange cheek'; ▒ = '*P.* aggressive' > 75mm SL; ░ = '*P.* aggressive' < 75mm SL.



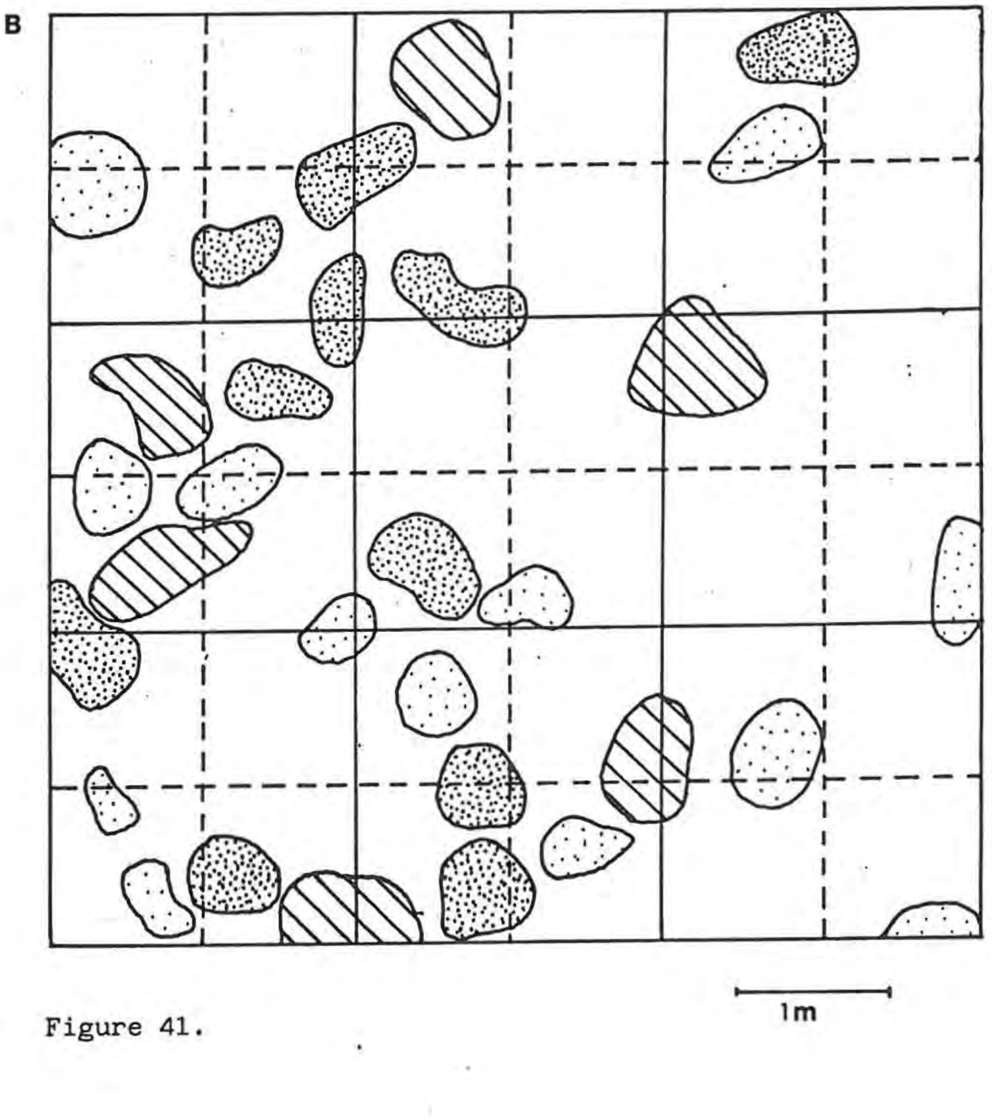


Figure 41.

2. Calothrix composition within the territory may be suitable for one species only.

It is unlikely that calothrix composition within a vacated territory is the sole factor affecting which species re-occupies that territory because:

a) in the shallows the calothrix composition within the territories of interspecifically territorial species is similar (Chapter 8, Figure 32) and
b) territories from which the majority of calothrix has been scrubbed are still repopulated by conspecifics of the original owner (Table 22).

Nonetheless,at five and ten metres there is a considerable difference in the composition within 'P. orange cheek' territories and the other territorial species (Figure 32). This could be an important factor affecting recolonization at these depths.

3. Species may specialize on (or be restricted by competition to) sites with a particular rock configuration.

The four territorial species were invariably asociated with characteristic rock configurations. This observation was quantified by classifying a random selection of territories between 2-4m depth, into one of the categories listed in Table 15. From this survey (Table 16) the following trends are apparent: 'P. orange cheek' often defend territories centred on a vertical face yet including some horizontal or sloping rock(s) at the bottom of the face; other territories of this species are situated in crevices. Territories of 'P. broad mouth' are invariably on a horizontal open rock and include a shallow crack or depression. The territories of large individuals of 'P. aggressive' (>75mm SL) are commonly found in crevices but may also

# Table 15

Categories of territory site based on rock configuration.

1. Horizontal Open Rock: Sites without shelter, situated on open rock with a slope of 0-45° from the horizontal
2. Horizontal Open Rock with Depression: Site on open rock with a slope of 0-45° from the horizontal and containing a small crack or depression.
3. Vertical Open Rock: Site without shelter, situated on open rock with a slope of 45-95° from the horizontal.
4. Crevices: Site situated in a crevice the sides of which do not diverge more than 90°.
5. Exposed Vertical Face with Shelter: Site on a vertical face, facing open water (i.e. not in a crevice) and containing shelter in the form of a crack or hole. The most common form is a territory situated on an unbroken vertical face and including some horizontal rock and shelter at the base of the face.
6. Small Rock: Site situated predominantly over rocks with a diameter of less than 20 cm.

use a site at the base of a vertical face. Territories of small 'P. aggressive' appear more frequently on open rock and over patches of small rock. Finally, 'P. sky blue' territories are almost entirely confined to small rock zones. A cross section of a typical field situation is given in Figure 42.

Chi-square tests on partially grouped data,(Table 16) show that all comparisons of the species' utilization of territory sites with different rock configurations are significantly different at the 1% level, with the exception of the 'P. orange cheek' - 'P. aggressive' (large) comparison, which is not significant. The reason for this high overlap is that both 'P. orange cheek' and large 'P. aggressive' occupy relatively high proportions of crevice sites and sites at the base of vertical faces. 'P. orange cheek' is, however, larger than 'P. aggressive' and occupies larger territories (Tables 4 & 9). The territories of 'P. orange cheek' may therefore be situated in larger crevices and on larger rock faces than those of 'P. aggressive'. This possibility was investigated by measuring the width and depth of crevices occupied by these species and the area of the largest vertical face incorporated either partially or wholly into their territories. It was found that 'P. aggressive' occupy sites which are smaller ($p > 0,02$) than 'P. orange cheek' sites in all these dimensions (Table 17). Thus there is a strong correlation between the rock configuration and/or size of a territory site and the species occupying that site.

