Ecological Interaction Between the Introduced and Native Rock-dwelling Cichlid Fishes of Lake Malawi National Park, Malawi

THESIS

Submitted in fulfilment of the
requirements for the degree of
DOCTOR OF PHILOSOPHY
of Rhodes University

By

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November 1995

Acknowledgements

I thank the following people, and organisations for contributing to the success of the studies reported in thesis: Mr. M.W. Matemba, the Director of Parks and Wildlife, Malawi, for approving, and obtaining permission from the Malawi Government for me to take a four year study leave. He also, assisted with transport and provided extra funds for field work, even at times when the Department had a meagre operational budget. I thank Dr. A.J. Ribbink, firstly for encouraging my interest in the fish of Lake Malawi, and bringing about an awareness of their importance to science. As my supervisor, I also thank him for his intellectual and moral support. He and his Assistant, Vanessa Jones also greatly assisted in the quarterly data collection on fish populations.

Dr. Eva Hert and Professor Miles Keenleyside assisted in the planning of the behavioural studies, and Dr. Hert provided valuable equipment and literature used in my studies. James Whiteman Maluza, Bosman Nkwazi, Pearson Chirambo and George Banda provided invaluable support as diving assistants, and in collection of data and fish.

Mr Aleke Kamanga, a forth year student at Bunda College of Agriculture spent many hours each vacation for two years, measuring and dissecting fish specimen. Messrs J. Smart, Chimbale, Dancan and Fisheries staff at Nkhata Bay and Likoma Island always provided logistic support, when called upon. Dr. Nelson Mwanyama helped in analysing the stomach content of some of the Mbuna species studied. Mr. Francis Mkanda, kindly provided his official vehicle when I needed it during my stay at Cape Maclear.

Mr. B. Singini, of Land Husbandry, Malawi assisted in tracing maps of the study sites, while Dave Voorvelt drew some of the illustrations in this thesis. Professor

Tom Hecht of DIFS, Rhodes University, Evadne Skelton and Vanessa Jones proof read and provided useful comments on some of the drafts of this thesis. Mr. Roger Bills kindly allowed me to use his latest literature on animal behaviour. Mr. O. Gon assisted greatly whenever I encountered computing problems during the phase of my thesis writing. I also thank the Director and all members of the J.L.B. Smith Institute of Ichthyology for the numerous logistical support rendered to me during the period of my thesis writing.

Funding for this study was provided by the WWF-SA. Other Organisations that assisted financially, or materially, include: WWF(US) provided funds for field research in 1993, and the Wildlife Society of Malawi purchased an out-board engine for the boat used during my field studies. I sincerely thank these organisations for their support.

I would also like to thank my parents for enduring and supporting the early stages of my education. Finally, I thank my wife Temweka, and daughters: Wanangwa, Mutinkheni, Lindani and Faith, for their continual love and support, and for putting up with my frequent absence and pre-occupation over the past few years. This thesis is dedicated to them.

Abstract

More than twenty years ago, over twenty species of the rock-dwelling cichlid species (Mbuna) were translocated from the northern Lake Malawi, where they are endemic, to Thumbi West Island, Lake Malawi National Park, in the southern part of Lake Malawi. Among these species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' are strongly territorial, and have increased substantially in number and are widely distributed, particularly in the three to seven metre depth band of the rocky habitats at the Island of Thumbi West. It is feared that the increase in population density of translocated species (hereafter referred to as introduced species) may be at the expense of ecologically equivalent native species which could be eliminated. In this thesis the following key hypotheses have been tested: (i) that the introduced species having originated from a region of Lake Malawi which is generally poor in nutrients and introduced in an area which is richer in nutrients, would cope better than the native species during periods of nutrient scarcity which occur frequently, often seasonally in oligotrophic lakes, such as Lake Malawi; (ii) that the introduced species are fitter than their ecologically equivalent native species in the acquisition of territorial space in which they breed, feed and seek shelter, and (iii) that introduced and native species coexist by utilizing different microhabitats. Results show that:

1. the introduced species, *P. callainos* and *P. tropheops* 'red cheek' may have responded positively to enhanced nutrient availability, as they were found to have better condition factors and fecundity indices at Thumbi West Island than at sites of their origin, in the northern lake Malawi. *Cynotilapia afra*, *P. callainos* and *P. tropheops* 'red cheek' also maximise their life-span fecundity by starting to reproduce at relatively smaller size than the native species with which they overlap in microhabitat requirements. Similarly, their breeding peaks precede the breeding peaks of the native species with which they overlap in microhabitat requirements.

Consequently, due to priority residence effects, the offspring of introduced species may have a competitive edge in the use of essential resources, *e.g.*, refuge over the offspring of the native species whose peak recruitment occurs later in the year.

2. There is an overlap between the introduced and native species in their microhabitat requirements. Consequently, interference competition between them for territorial sites occurs. The choice of optimal territory sites is constrained by the fact that females preferentially mate with males that defend significantly smaller holes, or crevices among the rocks, probably as a means of minimizing egg predation during spawning.

3. The population of territorial males of introduced species seems to grow exponentially, depending on the availability of suitable microhabitats, and an equilibrium between them and males of the native species may be reached. Competition for optimal territory sites seems to intensify, once the carrying capacity in a particular area has been reached, and it is at this stage that some territorial males of the introduced and native species with similar microhabitat requirements, *e.g.*, *C. afra* and *P. zebra*, or *P. tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest' displace each other. However, it seems unlikely that any of the native species which were compared with the introduced species would be driven to extinction because: (a) there is a considerable interspecific territory turn-over between the introduced and native species that overlap in microhabitat requirements. (b) Even in situations where some of the native species occur in microhabitats that are not of their preference, they occupy patches of suitable sites and are capable of breeding. (c) It has been suggested that since introduced and native species breed throughout the year and are polygamous and have intraspecifically shared paternity, they are capable of fertilizing many gravid females of their own species. Therefore, the population of native species may not be detrimentally limited by the presence of introduced species. (d) The introduced and native Mbuna species that prefer small rocks coexist in the same microhabitats, partly by feeding at different sites with different intensity and they also feed at different heights in the water column.

4. The following studies have been recommended before any management intervention, such as culling is adopted: (i) interaction between the introduced and native species in the shallow and deep rocky habitats; (ii) space utilization and survivorship of juveniles of the introduced and native species; (iii) laboratory studies to confirm the role of different nutrient regimes on the fecundity of Mbuna; (iv) the possibility of hybridization between the introduced and native species; (v) monitoring of population growth and distribution of the introduced species around Thumbi West Island should continue in order to detect their long-term effects on the native species.

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Chapter 1

Introduction

Lake Malawi, located between 9°30'S and 14°30'S, is the southernmost of the African Great Lakes (Fig. 1.1). It is the third largest in Africa (28800 km^2) after Lakes Victoria and Tanganyika. Its maximum depth has been estimated at between 770m (Beadle 1981) and 785m (Gonfiantini *et al.* 1979).

Based on the geological evidence, it has been suggested that Lake Malawi might originally have occupied only the northern part of its present basin (Fig. 1.1) and that it stood at a relatively higher elevation than it does today, but later acquired its present form and level after much complex faulting and collapsing of the landscape (Fryer & Iles 1972). Based on evidence from the sediment thickness in the northern basin, it has been suggested that Lake Malawi may be about 26 million years old for the original depression (Johnstone & Ng'ang'a 1990). However, major geological activities continued in the region until about two million years ago, and it is only from this time that there is evidence for continuous existence of the lake (Patterson & Kachinjika 1994).

Gross primary productivity in the Lake Malawi is primarily influenced by solar energy and nutrient availability (Beadle 1981). The latter is supplied through the upwelling of nutrient rich waters from the metalimnion to the epilimnion under the influence of the strong southeast trade winds from May to August, annually, or short-term setups and seiches (Eccles 1974; Beadle 1981; Twombly 1983). However, lack of nutrients may limit primary productivity in aquatic ecosystems when light and temperature are adequate for photosynthetic growth to proceed (Hecky *et al.* 1991). In the Lake Malawi, this limitation is attributed to the physiographic features

of the lake, its surrounding landscape, and its depth. In many places, Lake Malawi is flanked by mountain ranges which fall as precipitous escarpments to the shore and continue under water with undiminished gradient to great depths (Beadle, 1981). At its deepest, around Nkhata Bay, Lake Malawi is 770m deep (Beadle 1981), and with this extensive depth, the northern Lake Malawi is permanently stratified, *i.e.*, having a warm epilimnion overlying a cooler hypolimnion (Fryer & Iles 1972; Eccles, 1974; Beadle, 1981; Ribbink *et al.* 1983a). This stratification is further reinforcement by increases in dissolved salts which invariably counterbalance the heat produced by the centre of the earth (Fryer & Iles 1972).

The consequence of the permanent stratification is that besides the lower layers (*eg.*, below 200m) being anoxic, and biologically unproductive, large quantities of nutrients in the abyssal zone are unavailable for primary production in the epilimnion zone. However, in the shallower southern part of Lake Malawi, including the Thumbi West Island (Fig. 1.2), seasonal winds and short-term seiches stir the deeper cooler waters, allowing both oxygen and nutrients to be thoroughly mixed and evenly distributed in the epilimnion (Eccles 1974). Consequently, this maintains gross primary productivity at relatively higher levels than in the deeper northern part of Lake Malawi (Eccles 1974; Marsh *et al.* 1986).

Lake Malawi also experiences marked seasonal variations in the wind, temperature and precipitation (Eccles, 1974; Twombly 1983; Haberyan & Mhone 1991; Bootsma 1993a). Such variations directly influence the lake's productivity (Twombly, 1983; Haberyan & Mhone 1991; Bootsma 1993a). This also implies that food in Lake Malawi is limited at certain times of the year.

One of the most remarkable attributes of Lake Malawi is its diverse ichthyofauna. Eleven fish families have been identified, comprising between 500 and 1000 species

(Ribbink *et al.* 1983a; Lewis *et al.* 1986). About 96% of these fish species belong to the family Cichlidae, of which 99% are endemic to Lake Malawi (Ribbink 1991). Lake Malawi is also characterized by a high degree of regional endemicity, which suggests that fragmentation of populations during the lake's history may have led to intralacustrine speciation.

The cichlids occupy all the major habitats, with communities characterizing the sandy, muddy, open water, vegetated and rocky habitats.

In recognition of this lake's rich biodiversity, the government of Malawi established the Lake Malawi National Park (Fig. 1.2) in 1980, primarily to protect examples of the endemic aquatic fauna, particularly the Mbuna (Lewis *et al.* 1986). The Mbuna are small, colourful rock-dwelling cichlid fishes. These fishes have a wide trophic diversity, and by virtue of their sedentary and philopatric nature, each of the thirteen islands in Lake Malawi National Park is inhabited by a unique community of species comprising: (a) fishes which are endemic to the island, (b) fishes which have a slightly wider distribution, but are endemic to the park and (c) fishes which have a distribution which extends beyond the park boundaries, with a few having a lake-wide distribution (Ribbink *et al.* 1983a). This park has a high biodiversity, and about 40% of the fish species occurring in the whole of Lake Malawi are protected in this park. Several endemic fish species of great economic importance in the southern part of the lake also occur and breed in the park (Smith 1993). By virtue of these unique features this park was declared a World Heritage Site by the UNESCO in 1984.

Besides their high degree of endemism and speciose nature, the Mbuna are aesthetically among the most appealing fishes in Lake Malawi. They attract ornamental fish hobbyists from all over the world. This attribute is amply exploited

in Malawi by the export trade of Mbuna to Europe, Asia and America. This trade started in 1962 and peaked in the mid 1970s when over 400,000 fishes were being exported by three companies (Ribbink *et al.* 1983b). Fishes from different parts of the lake, such as Nkhata Bay and Likoma Island were being translocated alive to Cape Maclear (Fig. 1.1), where the exporter was based, in order to reduce the time and expense required to travel to more remote parts of the lake (Stauffer & Hert 1993). After selecting what to export, the remaining fish were being released back into the lake, mainly at Otter Point and Thumbi West Island, Cape Maclear, now falling within the Lake Malawi National Park (Ribbink *et al.* 1983a; Lewis *et al.* 1986; Trendall, 1988a). As a consequence of these translocations, many Mbuna species have been introduced at sites where they do not occur naturally.

Of concern to park authorities is the occurrence of over twenty Mbuna species endemic to the northern part of Lake Malawi in the unique communities of at least three islands of the park, *i.e.*, Thumbi West, Otter Point and Maleri (Fig. 1.2). Since the intra-lacustrine translocations more than 20 years ago, many of the introduced species have become established in the park and increased numerically (Ribbink *et al* 1983a; Trendall 1988a). The impact these alien species have on the native Mbuna community structure is not known, but it is feared that they may be competitively excluding the fishes native to the area. From a conservation point of view, this would be unacceptable because the long-term objective of Lake Malawi National Park is to maintain the biodiversity of the species endemic to the area. Consequently, the studies reported in this thesis were launched primarily to assess the interaction between the species translocated from the northern part of Lake Malawi and the native species in the park. Primarily, the aim was to ascertain if the alien species have any impact on the native rock-dwelling fishes of Lake Malawi National Park, before any management intervention, such as culling of the alien species can be adopted.

Throughout the world, it has been argued that fish introductions are harmful to the native fishes and other taxa through predation (McDowall 1968; Vooren 1972; Zaret & Paine 1973; Meffe 1985; Bruton 1990; Fernando 1991; Oguto-Ohwayo & Hecky 1991; Fryer 1991; Crowl *et al.* 1992), competition (Meffe *et al.* 1983; Bruton 1990; Allendorf 1991), habitat alteration (Ferguson 1990; Ross 1990; Arthington 1991), hybridization (Billington & Hebert 1991; Kapuscinski 1991; Stauffer 1984) and introduction of diseases (Allendorf 1991; Fernando 1991; Bruton 1990). However, most studies of fish introductions have dealt exclusively with inter-lacustrine introductions. Consequently, little is known about the consequences of intra-lacustrine fish introductions.

Previous studies of the introduced species in the Lake Malawi National Park only focused on population growth and distribution (Ribbink, *et al.* 1983a; Trendall 1988a), habitat partitioning and site fidelity of an introduced species, *Pseudotropheus aurora* (Hert 1990; 1992) and feeding habits of some introduced species (Reinthal 1987). Therefore, the studies reported in this thesis are the first to provide a detailed assessment of the interaction between the intra-lacustrine translocated species and native species in the Lake Malawi National Park.

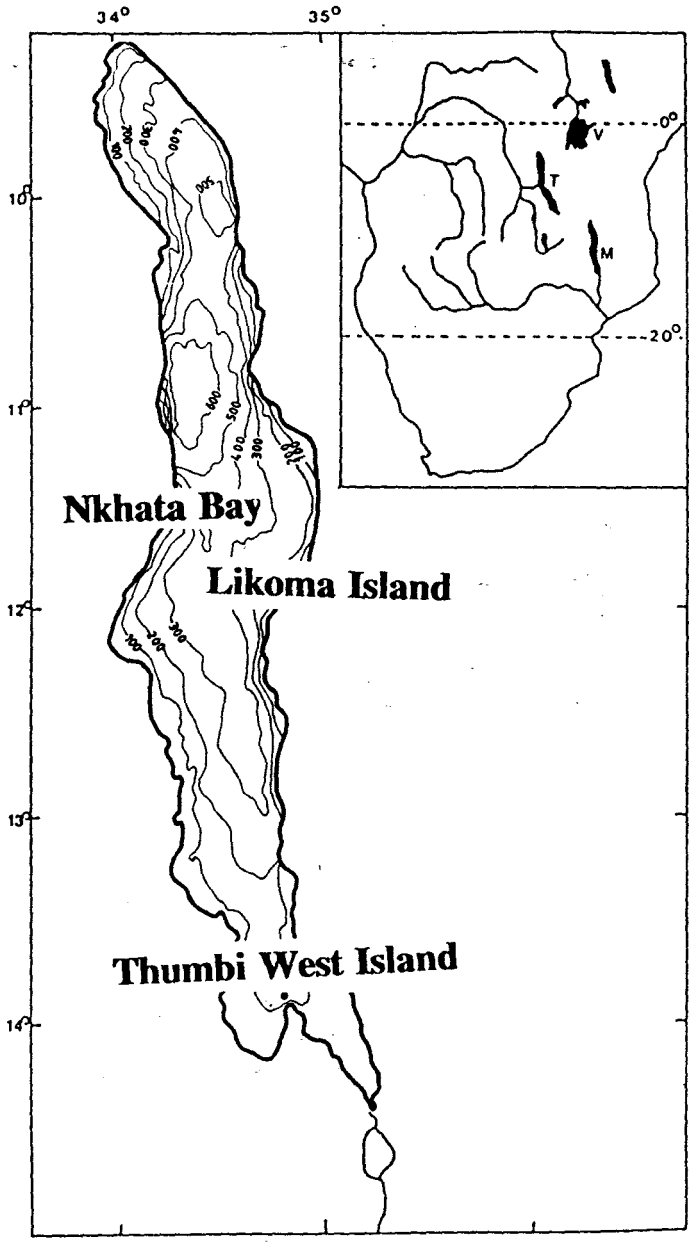


Fig. 1.1. Map of Lake Malawi with an insert of Africa, showing the African Great Lakes; Lake Victoria (V), Lake Tanganyika (T), Lake Malawi (M) and inserts of Nkhata Bay, Likoma Island and Thumbi West Island.