4. Position of the territory site relative to habitat variables such as rock size, depth and sediment levels may be important.

There were no sites available around Monkey bay which exhibited a smooth gradation from very large rocks to very small rocks. The correlation between the rock configuration and size of territory site and the species occupying it suggests that if a site with graded rock size was found the distribution of territorial fish would be as follows:

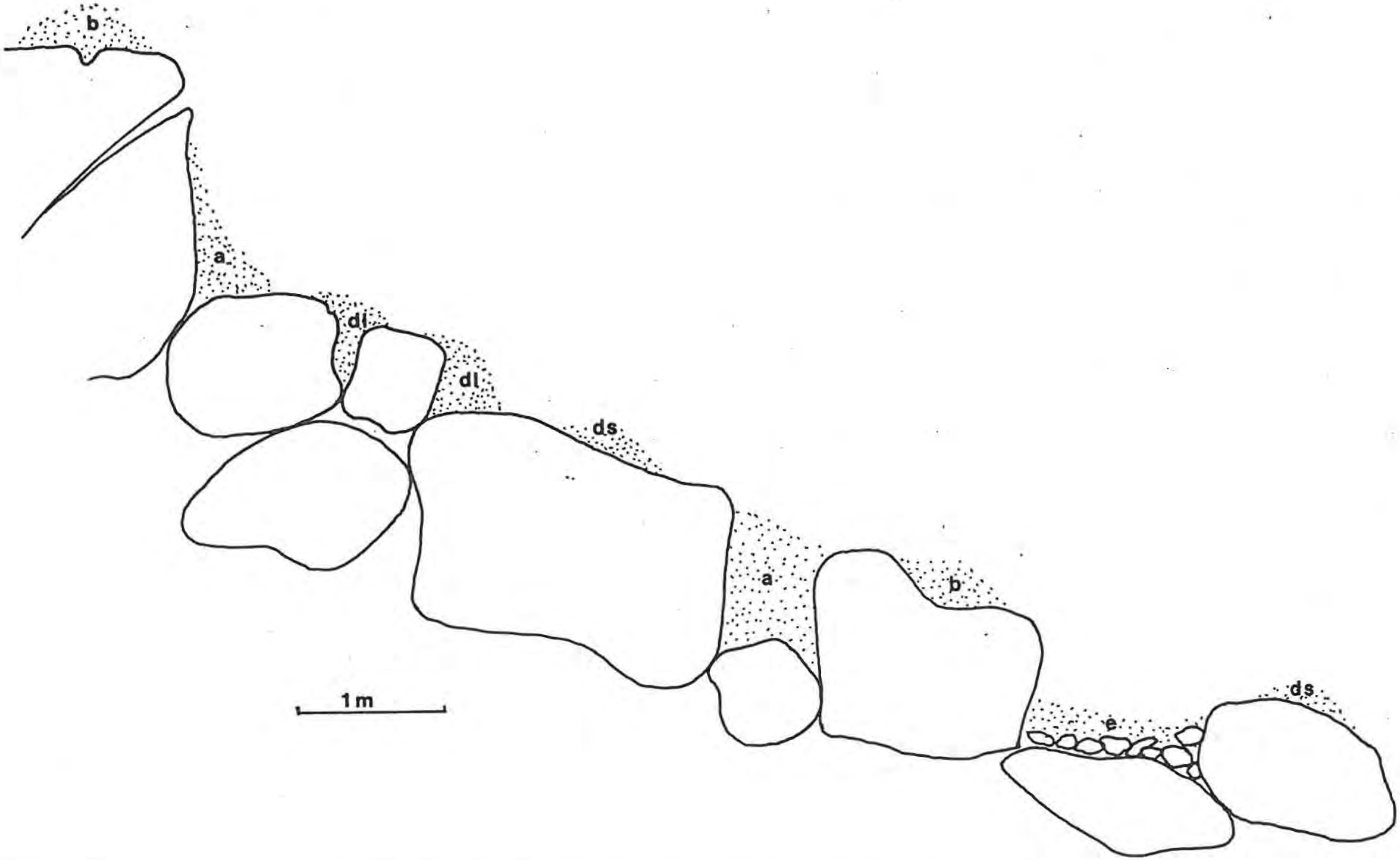


Figure 42. Diagram showing typical partitioning of territory sites on the rocky shores near Monkey Bay. a = 'P. orange cheek'; b = 'P. broad mouth'; dl = 'P. aggressive >75mm SL; ds = 'P. aggressive' <75mm SL; e = 'P. sky blue'. The stippled area represents the portion of the water column in which the territorial fish is commonly found.

### Table 16

The proportion of different territory site categories occupied by the interspecifically territorial species between 2-4m depth. All readings were taken on Thumbi East except for those of '_P_. broad mouth' which were taken at Chisali.

| Species | Horizontal Open Rock | Horizontal Open rock with depression | Vertical Open rock | Crevice | Exposed Vertical face with shelter | Small Rock | n |
|---|---|---|---|---|---|---|---|
| '_P_. orange cheek' | – | 0,019 | 0,096 | 0,385 | 0,462 | 0,038 | 52 |
| '_P_. broad mouth' | 0,05 | 0,7 | – | 0,175 | 0,075 | – | 40 |
| '_P_. aggressive' >75 mm SL | 0,085 | 0,017 | 0,017 | 0,59 | 0,186 | 0, 10 | 59 |
| '_P_. aggressive' <75 mm SL | 0,545 | 0,125 | 0,068 | 0,136 | 0,023 | 0,102 | 88 |
| '_P_. sky blue' | – | – | – | 0,042 | – | 0,958 | 24 |

Table 17

Critical dimensions of territory sites used by '_P._ orange cheek' and '_P._ aggressive' >75 mm SL between 2-4 m on Thumbi East. (Mean ± 1 S.E.)

| | '_P._ orange cheek' | '_P._ aggressive' |
|---|---|---|
| Crevice width (cm) | 57,2 ± 3,67 (n=37) | 29,5 ± 2,4 (n=50) |
| Crevice depth (cm) | 99,9 ± 7,9 (n=37) | 49,3 ± 3,8 (n=50) |
| Area of largest rock face ($m^2$) | 1,77 ± 0,59 (n=20) | 0,30 ± 0,034 (n=20) |

Over large rocks where faces and rocks are largest, 'P. broad mouth' and small 'P. aggressive' would be common on the faces and 'P. orange cheek' in cracks. Large 'P. aggressive' densities might peak at intermediate rock sizes and 'P. sky blue' and small 'P. aggressive' (again) over very small rocks.

Other habitat continua such as depth and sediment levels also appear to affect space resource subdivision and may compliment subdivision by rock configuration. The overlap of territory distributions with respect to depth and abundance on the two work sites, one of which (Chisali) has higher sediment levels than the other (Thumbi East), was calculated using Pianka's (1973) formula on the data presented in Chapter 7. These overlaps are given in Table 18. The overlap was also calculated for the usage of sites of different rock configurations (Table 19). The combined overlaps considering distribution by both depth and rock configuration is the product of the overlaps along individual dimensions. These overlaps are all small (Table 20) (a complete overlap would equal one). The largest overlaps are between 'P. orange cheek' - 'P. aggressive' (large) and 'P. aggressive' (large) - 'P. aggressive' (small). The true 'P. orange cheek'-'P. aggressive' (large) overlap has been shown to be lowered by their utilization of different sized cracks and faces. The high interspecific overlap need not be considered here. The remaining species have very small overlaps indicating that they are efficiently subdividing the space resource by 3 and 4 above.