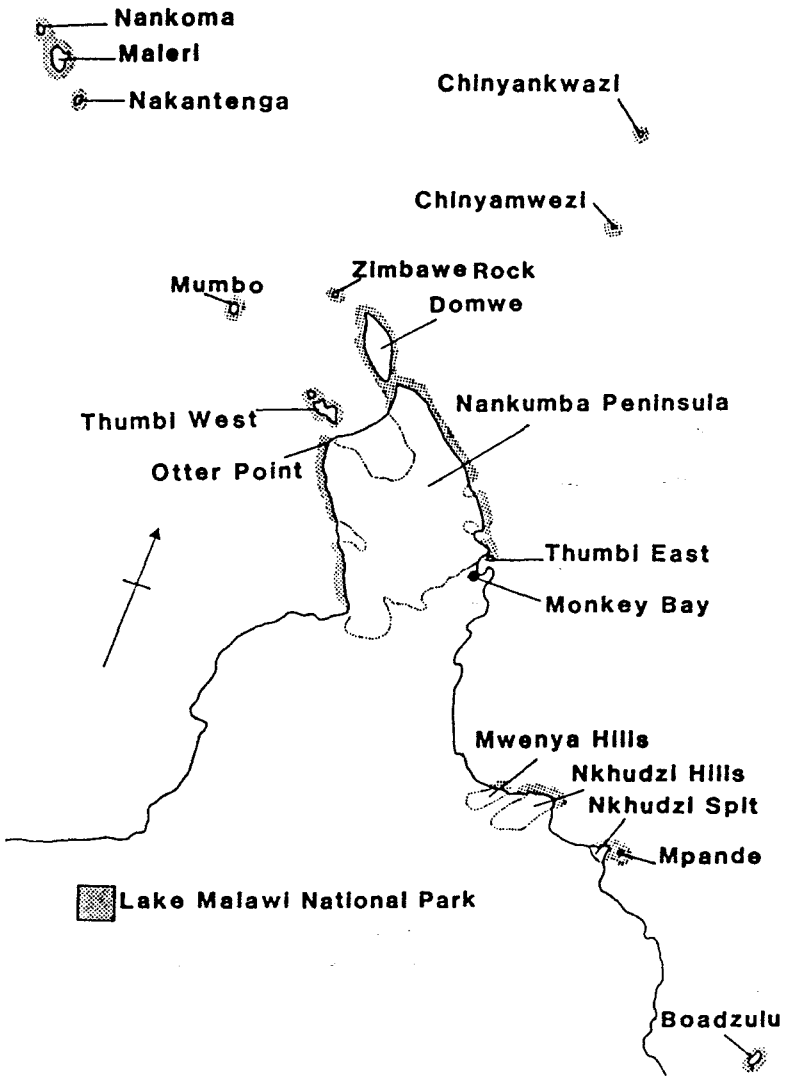


Fig. 1.2. Map of Lake Malawi National Park, showing the different islands; including Thumbi West, Otter Point and Maleri where the rock-dwelling cichlid species translocated from the northern part of Lake Malawi have been introduced.

Study objectives

The main objectives of the studies reported in this thesis were:

1. To find out why some introduced Mbuna species have successfully established themselves in the seemingly crowded community at Thumbi West Island, and increased in their population densities. The guiding hypotheses were that: (a) since the introduced species are from the part of Lake Malawi which is generally poor in nutrients and have been introduced into an area which is richer in nutrients (Eccles 1974; Twombly 1983; Haberyan & Mhone 1991; Bootsma 1993a, 1993b), they could probably cope better than the native species with periods of limited primary productivity and nutrient scarcity, which occur seasonally and frequently in an oligotrophic lake, such as Lake Malawi (Lowe-McConnell 1975). Consequently, they may improve in their condition and fecundity, and this could account for their increase in population densities at Thumbi West Island, where they have been introduced. This hypothesis has been evaluated in chapter two of this thesis. (b) The introduced species may have succeeded in their new environment, probably because they coexist with the native species by occupying, breeding and feeding in different microhabitats. (c) The introduced species may be superior competitors in the use of essential resources. This may be pertinent because the introduced and many of the native species seem to have similar ecological requirements (see Ribbink *et al.* 1983a). Consequently, they may exclude each other, particularly if the essential ecological resources are limited. The possibility of coexistence, or competitive exclusion between the introduced and native species has been evaluated in chapter three of this thesis.

2. To quantify the population size of territorial males of the introduced and native species and find out the distribution pattern of the introduced species around Thumbi West Island. It was assumed that for the introduced species to have a negative impact on the native species, their increase in numbers should correlate

with a decline in the population size of some native species, particularly those that have similar microhabitat requirements as the introduced species. This hypothesis is examined in chapter four of this thesis.

3. To highlight the values of Mbuna, and the need for their conservation in Lake Malawi. Since Lake Malawi is vast and it has a high regional endemicity of fish species, of which not all are represented in the Lake Malawi National Park, it has been suggested in chapter five of this thesis, that the aim should be to prevent extinction of any species, regardless of where it occurs in the lake.

Study sites

This study was conducted at Maingano, Likoma Island, at south bay, Nkhata Bay peninsula and at Thumbi West Island in Lake Malawi National Park (Fig. 1.3). Likoma and Nkhata Bay represent sites from which the introduced species originated, while Thumbi West Island represent one of the recipient communities to which translocated species were introduced.

The rocky shores at all study sites predominantly consist of small (≤ 65cm diameter) and large (> 65cm diameter) rocks (see chapter 3 for the classification of rock sizes). Boulders (> 400cm diameter) and slabs, *i.e.*, flat rock surfaces of various sizes were also common on the steeply shelving regions, mainly at Nkhata Bay and Likoma. Detailed descriptions of habitats at these study sites have been provided by Ribbink *et al.* (1983a).

The rock surfaces at all study sites were covered by attached algal mat (aufwuchs), which is composed of firmly attached filamentous algae, algal epithytes, diatoms, bacteria as well as fine organic detritus (Ribbink *et al.* 1983a; Reinthal 1987). Forty-four types of benthic and pelagic algae have so far been identified in Lake

Malawi (Haberyan & Mhone 1991). The variety of food in Lake Malawi is also demonstrated by the wide trophic diversity exhibited by its ichthyofauna: *e.g.*, plankton feeders, invertebrate feeders, mixed feeders, lepidophages, loose aufwuchs feeders, filamentous algal feeders, egg and parasite feeders and piscivores (Fryer & Iles 1972; Ribbink *et al.* 1983a).

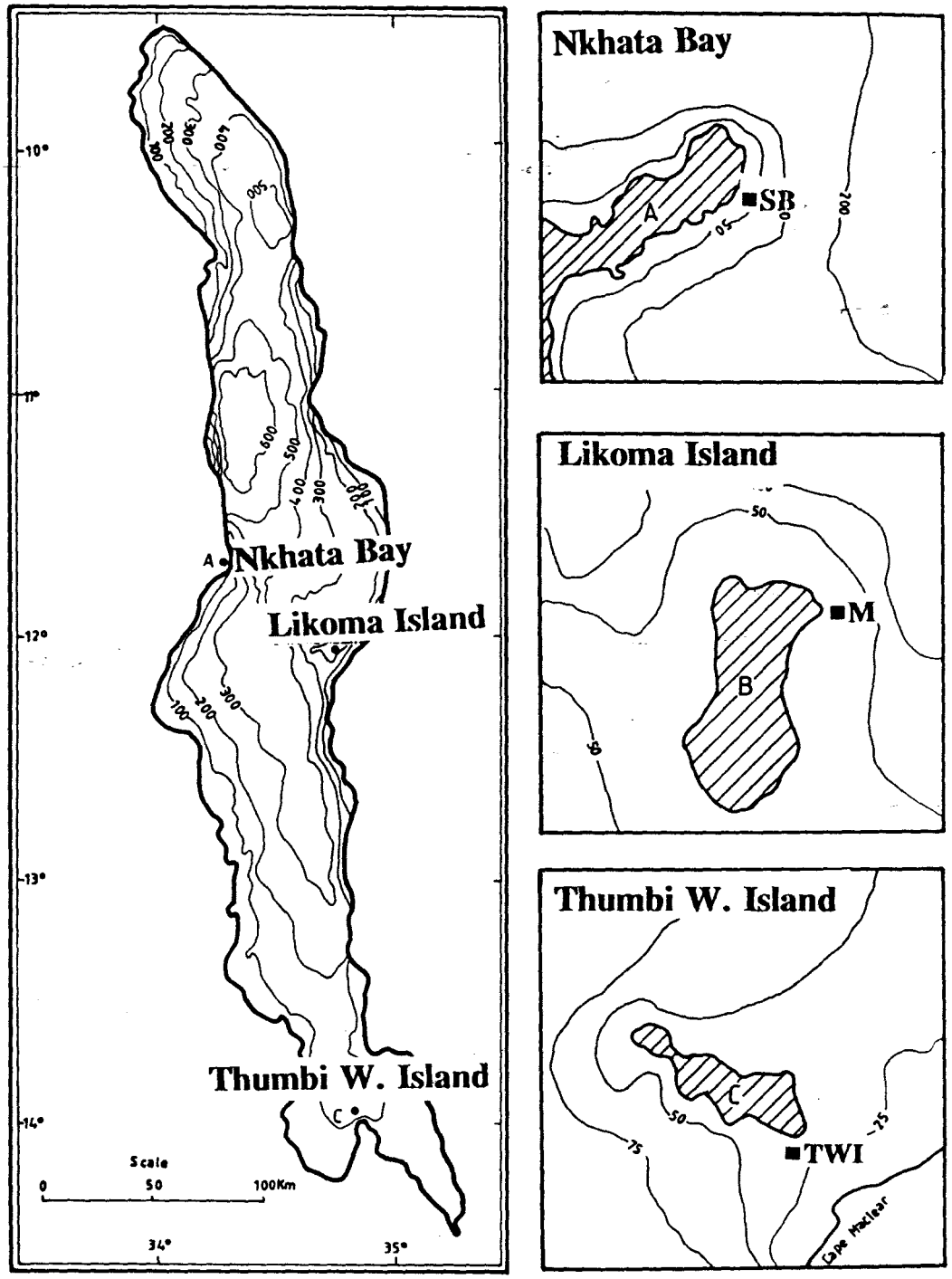


Fig. 1.3. Map of Lake Malawi with insets of the study sites: Nkhata Bay (showing south bay, denoted as *SB*), Likoma Island (showing Maingano, donoted as *M*) and Thumbi West Island, shown as *TWI*, where sampling was done.

The species studied

The following sub-communities occur within the community of the rocky-habitat at Thumbi West Island, where detailed studies of the interaction between the introduced and native species were carried out. These include: (a) the shallow water sub-community from 0-3m, characterised by species that live in the extreme shallows, and others which live in shallows as well as deeper waters, (b) the 3-10m sub-community, characterised by lithophilous species which are most numerous at this depth range, (c) the deep community which is characterised by lithophilous fish which are found beyond 10m depth, and (d) the community at the interface and intermediate zones which are areas where rocky habitat meets the sandy habitat, often as a sharply demarcated zone (interface zone), or as a mixture of rock and sand (intermediate zone). More than thirty native Mbuna species, fourteen introduced Mbuna species, and at least thirty-eight cichlid species which are not Mbuna, as well as representatives of the non-cichlid families occur at Thumbi West Island (Ribbink *et al.* 1983a; also see Appendix 1). Not all the fish at this site have been formly described. Consequently, the undescribed fishes have been referred to by the chironyms of Ribbink *et al.* (1983a).

Principally, the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' were studied. These species are strongly territorial, have increased substantially in numbers and are widely distributed around Thumbi West Island in the 3-7m habitat belt of the rocky areas. Consequently, one of the fundamental aims of the studies reported in this thesis was to find out if these species' population growth and increased distribution also reflect a process by which the native species are being eliminated.

Since the introduced species occur in all the sub-communities at Thumbi West

Island, the studies reported in this thesis only focused on the community occurring between 3 - 7m depth zone, because this zone appeared to have more territorial males of the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' than any other introduced species in this depth zone. Also, although the impact of introduced species was evaluated on all the native species occurring in the study zone, the main focus was on the native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest'. The former is a congeneric of an introduced species, *Pseudotropheus callainos*, while the latter is a congeneric of an introduced species *P. tropheops* 'red cheek'. Besides being congenerics, these species also appeared to be ecological equivalents (see Ribbink *et al.* 1983a). Consequently, it was assumed that they would compete for territorial space, in which these fishes breed, feed and seek shelter.

Chapter 2

Condition Factor and Fecundity of the Introduced and Native Rock-dwelling Fish Species (Mbuna), Cichlidae of Lake Malawi, Africa

Introduction

The reasons the introduced Mbuna species have increased numerically at Thumbi West Island, Lake Malawi National Park, to the extent that they now dominate at many sites (Ribbink *et al.* 1983a; Trendall 1988a) are not known. But since these fishes were translocated from a region of Lake Malawi that is relatively poor in nutrients and introduced into an area which is richer in nutrients (Eccles 1974; Twombly 1983; Haberyan & Mhone 1991; Bootsma 1993a, 1993b), it can be assumed that they would respond positively to enhanced nutrient availability in their new environment. Consequently, this may lead to improved nutritional condition and fecundity, which would account for their increase in abundance. This seems likely because the energetic cost of egg production in fish is high and food has been singled out as being one of the most important factors determining fecundity (Scott 1962; Bagenal 1969; Wootton 1973; Messieh 1976; Marsh *et al.* 1986). Being mouth-brooders, the Mbuna may require even more energy for both egg production and for the fast period of about three weeks while holding developing fry in their mouths (Marsh *et al.* 1986) than other fish.

To test the hypothesis that fish from the nutrient-poor northern part of Lake Malawi may be in better condition and more fecund in the nutrient-rich southern part of Lake Malawi, the condition factor and fecundity of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' were assessed and compared with some of the native species that overlap with them in microhabitat requirements. The introduced and native species that overlap in microhabitat requirements have been identified in chapter 3 of this thesis. The main objectives were: (i) to find out if the introduced species in the park were in better condition and more fecund than the conspecifics in the northern part of Lake Malawi where they originated and (ii) to find out if the introduced species were in

better condition and more fecund than the native species in the park that overlap with them in microhabitat requirements. In addressing the second objective, it was further assumed that since introduced species come from a nutrient-poor region, they may be more capable of coping with periods of limited primary productivity and nutrient scarcity, which occur seasonally and frequently in an oligotrophic lake such as Lake Malawi than the native species, and would therefore, be in better condition and more fecund than the native species. Of particular interest were the native Mbuna species, *Pseudotropheus zebra and P. tropheops* 'orange chest'. The former overlaps in microhabitat requirements with the introduced species, *C. afra* and *P. callainos,* while the latter overlaps with its sibling introduced species, *P. tropheops* 'red cheek'.

Methods

This study was undertaken from August, 1992 to December, 1994. Samples were drawn from Thumbi West Island, Lake Malawi National Park, Likoma Island, mainly at Maingano and Nkhata Bay, at the south bay (Fig. 2.1). Thumbi West Island is the recipient community of the introduced species, Likoma is the site from which *Cynotilapia afra* and *Pseudotropheus tropheops* 'red ckeek' were translocated, and Nkhata Bay is a site from which *Pseudotropheus callainos* was translocated.