## Table 18

Overlaps of distribution with depth at the two work sites (Thumbi East and Chisali) calculated for the four interspecifically territorial species using Pianka's formula (1973).

| | '*P*. sky blue' | '*P*. broad mouth' | '*P*. orange cheek' | '*P*. aggressive <75 mm SL |
|---|---|---|---|---|
| '*P*. aggressive' >75 mm SL | 0,7666 | 0,4386 | 0,8060 | 1,000 |
| '*P*. aggressive' <75 mm SL | 0,7666 | 0,4386 | 0,8060 | |
| '*P*. orange cheek' | 0,1806 | 0,6539 | | |
| '*P*. sky blue' | 0,2088 | | | |

## Table 19

**Overlaps of the utilization of territories according to their rock configurations, calculated using Pianka's fomula (1973).**

| | '*P*.sky blue' | '*P*.broad mouth' | '*P*. orange cheek' | '*P*.aggressive <75 mm SL |
|---|---|---|---|---|
| '*P*. aggressive' >75 mm SL | 0,2001 | 0,2894 | 0,8263 | 0,3924 |
| '*P*. aggressive' <75 mm SL | 0,1834 | 0,3275 | 0,2114 | |
| '*P*. orange cheek' | 0,0906 | 0,2606 | | |
| '*P*. broad mouth' | 0,0179 | | | |

## Table 20

Combined overlaps from rock configurations (Table 18) and depth (Table 19).

| | '*P*. sky blue' | '*P*. broad mouth' | '*P*. orange cheek' | '*P*. aggressive' <75 mm SL |
|---|---|---|---|---|
| '*P*. aggressive' >75 mm SL | 0,1534 | 0,1269 | 0,6659 | 0,3924 |
| '*P*. aggressive' >75 mm SL | 0,1406 | 0,1436 | 0,1704 | |
| '*P*. orange cheek' | 0,0164 | 0,1704 | | |
| '*P*. broad mouth' | 0,0025 | | | |

5. A learning process may occur whereby individuals 'know' that a conspecific previously occupied the vacant site which is therefore suitable for them.

Since a learning process alone could not account for the differential use of sites according to rock configuration and depth it is assumed that learning does not play an important role in territory re-occupancy.

It is concluded that space is divided between the four interspecifically territorial species by the differential use of territory sites according to their rock configuration, size, position on the shore and possibly, in the case of 'P. orange cheek', calothrix composition.

The next step was to determine whether these differences in space utilization are a result of chance processes, specialization or competitive exclusion (see Chapter 3 for a review of these).

The distribution of fish in territory sites at Monkey Bay is clearly non-random thus ruling out the possibility that chance plays an important role in site allocation. This leaves the possibilities of subdivision by specialization or competitive exclusion, either of which are feasible.

Competitive exclusion is indicated by the sparsity of 'P. orange cheek' territories in the shallows of Thumbi East (Figure 20). They may be excluded from this (assumed) optimal zone by the abundant 'P. aggressive'. On the other hand,specialization is indicated by the correlation between fish size and territory site size and between diet and calothrix composition in the territories.

An experimental approach was adopted to distinguish between competition and specialization. Originally an enclosure was constructed for this purpose but it was of no value because the fish did not form territories under these artificial conditions. Mass removals were therefore conducted whereby one species was repeatedly removed from designated areas thus giving the other species maximum opportunity to occupy the vacated sites. Despite the small areas involved this was surprisingly successful at keeping the densities of the removed species down (Table 21).

Before it could be assumed that the vacated territories were available for occupation by the undisturbed species it had to be shown that the failure of the conspecifics of the removed species to repopulate was due to depletion of potential colonizers in the immediate neighbourhood and not to reduction of the Aufwuchs standing crop within the undefended territories. With this aim, the territories of ten '_P._ orange cheek' and ten '_P._ aggressive' were scrubbed with a wire brush to remove most of the Aufwuchs (the remaining standing crop was only $1{,}8 \pm 0{,}26$ $gm^{-2}$). The territory owners were removed and re-occupancy was monitored after 1 day and 1 week. Scrubbed territories were still rapidly re-occupied by conspecifics of the original tenant (Table 22) indicating that reduction of standing crop alone cannot account for any lack of recolonization of vacated territories within removal quadrates.

It can therefore be assumed that under the above conditions, no interchange of territories will occur between species if specialization is the only means of space subdivision. If competitive exclusion is occurring, however, the removal of the dominant species will be followed by rapid replacement by the subordinate species, but territories vacated by the subordinate species will not be taken over by the dominant species.

A third possibility is a combination of the above two extremes. The species involved may specialise on different types of territory site yet be in competition for sites with characteristics between the two.

## Table 21

Rate of influx of fish into repetitive mass removal quadrates as measured by the rate of removal of fish from these quadrates. Numbers represent the combined number of fish removed from two replicate quadrates (each 6 x 6 m) on consecutive days. The high removal on day one is a result of movement of individuals into the quadrate during the course of the removal operation.

| | No. of fish initially present. | No. of fish removed on day: 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| 'P. orange cheek' | 16 | 16 | 9 | 7 | 5 | 4 | 1 | – |
| 'P. aggressive' 60–75 mm SL | 12 | 34 | 14 | 1 | – | – | – | – |
| 'P. aggressive' > 75 mm SL | 37 | 53 | 11 | 2 | 1 | 1 | – | – |

## Table 22

Recolonization of artificially vacated territories from which the calothrix mat had been scrubbed. Territories were monitored 1 day and 1 week after the removal of the owner. (n=10)

| | 'P. orange cheek' Removal | | 'P. aggressive' Removal | |
|---|---|---|---|---|
| | 1 Day | 1 Week | 1 Day | 1 Week |
| Replaced by 'P. orange cheek' | 5 | 6 | 2 | – |
| Replaced by 'P. aggressive' | – | – | 7 | 8 |
| Still vacant | 5 | 4 | 1 | 2 |

In this case the removal of either species will be followed by the occupation of some of the vacated territories by the other species.

The results (Table 23, Figures 43 & 44) are closest to the latter of the three possibilities presented above since both species occupy some of the vacated sites of the other species when they are available.

A summary of the results in point form, follows.

1a) 52 territories were made available by the removal of '*P.* aggressive'. After six months five of these were occupied by '*P.* orange cheek'.

1b) 16 territories were made available by the removal of '*P.* orange cheek'. After six months eight of these were occupied by '*P.* aggressive'.

2a) After six months the total number of '*P.* orange cheek', in the quadrates from which '*P.* aggressive' had been removed, had increased by 50%.