Sampling

Sampling was done by means of SCUBA at 3 - 7m depth, where the studied species were most abundant. A minimum of thirty males and thirty females of each of the studied species, *C. afra, P. callainos, P. tropheops* 'red cheek, *P. zebra* and *P. tropheops* 'orange chest' were caught monthly, using a nylon, 6 millimeter mesh size multifilament net (6m long x 1,5m deep). Males and females were readily distinguished from each other by their colour and the size of their genital pore. The

genital pore in all size classes is larger in females than in males. Due to transport costs and logistical problems, samples from Nkhata Bay were only collected in April, May, August, October and November.

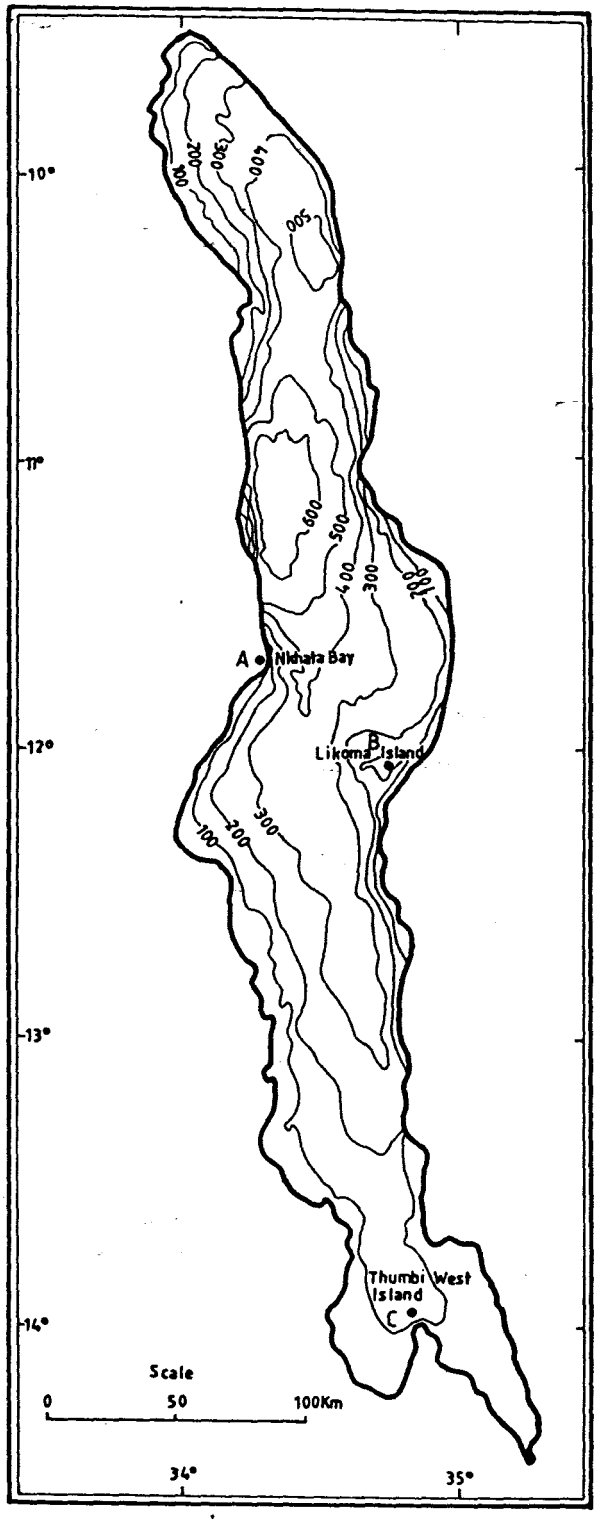


Fig. 2.1. Map of Lake Malawi with inserts of the study sites; (A) Nkhata Bay, (B) Likoma Island and (C) Thumbi West Island.

Condition factor

A number of indices can be used to determine the condition of fish. These include: the length-weight relationship (*e.g.*, Le Cren 1951; Craig 1974; Reimers 1974; McNeely & Pearson 1974; Sekavec 1974; DeSilver 1985; Nash 1981; Bolger & Connolly 1989); a liver index, or hepatosomatic index (Htun-han 1978; body water content (Elliot 1976); visceral-somatic index (Delahunty & de Vlaming 1980; Adams & McLean 1985); protein energy ratio (Bolger & Connolly 1989) and partial condition factors (Bolger & Connolly 1989). However, all of these condition indices, except the length-weight relationship require time consuming laboratory analyses. For this reason, the length-weight relationships was used in assessing the condition of the introduced and native Mbuna species in this study. This method was the most suitable under field conditions where laboratory facilities were not available. The assumption inherent in the use of this index was that heavier fish of a given length were in a better condition (Bolger & Connolly 1989). The length-weight measurement is also believed to be a good indicator of the general "well-being" of the population under consideration, and it has been used in the following population analyses:

(i) in comparing monospecific populations living under apparently similar, or different conditions of food density and climate (Stucky & Klaasen 1971; Wiemer & Hannenan 1982);

(ii) in determining the timing of gonad maturation (Htun-han 1978; Dadzie & Wangila 1980; Chang & Navas 1984), and

(iii) as an indication of changing gross nutritional balance during chronic alterations in feeding activity and food supply (Caulton & Bursell 1977; DeSilver 1985; White & Fletcher 1985; Booth & Keast 1986).

Measurements

The standard lengths (SL) of the captured fish, *i.e.*, the length between end of the

snout and the base of the caudal fin were measured and the fish were weighed on a sensitive balance (Model 400D, DE Series) to obtain the fresh weights. The fish were later sun-dried to constant weight to obtain dry weight which was used in computing the condition factors and fecundity. Drying of fish was necessary to circumvent biased effects of moisture on condition and fecundity. The length and weight data were categorised by species, sex and locality.

Data analysis

The condition factor (K) (Le Cren 1951; Bolger & Connolly 1989; Reimers 1974; McNeely & Pearson 1974) was used in assessing the condition as follows:

$$K = \frac{\text{Weight in grams x 100 000}}{\text{[Standard length (mm.)]}^b}$$

The exponent *b* in this formula is the length-weight regression coefficient, assumed to be 3 (Reimers 1974; Bolger & Connolly 1989). But since it varies, both within and between populations (Le Cren 1951; Weatherley 1972), in this study the log transformed length to mass relationship was empirically derived by linear regression, and the values used for each species were as follows:

C. afra, Likoma:

Males: $\log_{10} W = -5.69 + 3.09 \log_{10} SL$ ($n = 786$, $r^2 = 0.68$)

Females: $\log_{10} W = -4.51 + 2.75 \log_{10} SL$ ($n = 735$, $r^2 = 0.87$)

C. afra, Thumbi:

Males, $\log_{10} W = -4.03 + 3.05 \log_{10} SL$ ($n = 784$, $r^2 = 0.63$)

Females, $\log_{10} W = -5.78 + 3.01 \log_{10} SL$ ($n = 786$, $r^2 = 0.60$)

***P. callainos*, Nkhata Bay:**

Males, $\log_{10}W = -4.40 + 3.10 \log_{10}SL$ (n = 586, $r^2 = 0.79$)

Females, $\log_{10} W = -6.06 + 3.04 \log_{10} SL$ (n = 454, $r^2 = 0.92$)

***P. callainos*, Thumbi:**

Males, $\log_{10} W = -5.19 + 3.07 \log_{10} SL$ (n = 721, $r^2 = 0.68$)

Females, $\log_{10}W = -6.49 + 3.00 \log_{10} SL$ (n = 723, $r^2 = 0.79$)

***P. tropheops* 'red cheek', Likoma:**

Males, $\log_{10}W = -6.46 + 3.28 \log_{10} SL$ (n = 734, $r^2 = 0.92$)

Females, $\log_{10}W = -5.10 + 3.08 \log_{10} SL$ (n = 726, $r^2 = 0.99$)

***P. tropheops* 'red cheek', Thumbi:**

Males, $\log_{10}W = -6.82 + 4.0 \log_{10} SL$ (n = 720, $r^2 = 1$)

Females, $\log_{10}W = -4.58 + 2.8 \log_{10} SL$ (n = 722, $r^2 = 0.44$)

***P. tropheops* 'orange chest', Thumbi:**

Males, $\log_{10}W = -7.00 + 4.00 \log_{10} SL$ (n = 333, $r^2 = 0.87$)

Females, $\log_{10}W = -6.5 + 3.04 \log_{10}SL$ (n = 298, $r^2 = 0.81$)

***P. zebra*, Thumbi:**

Males, $\log_{10}W = -7.23 + 4.00 \log_{10} SL$ (n = 371, $r^2 = 0.80$)

Females, $\log_{10} W = -4.76 + 2.88 \log_{10} SL$ (n = 299, $r^2 = 0.81$)

Fecundity

The same fish captured for condition measurements were also used in the assessment of fecundity. Females of the captured fish were measured (SL), weighed, dissected to remove their gonads which were weighed, and the number of eggs in

the ovaries and/or mouth were counted. Fecundity in this study was considered as the number of ripe eggs in the ovary and/or mouth. After counting eggs, the fish were dried to constant weight, as described above.

Data analysis

Fecundity (absolute) was expressed as the number of eggs per female, while the relationship between fecundity and length, was transformed to the logarithmic form and linear regression. The fecundity index (*FI*) and gonad index (*GI*) (Messieh 1976) were calculated as follows:

$$FI = F/SL^b \times 100$$

$$GI = G/SL^b \times 10^5$$

where F = number of eggs per female, G = gonad fresh weight in milligrams, SL = standard length in millimetres and b = the length-weight regression coefficient. For comparative studies like this one, values of relative fecundity (fecundity index) are more useful than absolute fecundity (Messieh 1976). The fecundity index can also be expressed as the number of eggs per unit of weight (*e.g.*, Shatunovskiy 1988), but this has been criticized and instead the use of length has been recommended (*e.g.*, Bagenal 1969; Messieh 1976). For instance, Bagenal (1969) reports that if the fish weight excludes gonads, it may lead to spurious correlation, while if the gonad weight is included, difficulties may arise if there were marked changes in condition of the fish. Therefore, to circumvent these anomalies, SL^b, in which b was empirically derived was used in computing both the fecundity and gonad indices.

Differences in condition and fecundity between the introduced species in the park and conspecifics at Nkhata Bay and Likoma, and between introduced and native

species in the park were evaluated by *t*-Test.

Results

Size and condition of introduced species

The size (SL) of both males and females of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' at Thumbi West Island did not differ significantly from that of conspecifics at sites of their origin, Nkhata Bay and Likoma Island (Table 2.1). However, when their condition factors were compared, both males and females of the introduced species, *P. tropheops* 'red cheek' (Fig. 2.2.2) and *P. callainos* (Fig. 2.2.3) at Thumbi West Island were in significantly in better condition than conspecifics at sites of their origin, Likoma and Nkhata Bay, in the northern part of Lake Malawi. Some of these introduced species, were also in better condition than the native species with which they were compared. Notable among these were males of the introduced species, *C. afra*, which were better than the males of a native species, *P. zebra* (Fig. 2.3b). These two species overlap in their microhabitat requirements (see chapter 3). Similarly, males of the introduced species, *P. callainos* and *P. tropheops* 'red cheek' were also in better condition than their sibling native species, *P. zebra* (Fig. 2.4b) and *P. tropheops* 'orange chest' (Fig. 2.5b), respectively. In contrast, females of the introduced species were either inferior to the native species in their condition factors (Fig. 2.3a) and (Fig. 2.4a), or there was no significant difference between them and the native species (Fig. 2.5(a))

Cynotilapia afra was the only introduced species that does not seem to have positively responded to enhanced nutrient availability in its new environment, as its condition factors at Thumbi West Island and at Likoma, in the northern Lake Malawi where it originated did not differ significantly (Fig. 2.2.1).

Also, with the exception of *C. afra*, the condition factors of females of all the Mbuna species studied were significantly better than the condition of conspecific males (Fig. 2.6.1, 2.6.2, 2.6.3 & 2.6.4). However, the condition factors of these fishes fluctuated seasonally. The major peaks in condition coincided with either the wind-induced upwelling from May to August, or the onset of rains between November and January (Fig. 2.6.1 - 2.6.4), while the lowest condition factors were noted during the months when the lake was stratified, *i.e.*, between February and April, with March, or April which marks the end of the rainy season being among the worst months for most of the Mbuna species studied.

Table 2.1. The size (SL), presented as mean ± standard deviation, in millimetres of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' at Thumbi West Island, southern Lake Malawi compared with the size (SL) of conspecifics at sites of their origin (Nkhata Bay and Likoma Island), in the northern Lake Malawi.

	N	Thumbi W. Island	*N*	Site of origin	*t* Value	*P* value
(a) Males						
C. afra	784	70.05 ± 3.24	786	69.57 ± 2.43	0.32	> 0.05
P. callainos	721	68.92 ± 2.22	774	68.77 ± 3.50	0.11	> 0.05
P. troph.'rc'	720	69.78 ± 6.32	734	73.89 ± 3.33	1.57	> 0.05
(b) Females						
C. afra	786	63.24 ± 3.70	735	60.29 ± 3.33	2.07	> 0.05
P. callainos	723	64.50 ± 1.74	454	63.32 ± 4.03	0.68	> 0.05
P. troph.'rc'	722	66.21 ± 1.70	726	65.11 ± 2.29	1.27	> 0.05

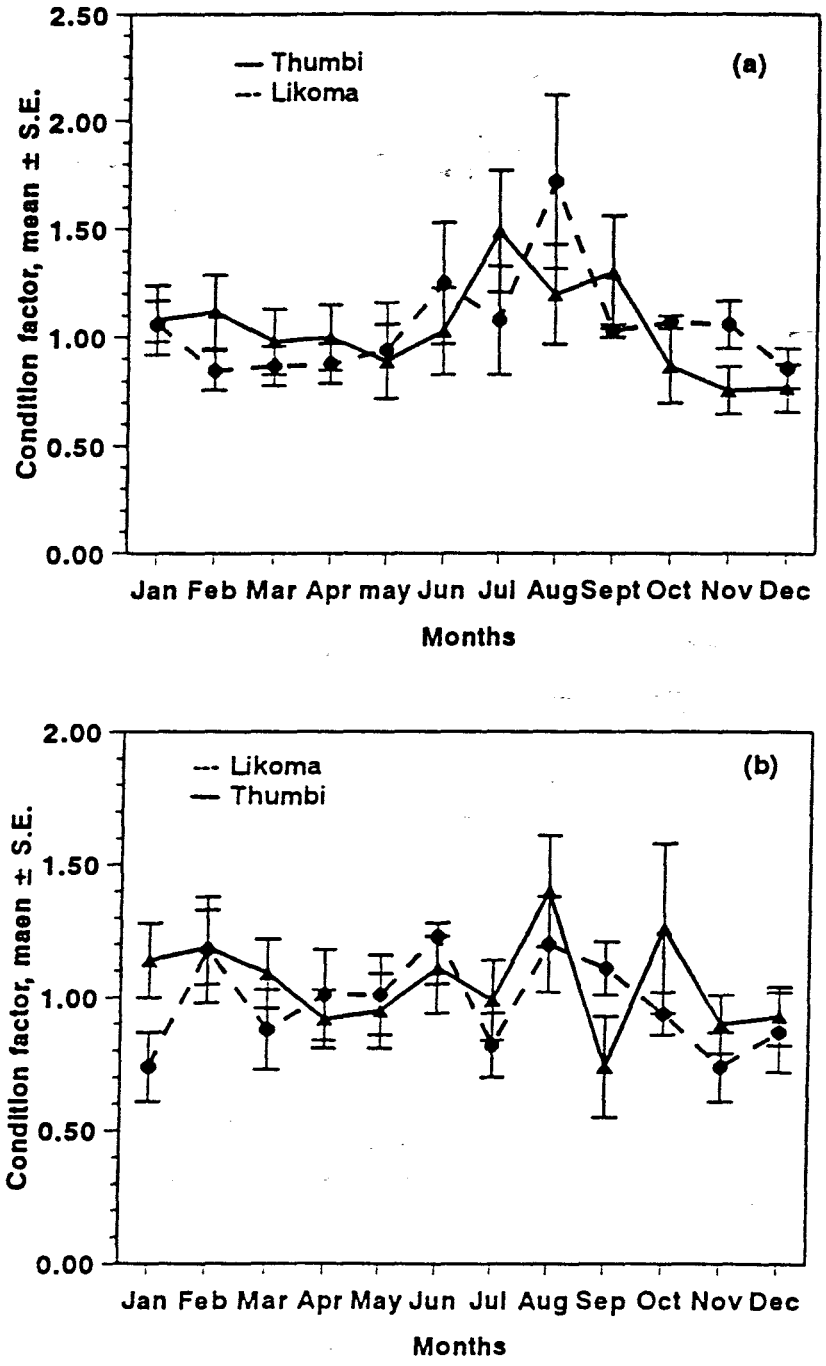


Fig. 2.2.1. Comparison of condition factors between (a) females and (b) males of the introduced species, *Cynotilapia afra* in the park, at Thumbi West Island, southern part of Lake Malawi and at its origin, Likoma Island, in the northern part of Lake Malawi.

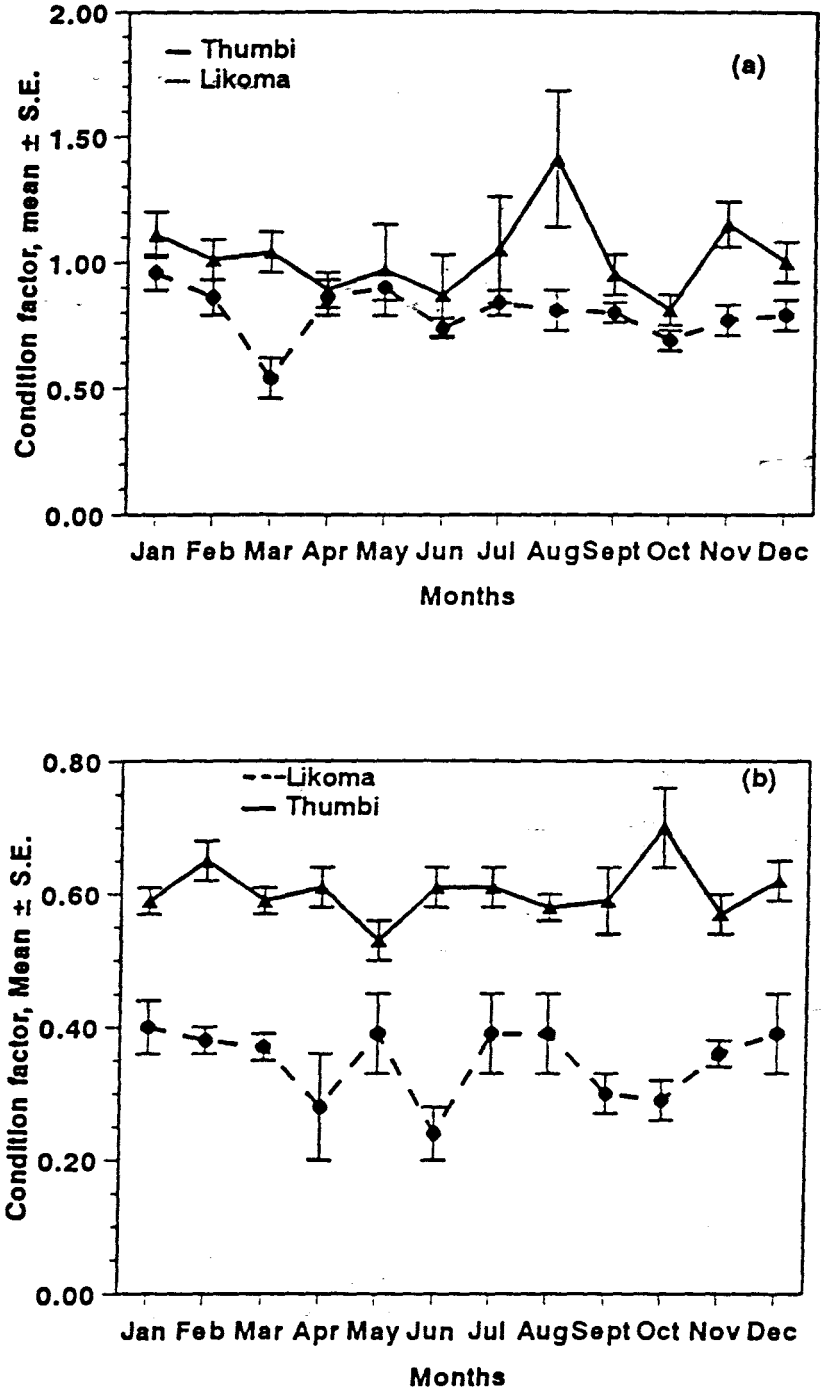


Fig. 2.2.2. Comparison of the condition factors between (a) females and (b) males of the introduced species, *Pseudotropheus tropheops* 'red cheek' at Thumbi West Island, southern part of Lake Malawi and at its origin, Likoma Island, in the northern part of Lake Malawi.

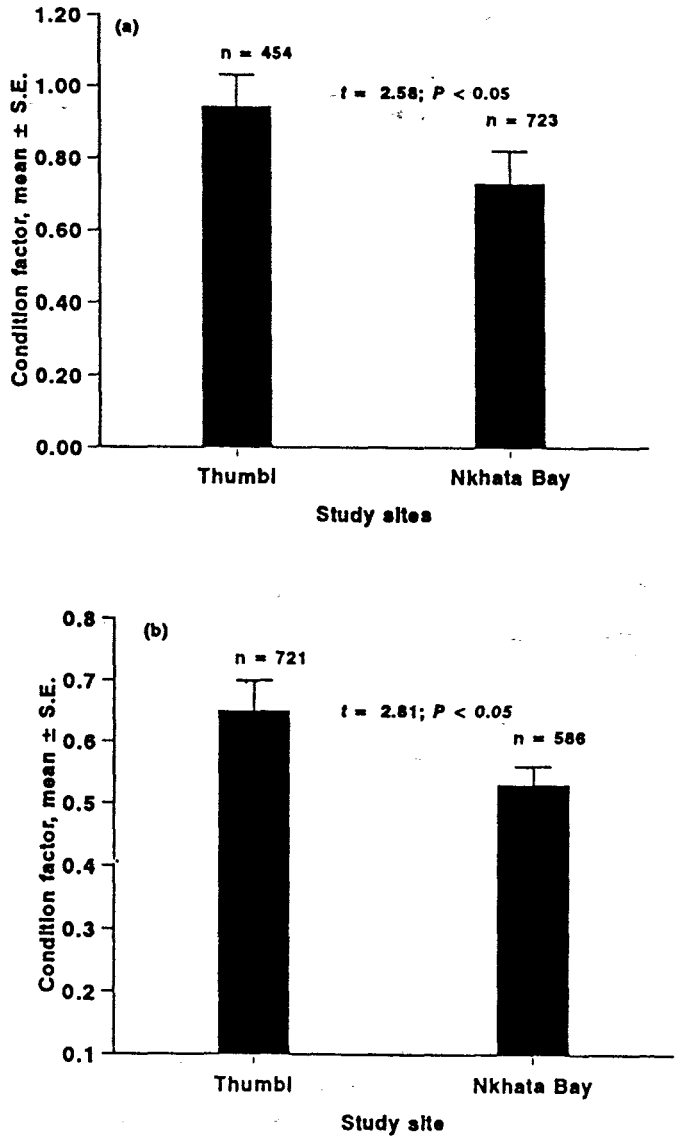


Fig. 2.2.3. Comparison of condition factors between (a) females and (b) males of the introduced species, *Pseudotropheus callainos* at Thumbi West Island, southern part of Lake Malawi where it has been introduced and at its origin, Nkhata Bay, northern part of Lake Malawi. The data from Nkhata bay were not collected every month, hence the data have been pooled and compared in a form of histograms.

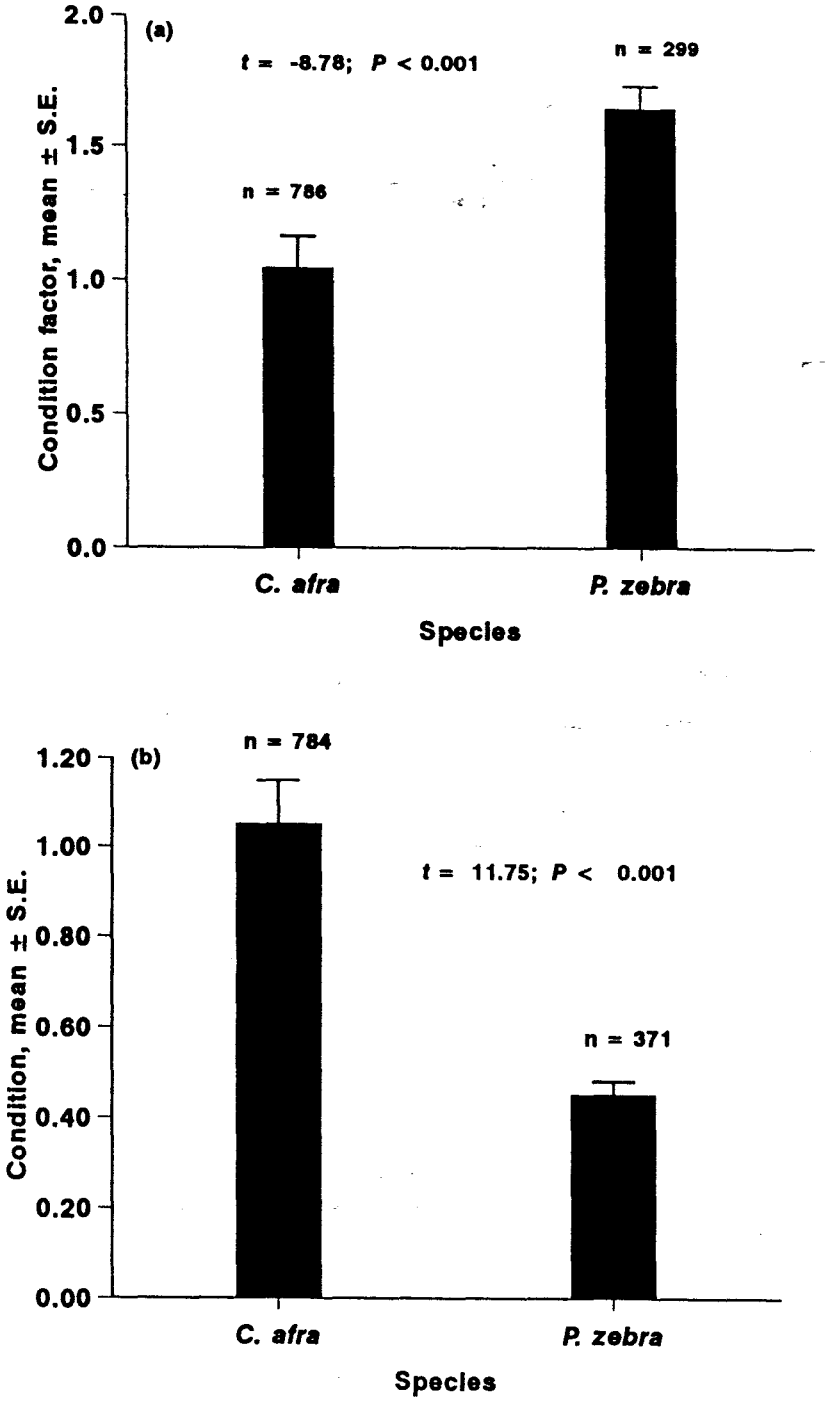


Fig. 2.3. Comparison of condition factors between (a) females and (b) males of the introduced species, *Cynotilapia afra* and a native species, *Pseudotropheus zebra*, with which it overlaps in microhabitat requirements (chapter 3).

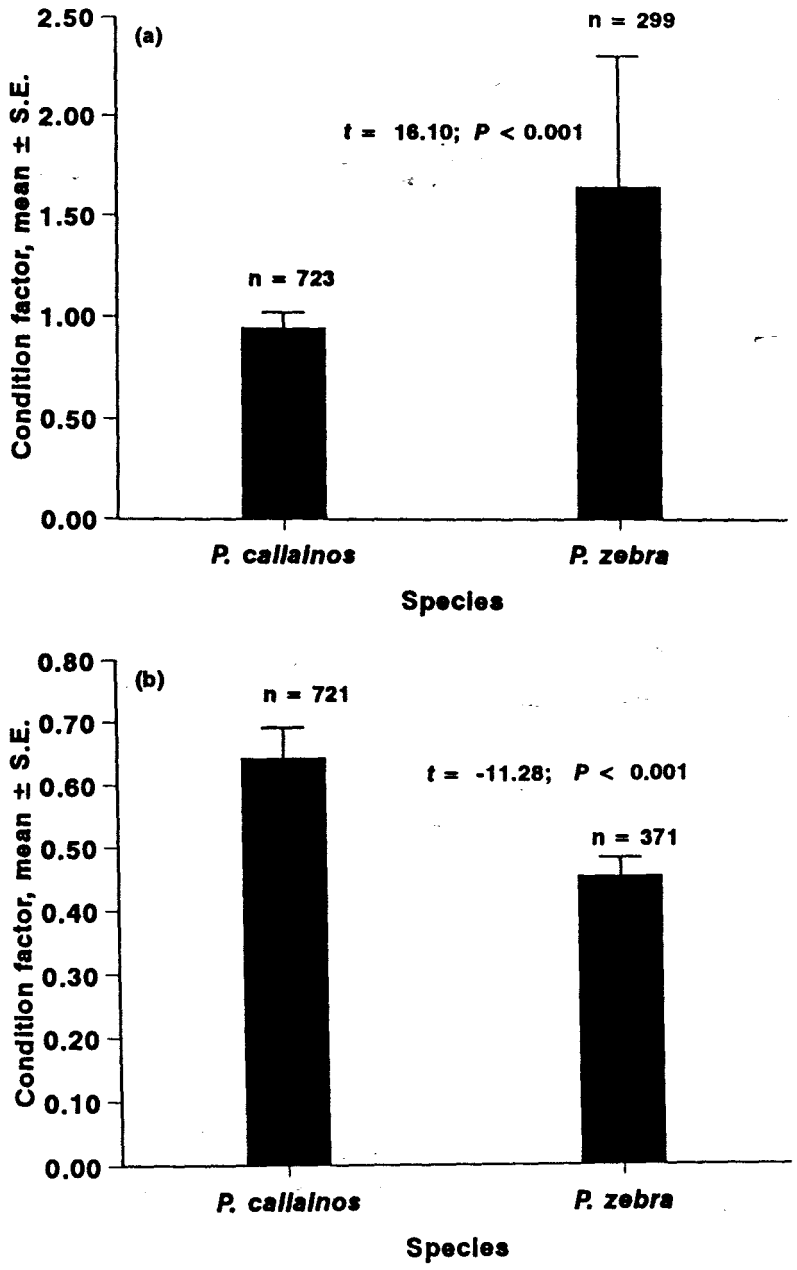


Fig. 2.4. Comparison of condition factors between (a) females and (b) males of the introduced species, *Pseudotropheus callainos* and its congeneric native species, *Pseudotropheus zebra*. The data from Nkhata Bay was not collected every month, hence the data had to be pooled and compared in a form of histograms.