2b) After six months the total number of '*P.* aggressive', in the quadrates from which '*P.* orange cheek' had been removed, had increased by 9,8%.

2c) After six months in undisturbed quadrates the total number of '*P.* orange cheek' had increased by only 6,6% while the '*P.* aggressive' population had decreased by 13,2%.

3a) After six months 41,7% of the '*P.* orange cheek' population, in the quadrates from which '*P.* aggressive' had been removed, was located in territory sites originally belonging to '*P.* aggressive'.

3b) After six months 12% of the '*P.* aggressive' population, in the quadrates from which '*P.* orange cheek' had been removed, was located in territory sites originally belonging to '*P.* orange cheek'.

3c) In the undisturbed quadrates there was no interchange of territory sites between '*P.* orange cheek' and '*P.* aggressive'.

## Table 23

Results of mass removal experiments. All figures represent totals from two 6 x 6 metre quadrates between 3-5m depth on Thumbi Eas
M = month.

### '*P.* orange cheek' Removals

| | No. initially present | No. removed (total) | Time After Removal. 2 Days | 1 Wk | 1 M | 2 M | 3 M | 4 M | 5 M | 6 M |
|---|---|---|---|---|---|---|---|---|---|---|
| Total no. of '*P.* orange cheek' | 16 | 40 | 1 | 1 | 1 | 1 | 2 | 4 | 5 | 5 |
| Total no. of '*P.* aggressive' >75 mm SL | 36 | | 38 | 37 | 35 | 35 | 32 | 36 | 36 | 39 |
| Total no. of '*P.* aggressive' <75 mm SL occupying '*P.*orange cheek' sites | | | 1 | 1 | 1 | 1 | ½ | | | |
| Total no. of '*P.* aggressive' >75 mm SL | 25 | | 27 | 27 | 29 | 32 | 32 | 29 | 26 | 27 |
| Total no. of '*P.* aggressive' <75 mm SL occupying '*P.* orange cheek' sites | | | | 1 | 3 | 5 | 4 | 8 | 8 | 8 |

### '*P.* aggressive' Removals

| | No. initially present | No.removed (total) | Time After Removal. 2 Days | 1 Wk | 1 M | 2 M | 3 M | 4 M | 5 M | 6 M |
|---|---|---|---|---|---|---|---|---|---|---|
| Total no. '*P.* aggressive' >75 mm SL | 36 | 68 | 6 | 6 | 7 | 6 | 7 | 8 | 10 | 9 |
| Total no. '*P.* aggressive' <75 mm SL | 16 | 49 | 13 | 8 | 6 | 7 | 5 | 12 | 22 | 23 |
| Total no. of '*P.*orange cheek' | 8 | | 12 | 13 | 15 | 12 | 9 | 11 | 11 | 12 |
| Total no. of '*P.* orange cheek' occupying '*P.*aggressive' sites | | | 4 | 6 | 8 | 6 | 4 | 5 | 5 | 5 |

Figure 43. Territories in a 6 x 6m quadrate at 3-5m depth on Thumbi East. A) before removal, and B) 6 months after the repetitive mass removal of all territorial '*P.* orange cheek'; ▨ = '*P.* orange cheek'; ▒ = '*P.* aggressive' > 75mm SL; ░ = '*P.*aggressive' < 75mm SL; □ = '*P.* sky blue'.

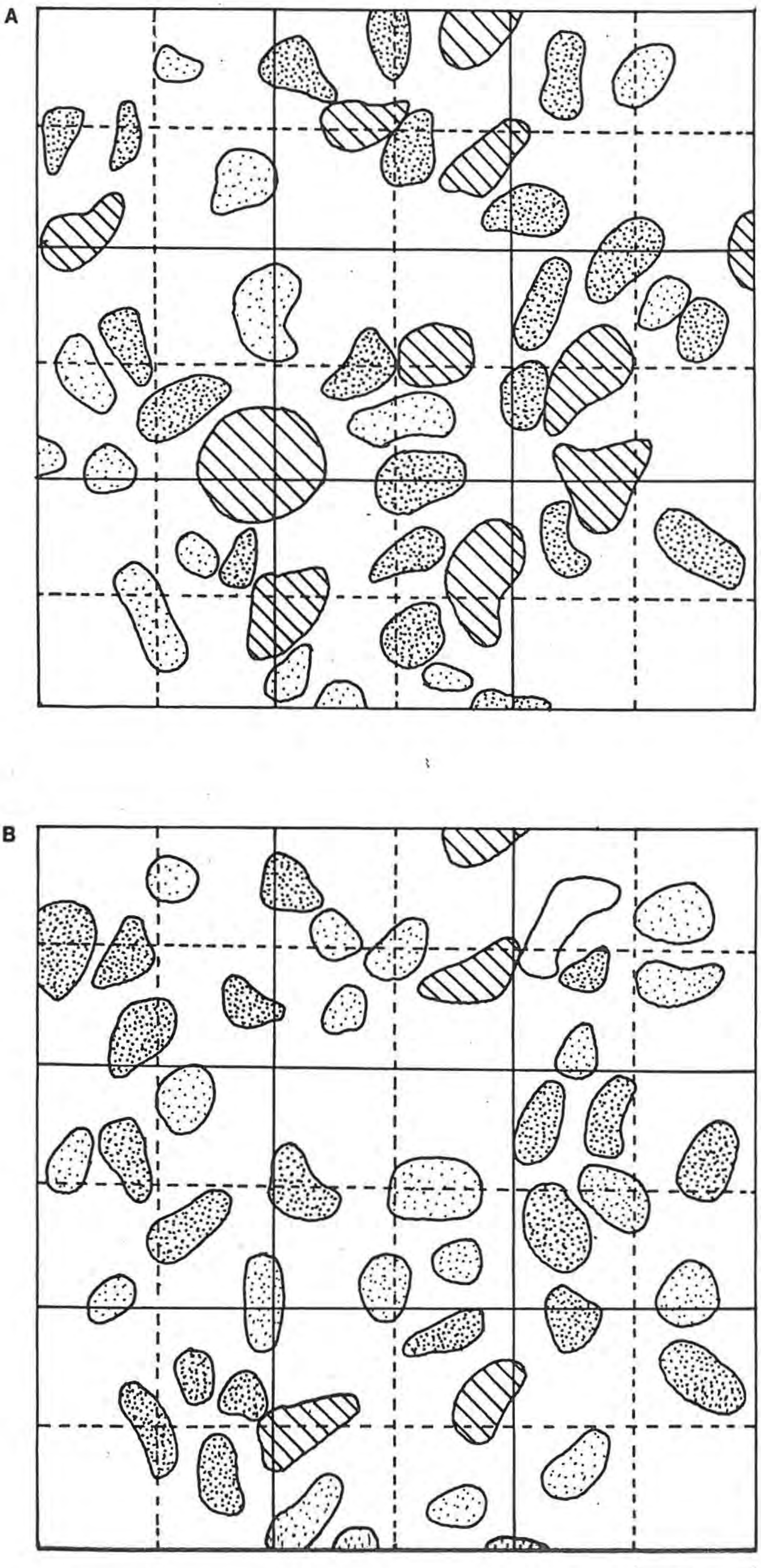


Figure 43.

Figure 44. Territories in a 6 x 6m quadrate at 3-5m depth on Thumbi East. A) before removal, and B) 1 months after the repetitive mass removal of all territorial '*P*. aggressive'. Individuals occupying the territories marked with a cross could not be caught. ▧ = '*P*. orange cheek'; ▒ = '*P*. aggressive' >75mm SL; ░ ='*P*. aggressive' <75mm SL' □ = '*P*. sky blue'.

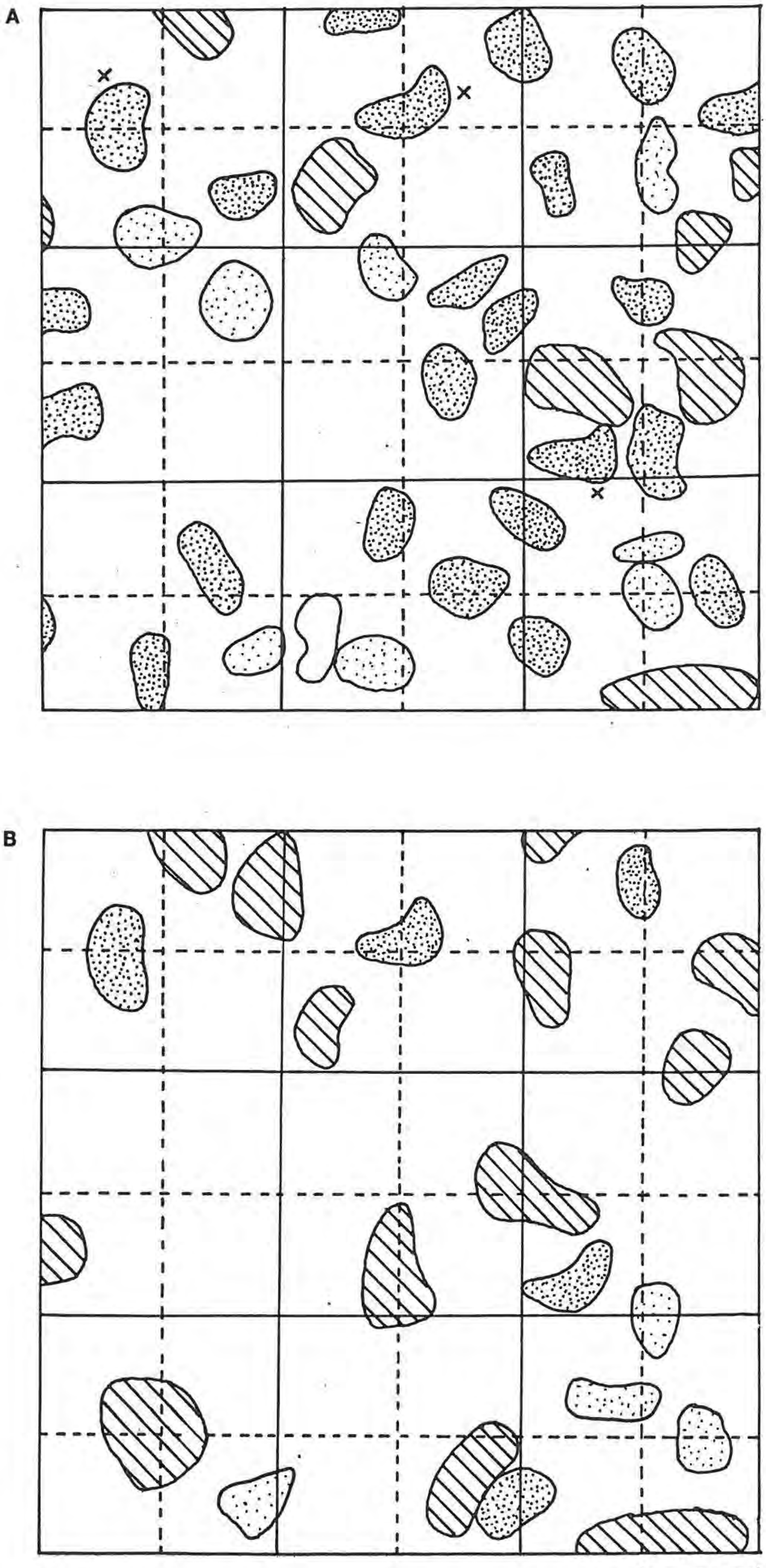


Figure 44.

From these results the following is concluded:

1. The incomplete colonization, by either species, of the territories originally belonging to the other species shows that some specialization is occurring.
2. The increase in numerical density in both species when the other is removed (compared to smaller or negative increases in undisturbed quadrates) suggests that competition is present.
3. The greater numerical increase shown by '_P_. orange cheek' relative to '_P_. aggressive' is probably due to the larger number of '_P_. aggressive' territories available for colonization.

These conclusions hold true only for the conditions under which the experiments were conducted i.e. between 3-5m depth on Thumbi East between April and October.

### Space as a limiting resource.

Sale (1974), working on a guild of coral reef fish, found that virtually all available rubble was occupied by interspecific territories of one or other of the guild species (pomacentrids) present. He concluded that the guild is space limited. In contrast the proportion of available space occupied by the four interspecifically territorial species at Monkey Bay seldom exceeds 30% (Table 24). Nonetheless artificially vacated territories in the shallows (1-4m) are rapidly re-occupied (Figure 40). This is true even when territories are scrubbed clear of Aufwuchs prior to removal (Table 22). From this it follows that territory sites in the shallows are in short supply and that the unoccupied space is unsuitable for one of the following reasons:

## Table 24

Percentage of the total available space occupied by interspecifically territorial species over broken rock. 'n' gives the number of mapped 6 x 6 m quadrates from which this data was calculated.

| Site | Depth | n | '*P.* orange cheek' | '*P.* aggressive' <75 mm SL | '*P.* aggressive' >75 mm SL | '*P.* broad mouth' | '*P.* sky blue' | Total |
|---|---|---|---|---|---|---|---|---|
| Thumbi East | 3-5 m | 8 | 8,6 | 6,6 | 10,5 |  | 3,7 | 29,4 |
| Thumbi East | 10 m | 2 | 13,7 | 1,0 | 2,8 |  |  | 17,5 |
| Thumbi East | 20 m | 1 | 16,3 |  |  |  |  | 16,3 |
| Chisali | 3-5 m | 3 | 12,8 | 6,1 | 5,5 | 0,6 |  | 25,0 |

1. The unused space may be unavailable if species other than the four interspecifically territorial species prevent its occupation. It would obviously be advantageous to non-interspecifically territorial species to restrict colonization by the interspecifically territorial species wherever possible. All space occupied by the four interspecifically territorial species is unavailable to the other guild members.

2. Territory boundaries seldom abut (Figures 43 & 44). It is therefore expected that some space between established territories will be unsuitable, either because it is too small or because it is too near to adjacent territories.