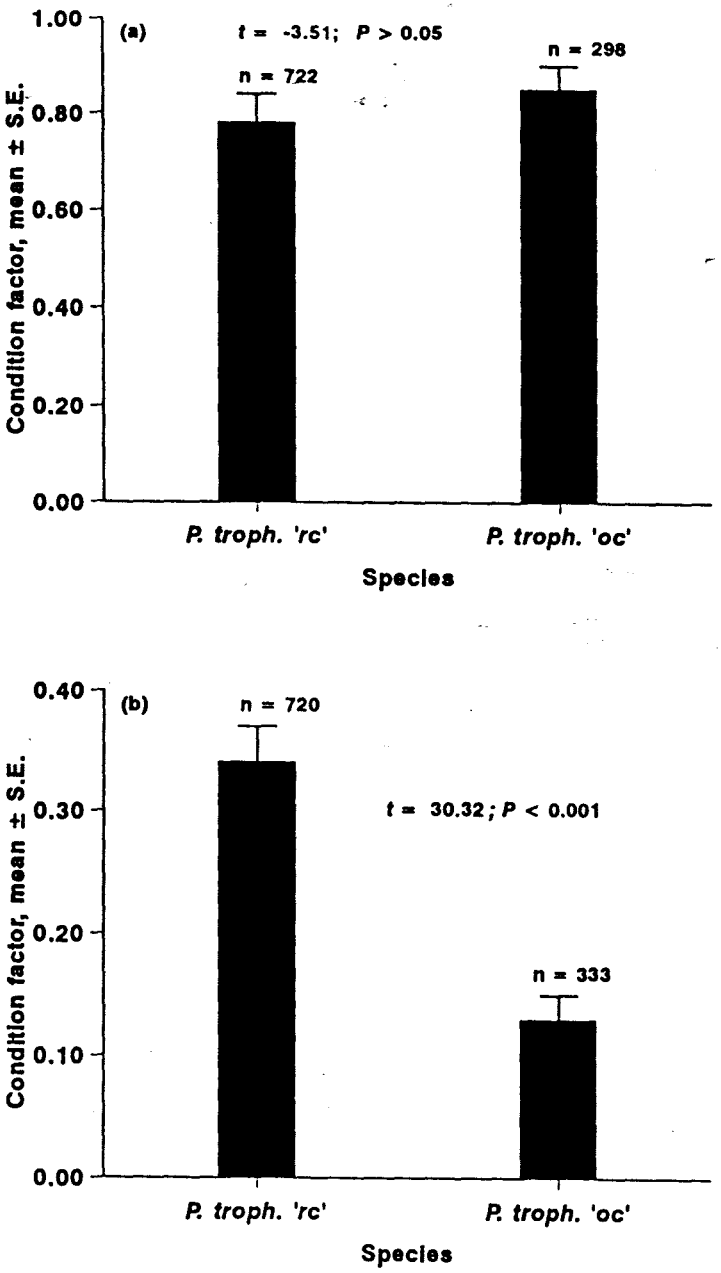


Fig. 2.5. Comparison of condition factors between (a) females and (b) males of the introduced species, *Pseudotropheus tropheops* 'red cheek' and its congeneric native species, *Pseudotropheus tropheops* 'orange chest'.

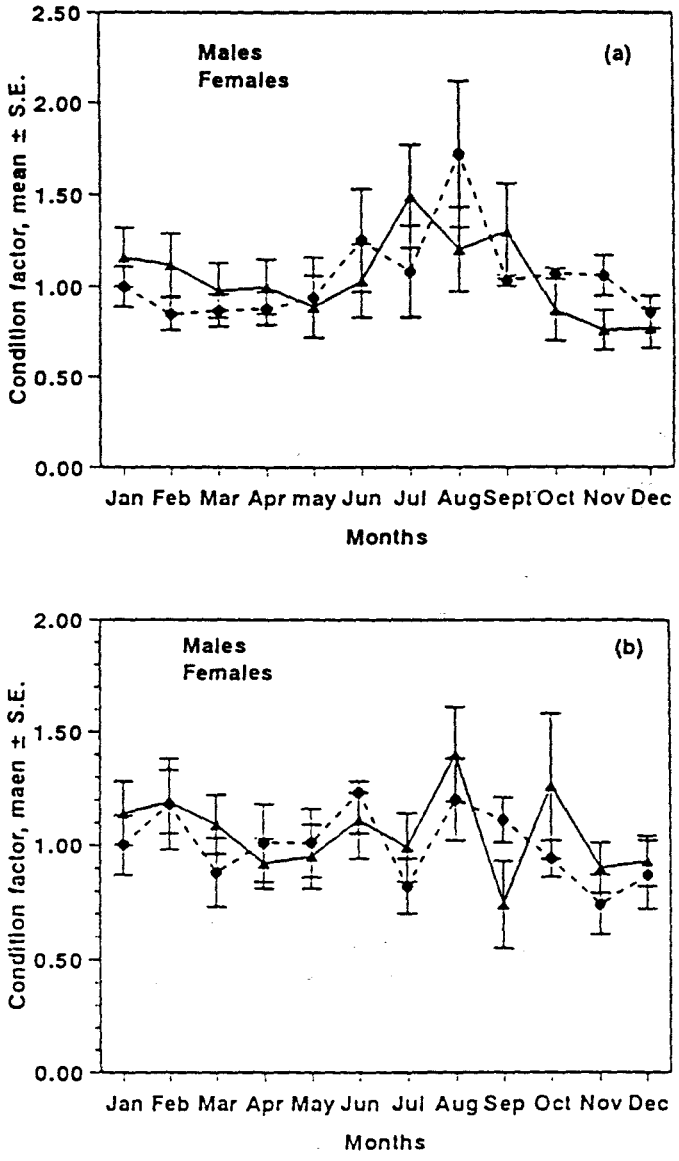


Fig. 2.6.1. Comparison of condition factors between males and females of the introduced species *Cynotilapia afra*, (a) at Likoma Island, in the northern Lake Malawi and (b) at Thumbi West Island, Lake Malawi National Park, in the southern Lake Malawi.

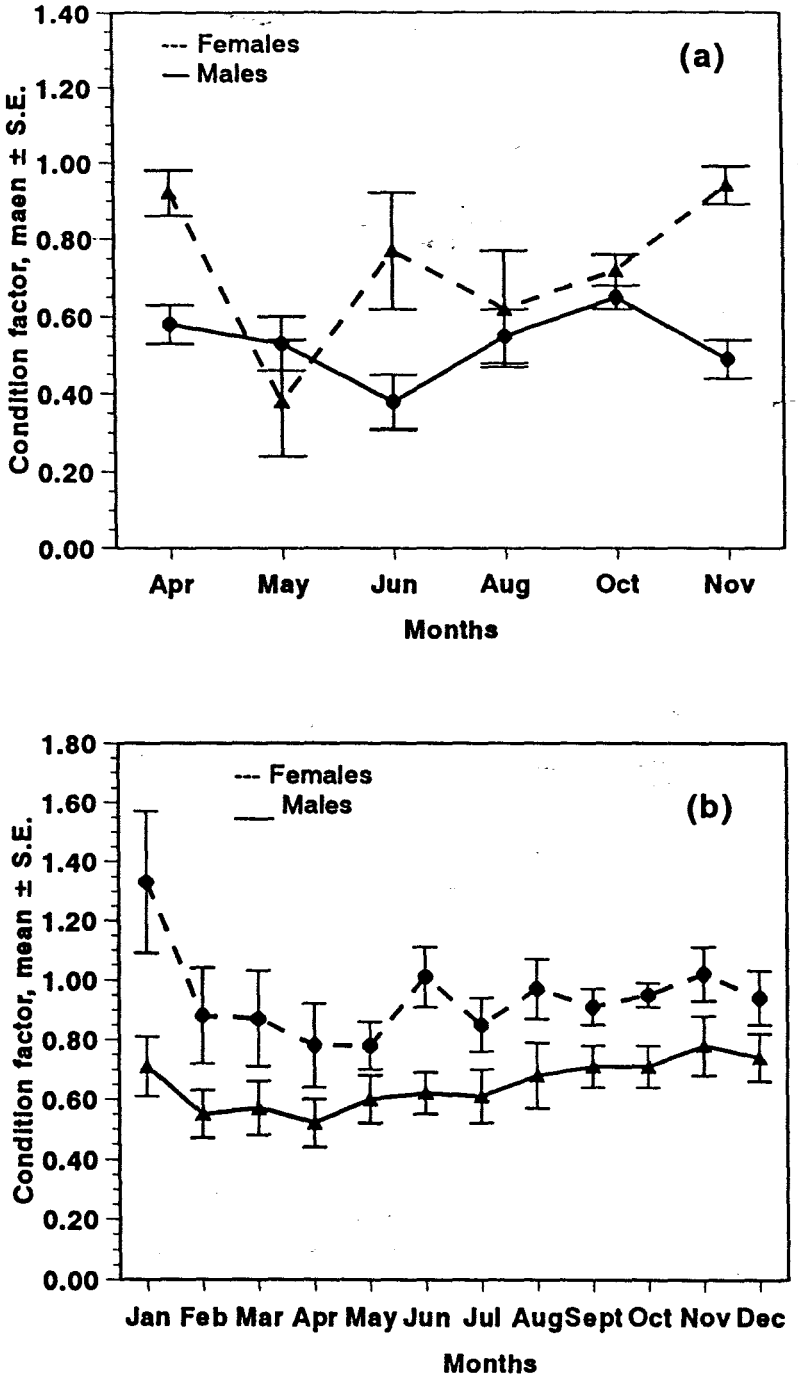


Fig. 2.6.2. Comparison of condition factors between males and females of the introduced species, *Pseudotropheus callainos* (a) at Nkhata Bay, northern Lake Malawi and (b) at Thumbi West Island, Lake Malawi National Park, in the southern Lake Malawi.

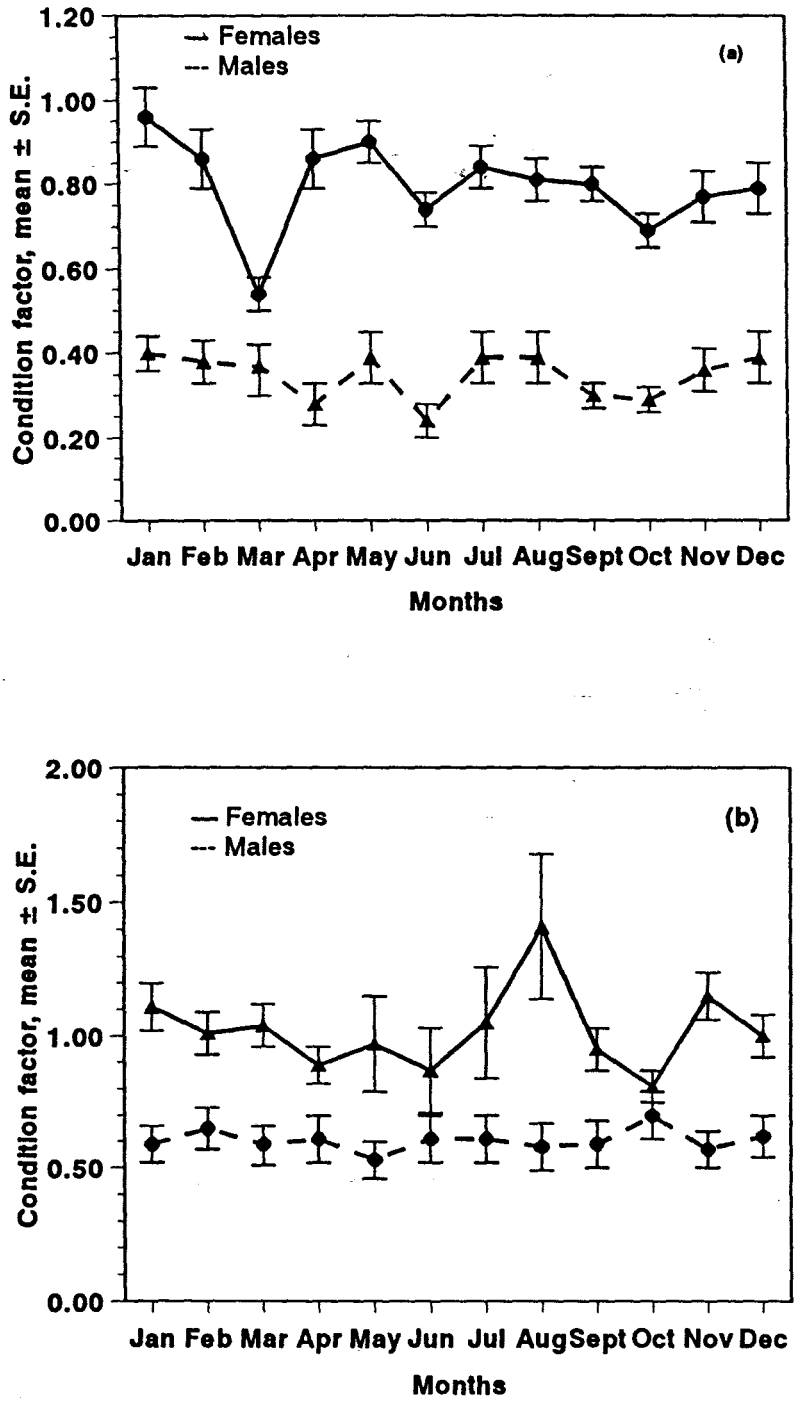


Fig. 2.6.3. Comparison of condition between males and females of *Pseudotropheus tropheops* 'red cheek', (a) at Likoma Island, northern Lake Malawi and (b) at Thumbi West Island, Lake Malawi National Park, in the southern Lake Malawi.

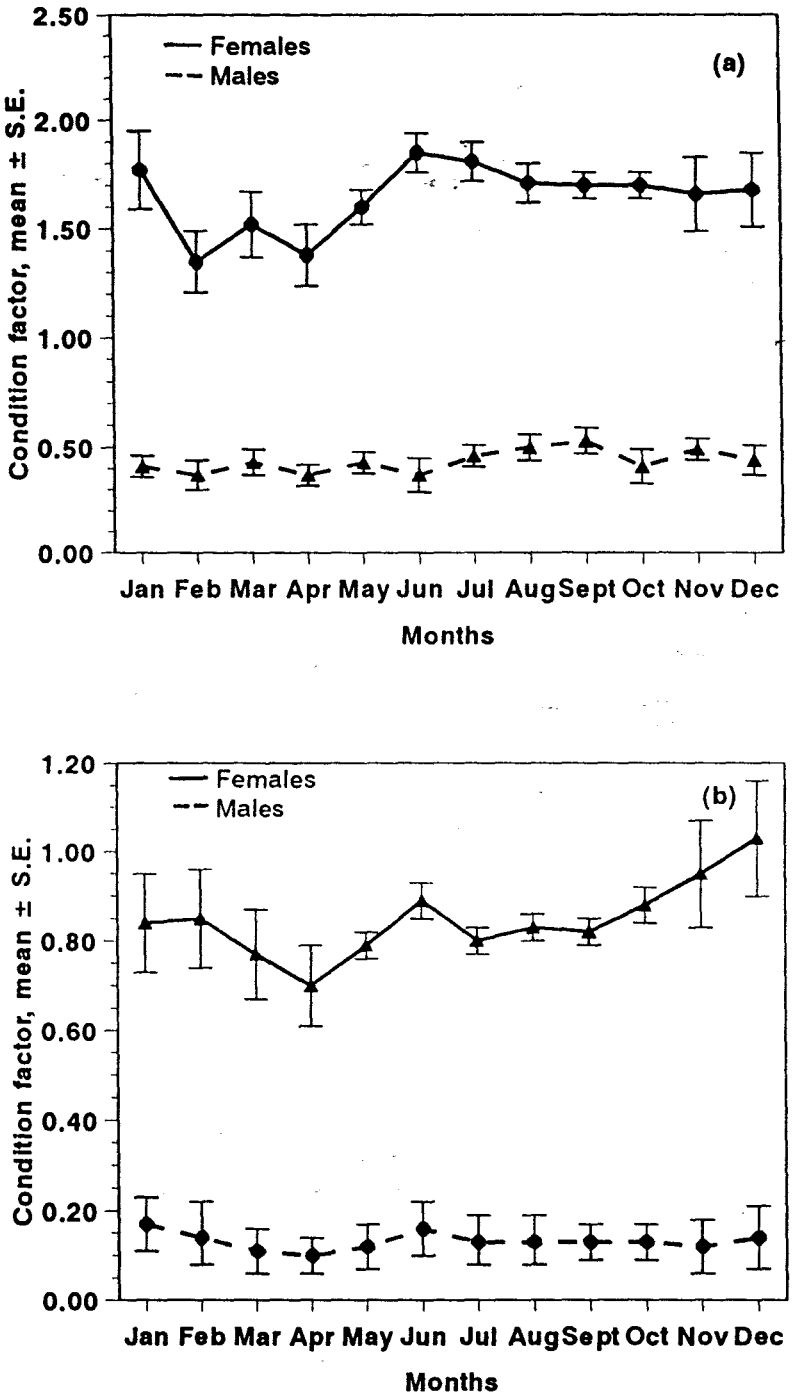


Fig. 2.6.4. Comparison of condition factors between males and females of native species, (a) *Pseudotropheus zebra* and (b) *Pseudotropheus tropheops* 'orange chest' at Thumbi West Island, Lake Malawi National Park, in the southern Lake Malawi.