3. Some rock configurations may be unsuitable for territories, particularly open rock without shelter. Although small 'P. aggressive' and 'P. broad mouth' may defend territories over open rock these sites are seldom utilized by large 'P. aggressive', 'P. orange cheek' or 'P. sky blue' (Table 16). That this is not due to a shortage of such sites is indicated by the slow and incomplete replacement of individuals removed from territories on these rocks (Figure 40) and by the presence of many large areas of undefended open rock, even in the densely populated shallows (unquantified personal observation). This suggests that open rock may be unsuitable for colonization by large 'P. aggressive', 'P. orange cheek' and 'P. sky blue'. It is unclear whether this is due to lack of shelter, increased energy expenditure required to defend these exposed sites (see Chapter 8) or some other factor.

It is concluded that although space in general does not appear to be in short supply on the rocky shores of Monkey Bay, the amount of space which is suitable for territories of 'P. orange cheek', 'P. sky blue' and large 'P. aggressive' is apparently limited.

# CHAPTER 10

# DISCUSSION

## Aufwuchs superabundance.

In the light of the present findings it is interesting to re-evaluate Fryer's (1959) conclusions i.e. that there is very little food subdivision between the members of the epilithic algal grazing guild and that their coexistence relies upon a superabundance of food.

From the present study it is obvious that there are in fact several mechanisms whereby food is subdivided between the species i.e. segregation by depth, feeding mechanism, mouth width, tolerance to wave action and territoriality. Although the presence of food subdivision does not indicate a food shortage, it is difficult to envisage how some of these mechanisms could have evolved without food shortage as the selective pressure. For instance, why did the specialized feeding structures of the Petrotilapia, Labidochromis and Labeotropheus species evolve if not in response to a shortage of food? Why expend energy defending a feeding territory if there is no shortage of food?

I conclude that, although a shortage of food in the evolutionary past does not necessarily indicate a shortage of food at the present, it cannot be assumed that all the epilithic algal grazing species are now so well adapted that they all have abundant food. Indeed there is no more need to propose a food superabundance for the Lake Malawi epilithic algae grazing fish than there is for the benthic algae grazing marine fish, which may show similarly high diet overlaps (Randall, 1961; Jones, 1968).

## Feeding territories in freshwater fish.

It is interesting to consider why interspecific territoriality is common among coral reef fish (see Chapter 3 for a literature review) whereas the present instance is the only clear case in which the interspecific defence of a food supply is known to occur in freshwater fish.

There are probably many requirements which need to be met before interspecific defence of feeding territories will evolve. I make no attempt to list all of these. However, three in particular are favourably met in Lake Malawi. They are that the food resource must be reliable and defensible and that the selection pressure for its defence must be present.

Taking these in order, a food resource that is subject to large fluctuations in abundance (usually annual) and periodic shortages would be a poor investment to defend since the territory owner may find itself without a food supply despite the time and energy put into its defence. From this point of view the resources in a tropical habitat, particularly an aquatic one, will be most likely to meet the requirements of reliability since they are not subject to the vagaries of climate found in higher latitudes.

Secondly, in order to be defensible, the food resource must be benthic. Obviously the defence of a planktonic or other mobile food resource is impractical. Furthermore the resource must be sufficiently productive that the area supplying the territory owner's needs is small enough to be economically defensible. Once again a tropical habitat is most likely to fulfil these requirements as the high productivity of the low latitudes is well documented (Brylinksy & Mann, 1973; Whittaker, 1975). It also follows that primary consumers will be more likely to evolve feeding territories than secondary consumer since productivity will decrease with each trophic level removed from the primary producers.

Finally, before interspecific defence of a food supply will evolve, the necessary selective pressure in the form of competitors for food must be present. Orians & Wilson (1964) have suggested that the presence of many species using the same resource will lower the chances of co-existence by specialisation (exploitation strategies) and hence increase the chance of interspecific territoriality evolving. It is in this feature that Lake Malawi has greater potential than any other fresh water lake (with the possible exception of Lake Tanganyika which has yet to be studied in detail). At Monkey Bay the epilithic algal grazing guild has 19 recorded members, and further north (Nkhata Bay and Likoma Island) similar guilds may contain twice as many species (Ribbink _et al._, in press). Although precise figures are not available for other tropical lakes only Lake Tanganyika can boast anywhere near as diverse an array of species (Fryer & Iles, 1972).

Of the three requirements for interspecific territoriality discussed above only the high diversity of competitors is unique to Lake Malawi (among fresh water lakes), and it may therefore be that this is one of the important differences explaining how interspecific territoriality evolved in Lake Malawi but not in other tropical lakes. A similar trend occurs in the marine environment where coral reefs, the other habitat in which interspecific territoriality is common, are similar to Lake Malawi in that they are also tropical and have a high diversity of species.

## Species Diversity.

It is now a well documented fact that tropical communities are, as a rule, more diverse (in species) than analogous communities in higher latitudes (Fischer, 1960; MacArthur, 1965; Paine, 1966). Lake Malawi is no exception to this rule in that it is situated in the tropics and has more fish species than any other freshwater lake. In the course of the last twenty years numerous theories to explain the high species diversity in the tropics have been proposed (Krebs, 1972; MacArthur, 1972; Pianka, 1974; Sale, 1977). I shall not add to this already enormous body of literature but shall merely discuss the possible effect the presence of interspecifically territorial species may have on the diversity within the guild to which they belong.

Wolf & Stiles (1976) suggest that the presence of the interspecifically territorial humming bird, Panterpe insignis, reduces the diversity in the community of which it is a member by monopolising a wider range of resources than would be possible by a non-territorial species (because competition with other species would force it to specialise). This reduction of diversity will only occur when the territorial species dominates all, or most, of the available resource and thereby markedly reduces the amount available to non-territorial species. At Monkey Bay the four interspecifically territorial species studied occupy only 30% of the available space in 3-5 metres of water and less in deeper water (Table 24). The remaining space is freely available for use by non-territorial species. Thus if one assumes that all available, non-territorial, niches are filled, the addition of territorial species to a community represents an increase in diversity which would not otherwise be possible.

Furthermore territories represent an added dimension to the niches of many non-territorial species. For instance, at Monkey Bay C. taeniolatus, P. zebra and P. auratus are regularly seen feeding within 'P. orange cheek' territories. It is possible that this gives them an advantage over other guild members, which may be critical to their coexistence In addition, the three species of Petrotilapia feed largely in the territories of 'P. orange cheek' and 'P. aggressive'. Marsh (1981) has shown that the males of each Petrotilapia species utilize the territories of different territorial species and size classes. Once again this could be an important factor governing the coexistence of these similar congeners.

I conclude that, far from reducing the diversity of the epilithic algae grazing guild at Monkey Bay, the presence of interspecifically territorial species may well increase diversity both directly, by their own presence increasing the number of species, and indirectly, by adding an extra dimension along which non-territorial species may subdivide resources.

## Community Stability

This is a large and controversial subject which shall not be reviewed in detail here. It is relevant, however, to briefly consider some of the literature on stability in coral reef fish assemblages. Again I turn to these assemblages for a comparison because of the many similarities in ecology between them and the epilithic algae grazing guild at Monkey Bay. What little information is available on the temporal stability in coral reef fish communities has been adequately reviewed by Sale (1980; in press). He points out that although the traditional view is that these ecosystems (along with other tropical ecosystems) are by nature stable, much of the data used in support of this theory in fact leads to the conclusion that "assemblages of reef fish are not particularly persistent in structure". That reef fish assemblages are temporally unstable with respect to species number and composition is further supported by Sale's own work and that of his co-workers (Sale, 1974, 1975, 1978a, 1978b, 1980b; Sale & Dybdahl, 1978). Two studies conducted at sites only 20km apart at the southern end of the Great Barrier Reef bear on this problem. Firstly the study of a guild of interspecifically territorial pomacentrids resident on rubble patches at Heron Island has shown that the species composition at a particular study site may vary with time, that space is apparently distributed by chance and that populations, when disturbed by removal, show no trend to return to the original species composition or distribution. A second study on the species composition on patch reefs in One Tree Island lagoon (Sale & Dybdahl, 1978; Sale, 1980a) resulted in a similar conclusion; once again species composition on a particular reef varied with time and reefs denuded of fish did not regain their original species composition during the period of observation.

Although there are no data for Lake Malawi cichlids which are directly comparable to Sale's studies, the present monitoring of 6 x 6m quadrates on Thumbi East, while of relatively short duration, does supply some information on the stability of the territorial populations of '_P_. orange cheek' and '_P_. aggressive'. These data (Tables 8 & 23, Figures 37 & 40) suggest that, unlike coral reef fish, these populations are both temporally stable (when undisturbed) and may rapidly regain their original species composition and distribution after limited disturbance.

What are the prime factors responsible for these differences in the otherwise similar populations? I suggest that the answer lies in the vastly different reproductive strategies used by coral reef fish and cichlids. All the species in the territorial guild studied by Sale have pelagic larvae, hence potential recruitment to a given habitat patch is probably entirely unrelated to fish density on that patch. This is an essential prerequisite to the lottery hypothesis proposed by Sale (1974, 1976, 1977) (see page 11) to explain the coexistence of the territorial reef fish guild.

Cichlids on the other hand do not have a pelagic stage in their life history, and the Mbuna are apparently highly sedentary both as juveniles and adults. The strong site attachment of adults is well illustrated by the present study and, although there is no proof as to the sedentary nature of juveniles, their occurrence in narrow cracks and among small stones (personal observation) makes the possibility of long range migrations by these individuals unlikely. As a consequence of this life history, the populations on a particular patch of habitat (in this case a rocky shore bounded on either side by a beach) are essentially closed i.e. their survival depends upon recruits from their own members only.

It is obvious that a certain amount of migration occurs between habitat patches because most species are distributed across several patches. On the other hand there may be marked differences in coloration between populations of a single species which are separated by less than 5km (personal observation). Migration is obviously limited and probably insufficient to ensure the continued existence of these species on patches where they are periodically forced to extinction by chance processes. It is therefore predicted that, in contrast to territorial coral reef fish, territorial cichlids will subdivide space in a predictable, non-random fashion and that chance will not play an important role in the allocation of space between the species. This is indeed the case as has been shown in Chapter 9.

Since territory sites are apparently in short supply (Chapter 9), the number of territorial fish on a given site is a function of the number of suitable sites, and this number is presumably constant. The relative proportion of the four territorial species present will be a function of the nature of the sites available and an interspecific competition function which dictates which species occupies sites which are suitable for two or more species. Thus the number of territorial fish present at a particular site is a function of three constants and is therefore expected to be constant allowing for some variation resulting from chance factors and possibly an annual cycle.

It is suspected that the lower stability apparent among the territories of small '_P_. aggressive' relates to the greater availability of sites on open rock which these individuals occupy (Chapter 9). If territory sites are not limiting, then the three functions controlling numbers in the other territorial fish will not apply. Small '_P_. aggressive' numbers are therefore expected to vary according to the extent of recruitment and mortality within the population. Since it has been shown that breeding is seasonal in many of these species (B.A. Marsh, pers.comm.), a longer monitoring of the 6 x 6m quadrates would probably reveal an annual cycle of abundance of fish on suboptimal, open rock territory sites.

It is concluded that the community of interspecifically territorial species at Monkey Bay are stable with respect to the species occupying a particular site and in numbers of territorial '*P*. orange cheek' and large territorial '*P*. aggressive'. This stability is a result of and neccessitated by the lack of a dispersive stage in these species which makes it essential that the space resource is subdivided in a non-random fashion if the adults are to coexist.

## Commercial exploitation

With the improved technology of the 70's and the simultaneously increasing interest in rearing aquarium fish as a hobby, an important export trade in live ornamental fish from Lake Malawi developed. Owing to their small size and often bright coloration, epilithic algae grazing fish form the majority of this trade. Although the number of fish removed by the ornamental fisheries is negligible when compared, for instance, to the quantity of food fish caught, studies by Ribbink (1976) and Ribbink *et al.* (in press) revealed that many of the exported species have very restricted distributions and hence small total population numbers. Ribbink concluded that some species may be in danger of overexploitation and made recommendations regarding the conservation of these fishes to the Malawian Fisheries Department.

One of the terms of reference of the Malawi ornamental fisheries project was to advise on the level of exploitation which the populations of fish exported by the ornamental fish trade could sustain. Since a large variety and number of species are regularly caught and exported it was impractical to attempt a detailed analysis of each species. Instead a work program was planned which focussed attention on certain species groups which occur at Monkey Bay. Prominent among these was the epilithic algae grazing guild reported in this thesis.

Although this guild differs markedly in species composition from homologous groups in other areas of the lake, the work carried out by project members at three widely dispersed sites, Monkey Bay, Likoma Island and Nkhata Bay, suggests that the basic community structure is similar in all epilithic algae grazing guilds throughout the lake. For example, each site studied has several interspecifically territorial species including P. tropheops-like, and P.fuscus-like species, similar to those dealt with in this thesis, although the actual species involved are often different. Also present are members of the genera Labidochromis, Labeotropheus and Petrotilapia and P. zebra-like species which are morphologically similar to species found at Monkey Bay and apparently fill similar ecological roles i.e. they are similar in diet, feeding mechanism, distribution and behaviour.

It seems likely that the same basic principles of resource subdivision, competition, etc. are acting in all these communities and others spread throughout the lake. Thus, if applied with caution, the data available for the epilithic algae grazing guild at Monkey Bay may be used to make predictions about the consequences of exploitation of similar guilds elsewhere in Lake Malawi.

One of the most important aspects of the ecology of these species revealed by this study is their sedentary nature. This is evident both from tagging and from the exceptionally slow migration of fish into areas in which their numbers had previously been reduced by repetitive mass removal ( Chapter 9 ). The implication of this to conservation is that an area under exploitation cannot rely on recruitment from other, unexploited areas, thus all estimates of sustainable exploitation levels must be based on the populations resident at the site being exploited. This is particularly critical for those species whose distribution is restricted to a single, small site.