Fecundity

All the Mbuna species studied breed throughout the year. But the number of eggs produced per month fluctuated widely, as shown by the large and overlapping standard errors (Fig. 2.7.1, 2.7.2, 2.7.3 & 2.7.4). However, there were obvious peaks and troughs in the number of eggs produced by each species. Two major peaks were evident, *i.e.*, at the end of the rainy season in April and at the end of the upwelling season in September. These peaks were most notable in the southern part of Lake Malawi, particularly exhibited by the introduced species, *C. afra* (Fig. 2.7.1) and *P. tropheops* 'red cheek' (Fig. 2.7.3). In contrast, *C. afra* and *P. tropheops* 'red cheek' in the northern part of Lake Malawi had a unimodal peak in their absolute fecundity, occurring in May for *C. afra* (Fig. 2.7.1) and September for *P. tropheops* 'red cheek' (Fig. 2.7.3).

The introduced and native species that overlap in their microhabitat requirements (see chapter 3) had non-synchronous breeding peaks, probably as a result of interference competition. Notable among these were the introduced species, *C. afra*, whose breeding peaks in April (mean $\pm$ *Sd* = 22 $\pm$ 4.56 eggs/female) and September (mean $\pm$ *Sd* = 25 $\pm$ 4.12 eggs/female) (Fig. 2.7.1) precede the breeding peaks of the native species, *P. zebra*, which occur in July (mean $\pm$ *Sd* = 13 $\pm$ 8 eggs/female) and in December (mean $\pm$ *Sd* = 12.73 $\pm$ 5.40 eggs/female) (Fig. 2.7.4). Similarly, the breeding peak of the introduced species, *P. tropheops* 'red cheek' (Fig. 2.7.3) preceded that of its sibling native species, *P. tropheops* 'orange chest' (Fig. 2.7.4).

Also, the introduced species in the park started to reproduce at relatively smaller size than the native species with which they were compared (Fig. 2.8.2). However, the *C. afra* (X^2 = 56, *df* = 4, $P < 0.01$), and *P. callainos* (X^2 = 40.41, *df* = 5, $P < 0.01$) in the northern Lake Malawi significantly start to breed at smaller size

than conspecifics that have been introduced at Thumbi West Island, (Fig. 2.8.1). The difference in absolute fecundity between the introduced species at Thumbi West Island and conspecifics at sites of their origin in the northern part of Lake Malawi was not significant (Table 2.2). But when the fecundity of these fishes was measured, based on relative fecundity which takes into account the size of the individual fish, the introduced species, *P. callainos* (t = 2.11, P < 0.001) and *P. tropheops* 'red cheek' (t = 7.56, P < 0.001) at Thumbi West Island had significantly higher fecundity indices than conspecifics at Nkhata Bay and Likoma (Table 2.3). This implies that they were more fecund in the park than at sites of their origin. Similarly, the introduced species, *P. callainos* (t = 2.44, P < 0.05) and *P. tropheops* 'red cheek' (t = 8.60, P < 0.001) had higher gonad indices in the park than at sites of their origin (Table 2.4). *Cynotilapia afra* was the only introduced species in the park whose fecundity and gonad indices did not differ significantly from its conspecifics at its site of origin.

Pseudotropheus tropheops 'red cheek' had significantly higher fecundity and gonad indices than its sibling native species, *P. tropheops* 'orange chest' (Fig. 2.9).

In all the Mbuna species studied, except *P. callainos* at Thumbi West Island, there was a positive relationships between size (SL) and absolute fecundity (Table 2.5), but this relationship was not significant in *C. afra* at Likoma, and *P. callainos* both at Thumbi and Nkhata Bay.

Table 2.2. Absolute fecundity, presented as mean ± standard deviation of the number of eggs per female of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek', at Thumbi West Island, southern Lake Malawi and at their sites of origin, Nkhata Bay and Likoma Island, in the northern Lake Malawi.

Species	*N*	Thumbi W. Island	*N*	Site of origin	*t* Value	*P* Value
C. afra	786	11.04 ± 8.00	735	9.75 ± 4.45	0.49	> 0.05
P. callainos	723	5.18 ± 2.47	454	2.79 ± 2.93	2.26	> 0.05
P. troph. 'rc'	722	9.21 ± 4.54	726	8.68 ± 3.85	0.50	> 0.05

Table 2.3. The fecundity indices (FI), presented as mean ± standard deviation of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' at Thumbi West Island, southern Lake Malawi, and at their sites of origin, Likoma and Nkhata Bay in the northern Lake Malawi.

Species	*N*	Thumbi W. Island	*N*	Site of origin	*t* Value	*P* Value
C. afra	786	0.005 ± 0.002	735	0.004 ± 0.002	0.11	> 0.05
P. callainos	723	0.004 ± 0.001	454	0.001 ± 0.001	2.11	< 0.05
P. troph.'rc'	722	0.008 ± 0.003	726	0.001 ± 0.001	7.56	< 0.01

Table 2.4. Gonad indices (GI), presented as mean ± standard deviation of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropeops* 'red cheek' at Thumbi West Island, southern Lake Malawi and at their sites of origin, Nkhata Bay and Likoma Island, in the northern Lake Malawi.

Species	*N*	Thumbi W. Island	*N*	Site of origin	*t* Value	*P* Value
C. afra	786	0.06 ± 0.03	735	0.06 ± 0.02	0.13	> 0.05
P. callainos	723	0.05 ± 0.01	454	0.02 ± 0.01	2.44	0.05
P. troph. 'rc'	722	0.12 ± 0.04	726	0.01 ± 0.01	8.60	< 0.001

Table 2.5. The relationship between size (SL) and absolute fecundity of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' and the native species, *Pseudotroheus zebra* and *Pseudotropheops tropheops* 'orange chest'

Species	Site	*N*	Slope	Intercept	Corr.coef.(*r*)	*P* Value
C. afra	Likoma	735	0.53	-11.63	0.861	0.139
	Thumbi	786	0.62	-11.62	0.992	0.003
P. callainos	Nkhata Bay	454	0.02	16.68	0.061	1.000
	Thumbi	732	-0.08	21.58	-0.270	1.000
P. troph.'rc'	Likoma	726	0.99	-41.33	0.815	0.048
	Thumbi	722	0.48	-11.60	0.891	0.043
P. troph.'oc'	Thumbi	298	0.65	-16.45	0.946	0.015
P. zebra	Thumbi	299	0.67	-18.60	0.690	0.002

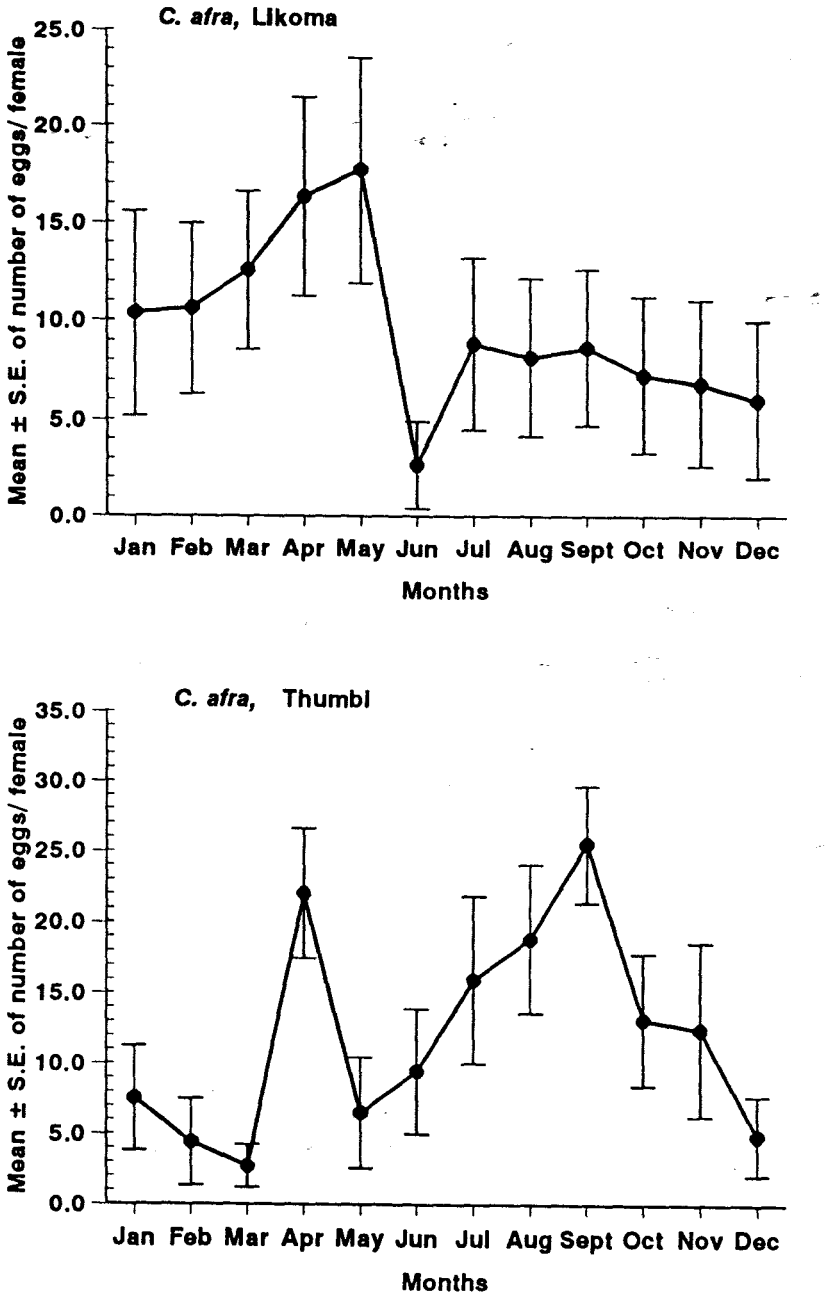
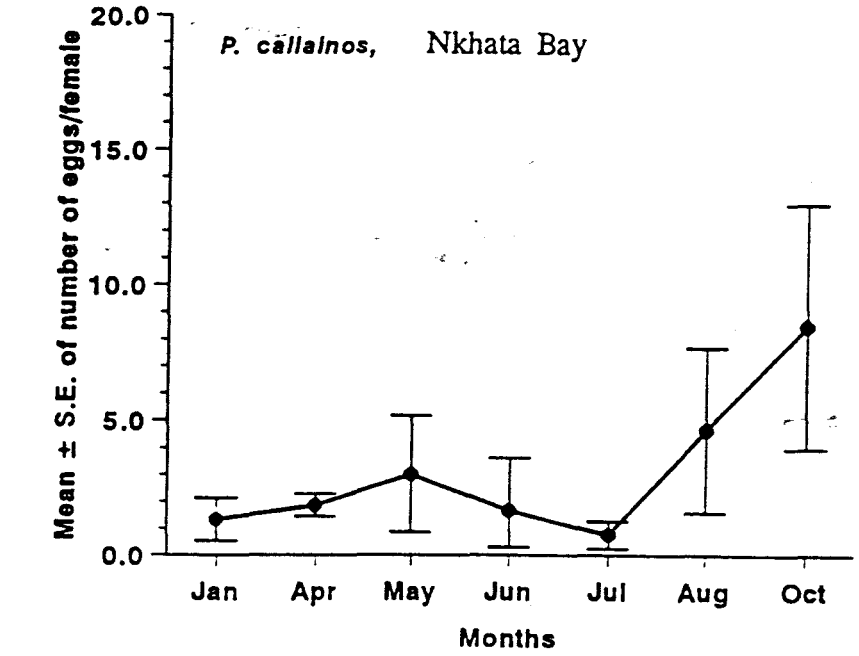


Fig. 2.7.1. The monthly absolute fecundity of the introduced species, *Cynotilapia afra* at its site of origin, Likoma Island and at Thumbi West Island, where it has been introduced.



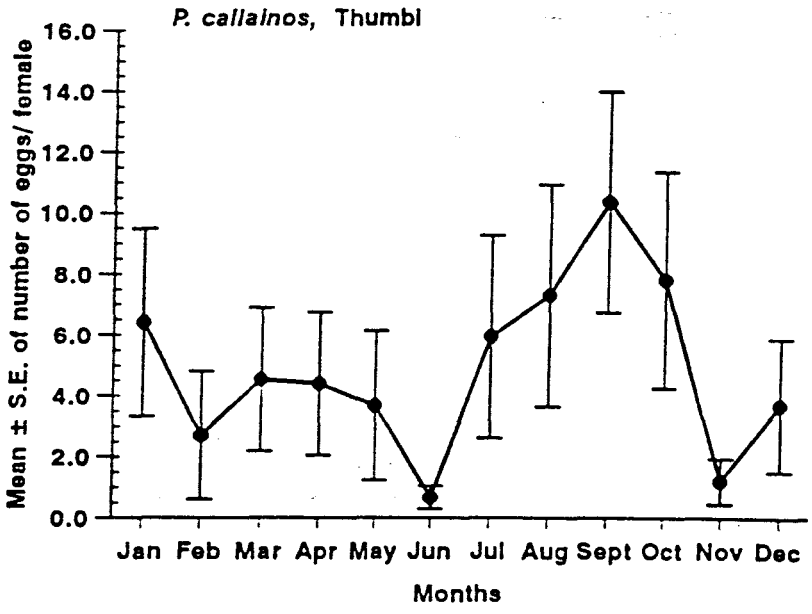


Fig. 2.7.2. The monthly absolute fecundity of the introduced species, *Pseudotropheus callainos* at Nkhata Bay, its site of origin and at Thumbi West Island, Lake Malawi National Park, in the southern Lake Malawi, where it has been introduced.

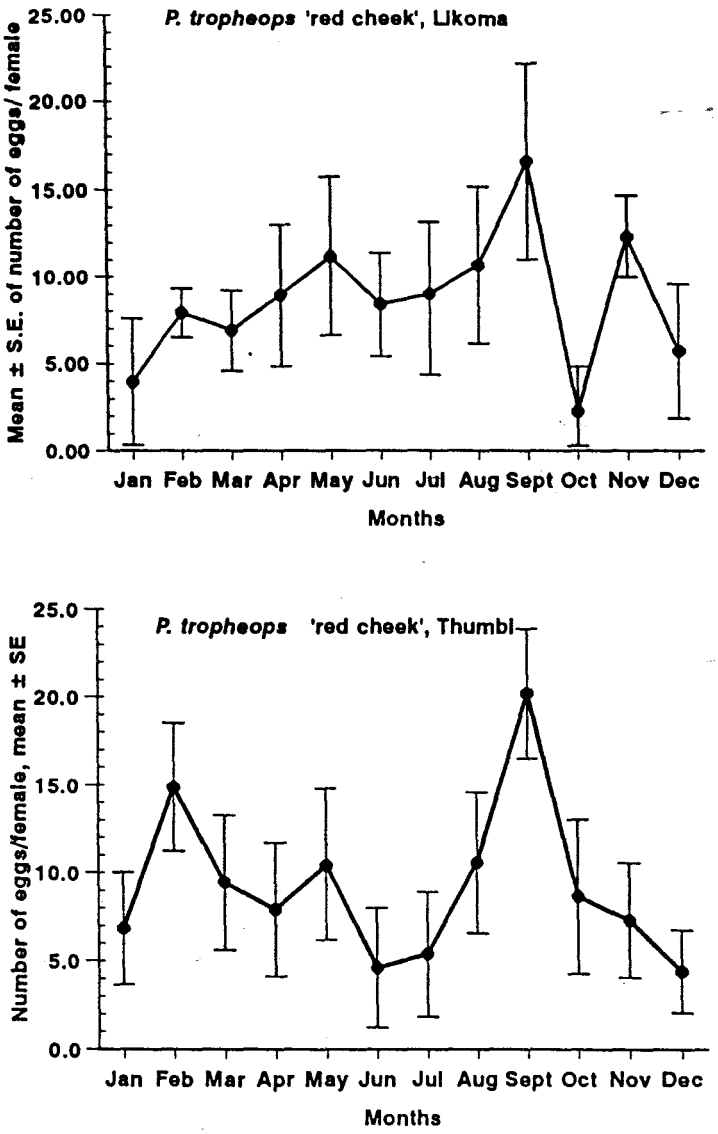


Fig. 2.7.3. The monthly absolute fecundity of the introduced species, *Pseudotropheus tropheops* 'red cheek' at Likoma Island, its site of origin and at Thumbi West Island, Lake Malawi National Park, where it has been introduced.