A further fact which must be taken into account when considering this problem of exploitation is the selective manner in which the fish are caught. The vast majority of fish taken by the ornamental fish trade are captured individually by divers who drive selected fish into fine meshed nylon nets where they become entangled. Fish which are not suitable for export are left almost completely undisturbed. This situation represents a potential threat to the ecological balance within the community. The research at Monkey Bay shows that there are at least two possible ways in which species specific exploitation could upset community balance:

a) Several non-territorial species utilize the interspecifically defended territories of '*P*. orange cheek', '*P*. aggressive' and possibly '*P*. broad mouth' and '*P*. sky blue' for feeding purposes. These include *C*. *taeniolatus* and *P*. *zebra* which frequently feed in '*P*. orange cheek' territories, the three *Petrotilapia* species (as yet undescribed) which may specifically seek out '*P*. orange cheek' and '*P*. aggressive' territories to feed in, and *P*. *auratus* which is suspected of "robbing" Aufwuchs from territories by means of stealth. If populations of territorial fish are reduced by exploitation this could also adversely affect these species which feed in their territories and may result in other changes in the population structure within the community.

b) The repetitive mass removal experiments conducted on '*P*. orange cheek' and '*P*. aggressive' at Thumbi East simulate, on a small scale, the conditions created by the ornamental fishermen in that one species was selectively removed while the other was left undisturbed. Under these conditions it was found that the undisturbed species took over territories which were previously occupied by the removed species. The removed species showed very little repopulation of the experimental site during the 6 months observation subsequent to removal, i.e. the undisturbed species increased at the expense of the removed species. It is reasonable to assume that commercial exploitation of interspecifically territorial guild species will have similar consequences. However, since commercial exploitation has been underway on a regular basis for several years the effect is probably more marked than that recorded at Monkey Bay and could reduce populations to the point where it would be difficult to recover in the face of competition from undisturbed species.

Thus the research reported here shows the necessity of controlling the exploitation of the epilithic algae grazing species by commercial fishermen. The level at which the exploitation must be curtailed depends on the reproductive potential and numerical density of the species involved. The data necessary to make this prediction has been collected by other members of the research team.

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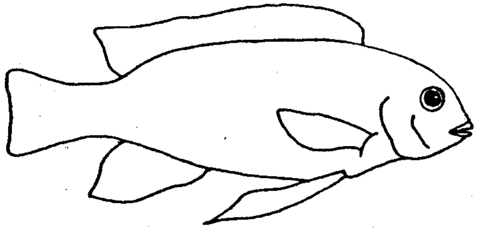
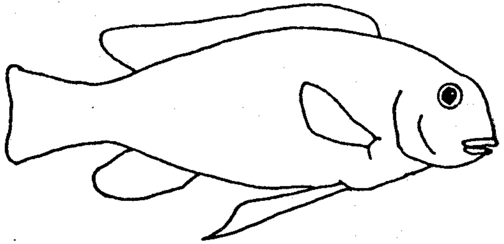
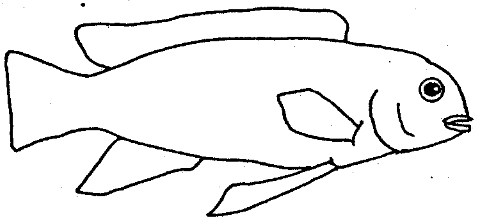
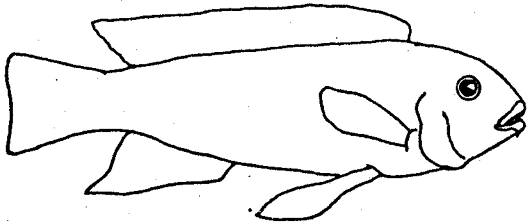
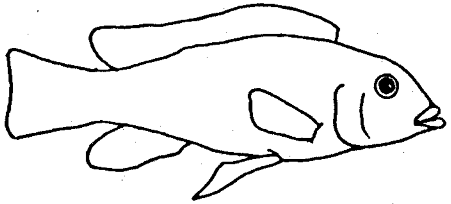
# APPENDIX I

One tailed Wilcoxons signed ranks test on the relative aggression shown by 'Pseudotropheus orange cheek' to intruders into its territories. The test shows which species pairs are attacked at significantly different distances from the territory centre. For each species pair the probability that there is no difference at which attacks occur is given. N.S. = Not Significant. C. taen. = Cyrtocara taeniolatus; P. aur = Pseudotropheus auratus; P.zeb = Pseudotropheus zebra; 'P.agg' = 'Pseudotropheus aggressive'; Petro. = Petrotilapia species; L.fuel = Labeotropheus fuelleborni; 'P.o c' = 'Pseudotropheus orange cheek'.

| | C.taen. | P.aur. | P.zeb. | 'P.agg' | Petro. | L.fuel. |
|---|---|---|---|---|---|---|
| 'P o c' | <,001 | <,005 | <,005 | <,005 | <,005 | <,001 |
| L.fuel. | <,001 | <,001 | ,025 <,01 | ,05<025 | N.S. | |
| Petro. | <,001 | N.S. | N.S. | N.S. | | |
| 'P.agg' | <,001 | ,025< ,05 | N.S. | | | |
| P.zeb. | <,001 | ,01< ,025 | | | | |
| P.aur. | N.S. | | | | | |

| SPECIES | MAX ♂ SL mm | MAX ♀ SL mm | TERRITORIAL BEHAVIOUR |  |  | GENERAL COMMENTS |  |
|---|---|---|---|---|---|---|---|
|  |  |  | Adult ♂ | Adult ♀ | Juveniles |  |  |
| '*Pseudotropheus* orange cheek' | 105 | 95 | Interspecifically territorial yet attacks some species more aggressively than others. | Usually non-territorial | Non-territorial. Shoal in extreme shallows | Common in deep water, equally common on both work sites. |  |
| '*Pseudotropheus* broad mouth' | 91 | 84 | Interspecifically territorial. | Usually non-territorial. | Non-territorial | Shallows only. Often associated with areas of high sediment cover. More common at Chisali than Thumbi East. |  |
| '*Pseudotropheus* dark' | 91 | 88 | Intraspecifically territorial | Non-territorial | Non-territorial | Deep water and sheltered shore fish often associated with areas of high sediment cover.<br>More common on Chisali than Thumbi East. |  |
| '*Pseudotropheus* aggressive' | 100 | 84 | Interspecifically territorial highly aggressive. | Interspecifically territorial, highly aggressive. | Interspecifically territorial when >65mm SL | Shallow water fish. More common on Thumbi East than at Chisali. |  |
| '*Pseudotropheus* sky blue' | 82 | 72 | Interspecifically territorial. | Interspecifically territorial. | Interspecifically territorial when >55mm SL | Confined to areas of small rock in shallows; not recorded at Chisali. |  |

UNDESCRIBED *PSEUDOTROPHEUS* SPECIES