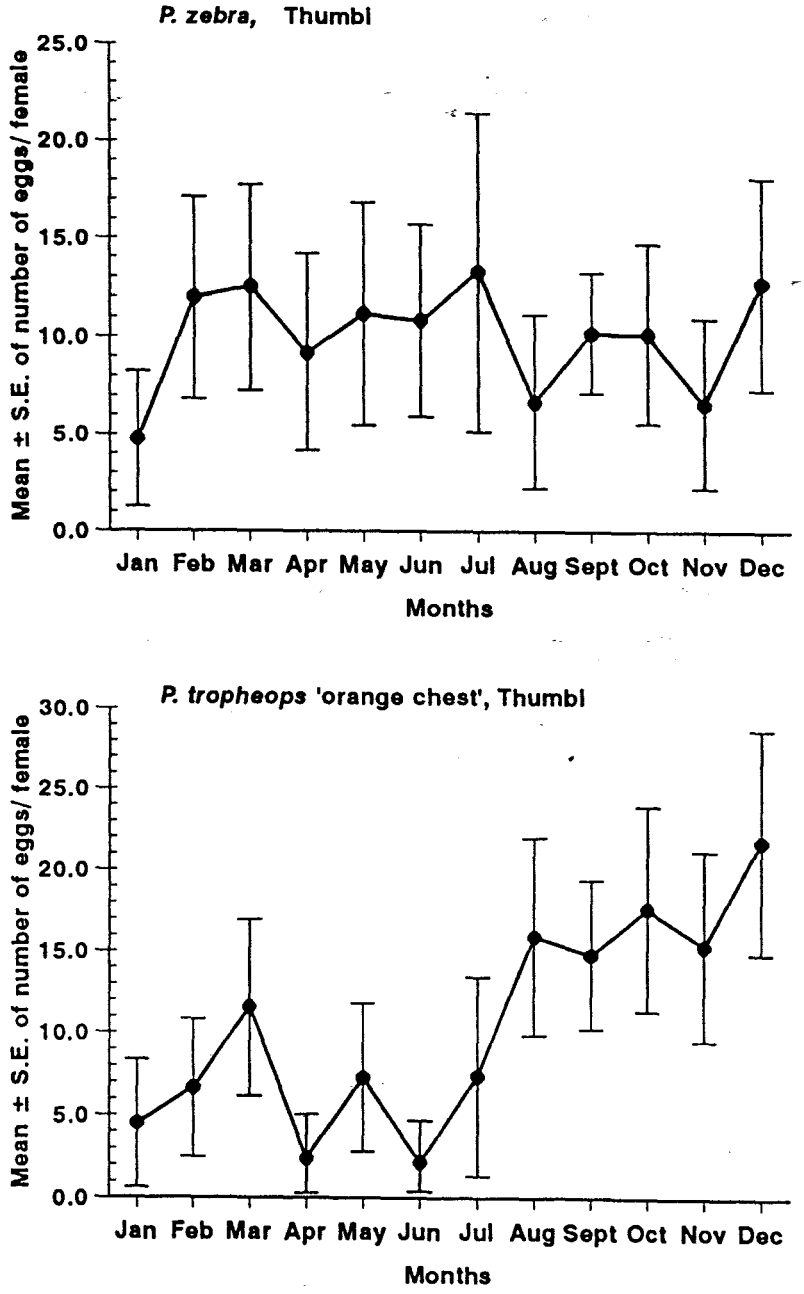


Fig. 2.7.4. The monthly absolute fecundity of the native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest' at Thumbi West Island, Lake Malawi National Park, Southern Lake Malawi.

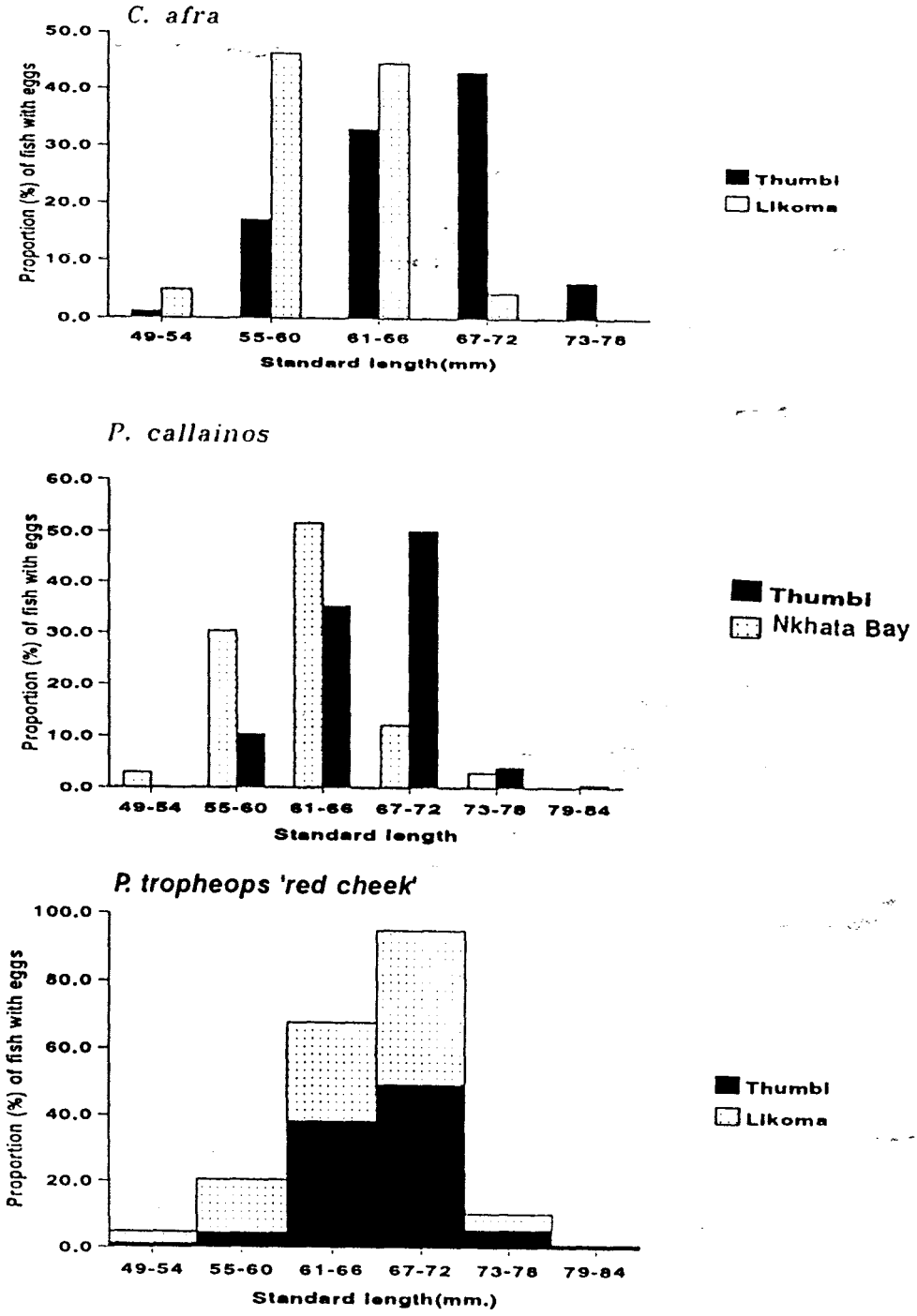


Fig. 2.8.1. The standard length (mm) at which the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' start to reproduce at Thumbi West Island, southern Lake Malawi, where they have been introduced and at sites of their origin, in northern part of Lake Malawi.

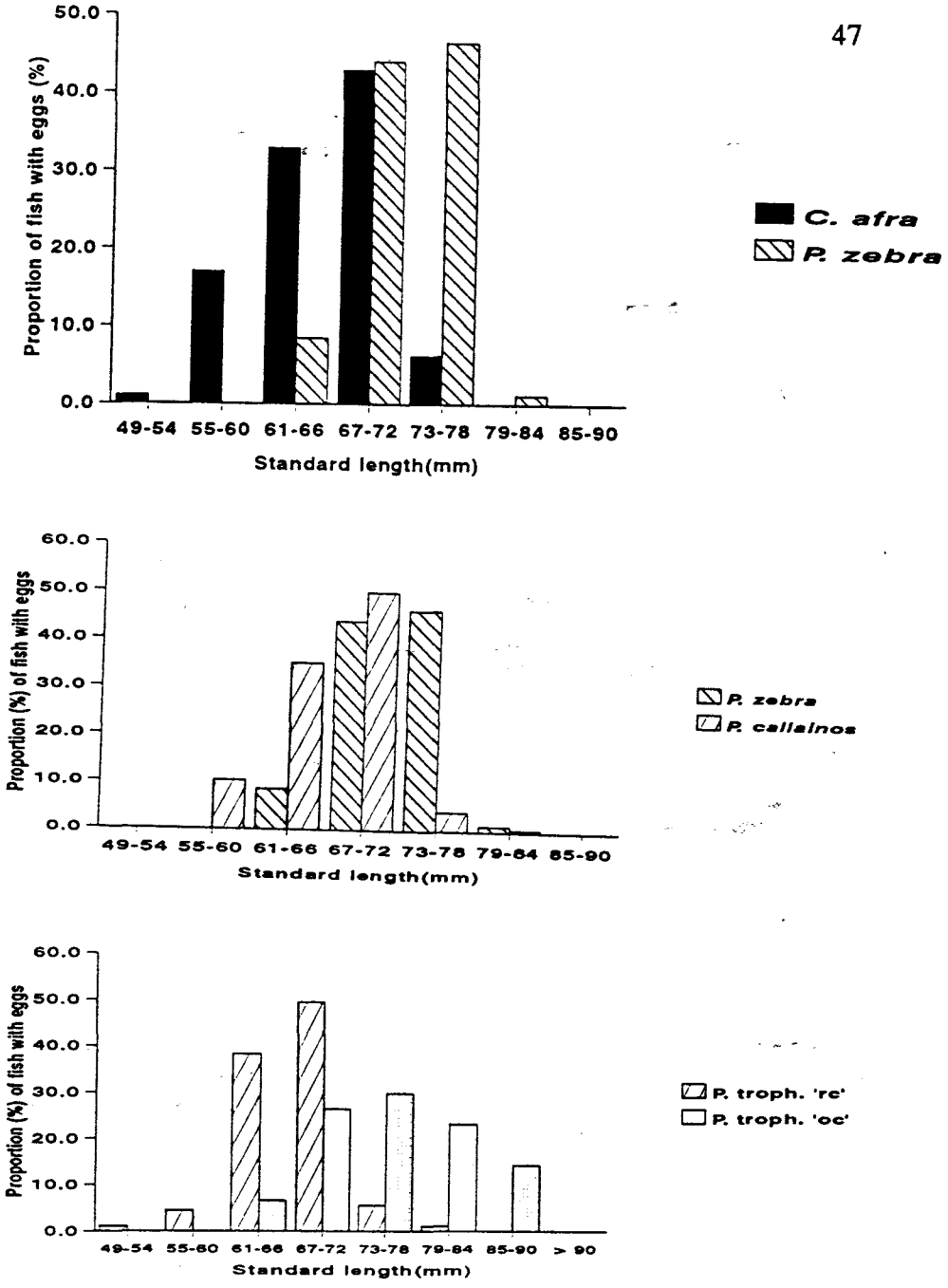


Fig. 2.8.2. Comparison of the standard length at which the introduced and native species that overlap in microhabitat requirements (chapter 3) start to reproduce.

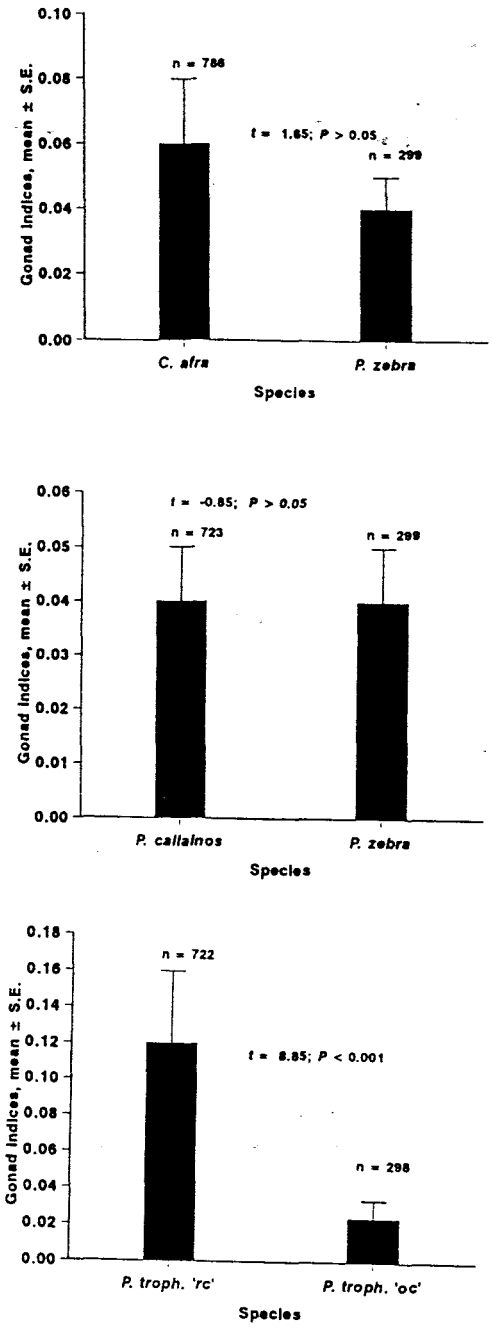


Fig. 2.9. Comparison of the gonad indices between the introduced and native species that overlap in their microhabitat requirements (see chapter 3).

Discussion

Results of this study show that some of the Mbuna which were translocated from the northern Lake Malawi and introduced into the southern part of Lake Malawi are in better condition (Fig. 2.2.1, 2.2,2 & 2.2.3) and are more fecund than the conspecifics at sites of their origin (Tables 2.3 & 2.4). This suggests that these fishes may have responded positively to enhanced food availability in the southern Lake Malawi. In many fish families, growth, condition and fecundity are influenced by food availability (Wootton 1990). Similarly, numerous studies relating to egg production and the population dynamics of fish, often imply that food supply is of primary importance in determining the reproductive potential of different fish stocks (Nikolskii 1969; Bagenal 1969). There are many examples that illustrate this. For instance, it has been shown in the convict cichlid, *Cichlasoma nigrofasciatum* (Townshend & Wootton 1985), the guppy, *Lebistes reticulatus* (Hester 1964), the three-spine stickleback, *Gasterosteus aculeatus* (Wootton 1973; Fletcher 1984; Wootton & Townshend 1984), the freshwater cottid, *Cottus gobio* (Mann *et al.* 1984), various salmonid species (Bagenal 1969; Springate *et al.* 1985), and many non-salmonid species (*e.g.*, Kuznetzov & Khalitov 1978) that the better fed fish grow faster and are more fecund than the poorly fed fish.

Improved food supply can also increase the gonad and egg sizes (Kuznetzov & Khalitov 1978). This seems also to be reflected in the introduced Mbuna species, *P. callainos* and *P. tropheops* 'red cheek', whose significant difference in the gonad indices between the individuals in the park and those in the northern Lake Malawi, where they originated (Table 2.4) may primarily be attributed to enhanced food availability because the lake is richer in nutrients in the south than in the north (Eccles 1974; Twombly 1983; Bootsma 1993a, 1993b).

The Mbuna's food requirement for somatic growth, maintenance and reproduction is not known, and has never been assessed in the wild. But despite this shortfall, it seems that the Mbuna species which were translocated from the nutrient-poor northern Lake Malawi and introduced into the nutrient-rich southern Lake Malawi may be finding it easier and energetically cheaper to obtain food than the conspecifics in the northern Lake Malawi. This seems likely because territories in which these fishes feed are larger in the north than in the southern Lake Malawi (see chapter 3). Therefore, the introduced Mbuna in the southern Lake Malawi may invest relatively more of their energy into gonadal development and vitellogenesis (*i.e.*, provision of the eggs with yolk) than conspecific in the northern Lake Malawi. This is probably the reason some of the introduced Mbuna in the park had larger gonad indices than conspecifics at sites of their origin (Table 2.4).

All the Mbuna studied produce a few ripe eggs at a time throughout the year (Fig. 2.7.1 - 2.7.4). This agrees with the observations made by Fryer & Iles (1972), Lowe-McConnell (1975), Ribbink *et al.* (1983a) and Marsh *et al.* (1985). Considering the oligotrophic nature of Lake Malawi (Lowe-McConnell 1975; Beadle 1981), the numerous Mbuna occupying the available trophic niches (Fryer 1959; Fryer & Iles 1972; Ribbink *et al.* 1983a) and the Mbuna's apparent competition for the essential resources, such as space for breeding, feeding and nursery ground for their young (Lowe-McConnell 1975; Sharp 1981; Marsh 1981; Ribbink *et al.* 1983a), fecundity may no longer be at a premium (Lowe-McConnell 1975). But the best reproductive response would be to put more energy into competition, maintenance and to reproduce larger eggs. Large eggs are associated with large yolk which provides the developing embryo with adequate reserves of energy and nutrients until the embryo is able to feed exogenously (*c.f.*, Balon 1990; Bruton 1990; Wootton 1990). This may be of great advantage, in terms of survivorship, because juveniles developed from large eggs may be bigger, may be able to take a

wide range of prey sizes, may be more capable of surviving periods of food shortage and may be more capable of eluding predators than the fry produced from small eggs (Ware 1975; Wootton 1990). This may be crucial for the Mbuna because as they reproduce throughout the year (Fryer & Iles 1972; Lowe-McConnell 1975; Ribbink *et al.* 1983a; Marsh *et al.* 1986; also see Fig. 2.7.1 - 2.7.4), competition for resources, such as food and hiding space among the resulting cohorts of fry may be quite intensive. The hiding places for the Mbuna's fry are crucial for their survival, as both the specialised ambush piscivores, such as *Nimbochromis linni, N. polystigma* and *N. livingstoni* and the pursuit predators, such as, *Protomelas kiwinge, P. macrostoma* and *P. woodi* are common in the rocky habitats of Lake Malawi (Ribbink *et al.* 1983a). Similarly, many Mbuna species, including the specialised herbivores within the genera *Pseudotropheus, Petrotilapia, Cynotilapia, Cyathochromis* and *Labeotropheus* eat fry of other fish opportunistically, while members of the *Melanochromis melanopterus* species-complex, which are morphologically and behaviourally adapted to piscivory feed regularly upon fry (Ribbink *et al.* 1983a). Under such a heavy predatory pressure, the Mbuna species that develop large gonads may have a high probability of producing large eggs and offspring that may have high survivorship advantage. However, it is not known if *P. tropheops* 'red cheek' which had significantly larger gonad indices than its sibling native species, *P. tropheops* 'orange chest' (Fig. 2.9), also produce larger offspring that may have survivorship advantage over those of the native species with smaller gonad indices. Similarly, the observed differences in the gonad size may simply reflect genetic differences between these species, probably with no overt implications on the size of eggs, or young which they produce. Future studies should also focus on the size of eggs and young produced by Mbuna and relate them to the young's ability to compete for nursery ground, or their survivor.

In the Mbuna, recruitment first occurs when the young are deposited among the

rocks by the female (Fryer 1959; Fryer & Iles 1972; Trendall 1988b), and the presence of one species in a habitat can decrease, or prevent subsequent recruitment of the same or different species in several ways, collectively termed priority effect (Sutherland 1974; Connell & Slatyer 1977; Trendall 1988b). In this respect, the introduced species, *C. afra* and *P. tropheops* 'red cheek', whose breeding peaks precede the breeding peaks of the native species with which they overlap in microhabitat requirements, such as, *P. zebra* (Fig. 2.7.1 & 2.7.4) and *P. tropheops* orange chest' (Fig. 2.7.3 & 2.7.4), respectively, may have an advantage of first recruiting their young in optimal habitats. Since agonistic behaviour has been observed in the juvenile Mbuna (Trendall 1988b), it is likely that the offspring of the introduced species recruited earlier in the year have a competitive edge in the use of essential resources over the late recruited offspring of the native species. This may have serious implications on the survival of the late recruited offspring of the native species, as they may be vulnerable to predation, particularly, if some are being excluded from optimal nursery grounds. Therefore, although this study did not look into juvenile mortality and space utilization by the offspring of the introduced and native species, it can be suggested that the successful population growth of some introduced species at Thumbi West Island may be partly attributed to the non-synchronous breeding peaks between them and native Mbuna species.

Cynotilapia afra, *P. callainos* and *P. tropheops* 'red cheek' start to breed at relatively smaller size at sites of their origin, in the northern Lake Malawi, than at Thumbi West Island, in the southern Lake Malawi, where they have been introduced (Fig. 2.8.1). In fish, crowding (Balarin & Hutton 1979) and lower food availability (Mironowa 1978) have been attributed to early sexual maturity and reproduction at smaller size. For instance, in various Tilapiines, crowding at very high densities can accelerate puberty and maturity (Balarine & Hutton 1978). However, it is unlikely that crowding may have influenced early puberty and early

reproduction in the Mbuna of northern Lake Malawi, because the population density of Mbuna and other rock-dwelling fishes is lower in the north (4.8 - 6.9 m^{-2}) than in the southern Lake Malawi (8.5 - 10.4 m^{-2}) (Ribbink *et al.* 1983a). Therefore, if crowding had any effect at all, it should have been on the Mbuna in the south, where the fish population density is higher. But since Lake Malawi is poorer in nutrients in the north than in the south (Eccles 1974; Twombly 1983; Bootsma 1993a, 1993b), the majority of Mbuna in the northern Lake Malawi start to breed at smaller size probably as an adaptive response to the poor nutrient regime. The remarkable difference in the condition factors between the introduced species at Thumbi West Island and conspecific in northern Lake Malawi (Fig. 2.2.2 & 2.2.3) may be a reflection of this lake's difference in nutrient status between the north and the south. Poor nutrition has also been associated with early sexual maturity and reproduction at smaller size in *Oreochromis mossambicus* (Mironowa 1979) and *Oreochromis niloticus* (Munro 1990) and in both cases, it has been assumed to be an adaptive response to harsh conditions (Munro 1990). Similarly, the introduced species at Thumbi West Island start to reproduce earlier than the native species with which they overlap in microhabitat requirements. It is also probable that enhanced food availability to the introduced species acts as a modifying influence through its effect on growth rate, and it thus acts in favour of those genotypes which, by entering sexual maturity at a particular size and/or younger age, maximise their life-span fecundity (*c.f.*, Munro 1990).

In this study, only size at which the individual species started to breed was taken into account when evaluating the fecundity of the studied Mbuna species. No attempt was made to relate fecundity with the age of the studied Mbuna species because no appropriate method for ageing adult Mbuna has been developed, and it was beyond the scope of this study to develop such a method. The existing ageing method, such as the daily growth rings of otoliths has proved inappropriate for

ageing Mbuna beyond their juvenile stage (Msukwa 1993). Similarly, the method based on the size-frequency which works on the premise that fish born at approximately the same time form a cohort, and that cohorts should form distinct modes in the size-frequency distribution of the population (Wootton 1990), also has limited application in ageing the Mbuna. This is because the Mbuna breed throughout the year, and therefore, there is a high probability that within a single year, there may be several distinct cohorts. Hence, the slow growing individuals may be indistinguishable from the younger cohorts. Therefore, it was not possible to age the Mbuna using the length-frequency method within the limited time of this study.

Of the introduced Mbuna species studied, only *C. afra* seems not to have positively responded to enhanced nutrients in its new environment, as both its condition factors (Fig. 2.2.1) and fecundity indices (Tables 2.3 & 2.4) were not significantly different between the population in the park and that of its conspecific at its site of origin, in northern Lake Malawi. This implies that *C. afra* in northern Lake Malawi also manages to obtain adequate food requirements, but probably at a higher searching cost than its conspecific in the south, as territories in which this species feeds are larger in the north than in the south (see chapter 3). Also unlike the other Mbuna that were studied, *C. afra* exclusively feeds on the pelagic diatom, *Melosira* (Reinthal 1987; 1990), and zooplankton (Ribbink *et al.* 1983a) which may be available even after the upwelling season, when food may be less abundant (Eccles 1974; Twombly 1983; Haberyan & Mhone 1991). For instance, *Melosira* whose growth depends on high silica level is most abundant during the upwelling season when silica is also high (Haberyan & Mhone 1991). During the calm, stratified season its cells sink to the botttom, but as Malawi is susceptible to storms, violent winds and abrupt changes in weather from November to April (Torrance 1972), Lake Malawi experiences some turbulence. Consequently the *Melosira* cells

that sink and settle on the rocky-shore are resuspended in the water column (Haberyan & Mhone 1991), where *C. afra* has access to it even during the stratified season when food is generally limited. Similarly, the rainfall-induced lake turbulence between November and April, induces some upwelling of nutrients which favours growth of zooplankton, and indeed short-term abundance of zooplanton have been reported both in the northern Lake Malawi (Degnbol & Mapila 1982) and southern Lake Malawi (Twombly 1983). Consequently, *C. afra* may also have access to this food resource at the time when food is generally scarce in the lake. Therefore, the insignificant difference in condition (Fig. 2.2.1) and fecundity (Tables 2.3 & 2.4) between *C. afra* in the northern and southern Lake Malawi may be due to *C. afra*'s diverse feeding opportunities, even at times when food is normally scarce in the lake.

The Mbuna species studied exhibited marked seasonality in their condition factors (Fig 2.2.1 - 2.2.3; Fig. 2.6.4) and absolute fecundity (Fig. 2.7.1 - 2.7.4) (also see Marsh *et al.* 1986), with peaks in both condition and fecundity often evident during particular months of the year. Similar observations have been made in other fish families, as well as other organisms, with evidence that reproduction, like other aspects of life history, tend to be seasonal both in the temperate and tropical environments (Munro 1990).

Many factors have been attributed to such seasonality. For example, in natural populations of the temperate fish, it is assumed, often implicitly, and sometimes explicitly stated that photoperiodism and temperature are the major initiating and synchronising environmental stimuli for reproduction, and examples in support of this have been given in a number of fish orders, such as Teleostei (Buxton 1990), Salmoniformes (Scott 1990), Gasterosteiformes (Wootton 1977; Boule & FitzGerald 1989; Baggerman 1990), Artheriniformes (Day & Taylor 1983, 1984; Taylor 1990)

and Perciformes (de Vlaming 1972a, 1972b). In all of these studies, the consensus is that the seasonal cycle of changing light and darkness is used as a predictive cue that initiates gametogenesis (Bye 1990). Whereas temperature on the other hand influences the rates of metabolic processes. For poikilotherms, such as fish, there is invariably a relationship between environmental temperature and the metabolically demanding processes related to reproduction. For example, growth, feeding rates and food conversion efficiency, as well as the availability of food are all affected by temperature, and these have important implications for gametogenesis and breeding seasonality in the temperate fish (Bye 1990).

In the tropics, temperature has also been identified as a potential proximate factor triggering reproductive seasonality in a variety of lacustrine cichlid species (*e.g.*, Henderson 1963; Payne & Collinson 1983), and field observations have identified the lower threshold temperature for the breeding of several species of *Tilapia* (*e.g.*, Cridland 1962; Maar *et al.* 1966; Bruton & Bolt 1975). For instance, it has been noted that sufficiently high temperature triggers reproduction in *Tilapia rendalli* in Lake Kariba (Donnelly 1969), while low temperature inhibits reproduction in *Oreochromis mossambicus* (Mironowa 1978), and inhibits territorial behaviour and reproduction in south American cichlids (Baerends & Baerends-Van Roon 1950; Peeke *et al.*1980). In Lake Malawi, while temperature is an important factor influencing primary productivity (Eccles 1974; Beadle 1981; Haberyan & Mhone 1991; Bootsma 1993a, 1993b), there is no evidence that the Mbuna's territorial behaviour, and/or reproductive performance may be influenced by temperature. Probably, this is because the euphotic temperature of Lake Malawi only fluctuates seasonally by a small amplitude, of between 22.5°C and 29°C (Eccles 1974; Twombly 1983; McKaye 1983).

Besides temperature, rainfall and floods have also been linked to reproductive

seasonality in some tropical lacustrine fishes (Fryer & Iles 1972), particularly those that migrate upstream to breed (Munro 1990). These fishes are mostly substrate spawners, that do not guard, or employ any parental care to their progeny. Therefore, they choose within the flooded streams, optimal microhabitats, where running water provides sufficient oxygen to the developing fry (Fryer & Iles 1972). This is however, not the case with the Mbuna of Lake Malawi, although they are descendants of the riverine haplochromine ancestor (Fryer & Iles 1972; Ribbink *et al.* 1983a). The Mbuna are capable of providing their own running water for their eggs and developing fry. This is achieved by the female Mbuna which immediately picks up the eggs during spawning, so fertilization takes place in her mouth, after which she broods them for a period of about 3 - 4 weeks (Fryer & Iles 1972; Ribbink *et al.* 1983a; Marsh *et al.* 1986). Throughout the brooding period, the eggs are well aerated by the normal respiratory current of the parent, which inevitably bathes the eggs, or young, as the water passes through the mother's mouth by churning movements which also help to clean the egg and young and thus, prevent fungal infections (Fryer & Iles 1972). Having achieved this level of adaptation, the Mbuna, and other Lake Malawi's cichlids, do not need to migrate upstream to breed. Therefore, rainfall and floods *per se* do not directly influence the Mbuna's breeding seasonality.

However, there is some evidence that the timing and intensity of spawning for some cichlid fish in Lake Malawi (Lewis 1981; Marsh *et al.* 1986) and Lake Victoria (Witte 1981) may be correlated with seasonal food availability. In this study, the peaks and troughs in the Mbuna's condition factors (Fig. 2.2.1 - 2.2.3 & Fig. 2.6.4) and absolute fecundity (Fig. 2.7.1 - 2.7.4) may also be due to seasonal fluctuations in Lake Malawi's nutrient regime.

Seasonal variations in primary production have been reported in all the African

Great Lakes (*e.g.*, Lake Malawi: Eccles 1974; Degnbol & Mapila 1982; Twombly 1983; Haberyan & Mhone 1991; Bootsma 1993a, 1993b, Lake Tanganyika: Hecky & Fee 1981; Hecky & Kling 1981 and Lake Victoria: Talling 1966; 1986). For Lake Malawi, three seasons have been recognised, with respect to primary productivity. These are: the upwelling season (May - August), the transition season (September - October) and the stratified season (November - April) (Haberyan & Mhone 1991).

The upwelling season is characterised by cool and dry weather, with daily average temperature of 20°C to 22°C (Bootsma 1993a). During this season the trade winds, known locally as *Mwera,* blow from the southeast and induce a pile-up of surface water in the northern sector of the lake, causing the permanent thermocline at 200 - 250m to tilt so that nutrient-rich water from the abyssal zone is mixed into the mixolimnion (Eccles 1974; Beadle 1981). The high turbulence and nutrient levels in the mixolimnion during this season favour growth of the diatoms (Haberyan & Mhone 1991; Bootsma 1993a, 1993b) and zooplankton (Twombly 1983) which are generally most abundant at this time of the year. Therefore, it is not surprising that most of the Mbuna species studied exhibited the highest condition factors during this season (Fig. 2.2.1 - 2.2.3 & Fig. 2.6.4) and *C. afra* at Likoma (Fig. 2.7.1) had its highest absolute fecundity in the upwelling season.

During the transition season, there is an increase in temperature and severe fluctuations in the relative biomass of the algal resources (Haberyan & Mhone 1991), but generally some of the diatoms, such as *Nitzschia* and chlorophytes (Haberyan & Mhone 1991) and some zooplankton (Twombly 1983) may still be abundant during this season. This is clearly reflected by high condition factors in some of the Mbuna species studied (Fig. 2.2.1 - 2.2.3 & Fig. 2.6.4), and *C. afra* at Thumbi West Island has a second peak in its absolute fecundity (Fig. 2.7.1) during this season, while others, *e.g., Pseudotropheus callainos* (Fig. 2.7.2) and

Pseudotropheus tropheops 'red cheek' (2.7.3) have their major peaks in absolute fecundity during the transition season. The delayed peak in reproduction by these fishes to the end of the season of food abundance, indicates a time lag between their exposure to abundant food and assimilation of food into gonad development and vitellogenesis.

During the stratified season the water temperature increases, and it reaches a maximum daily average of around 28°C in November and stratification develops (Bootsma 1993a, 1993b). Often this stratification is in the form of several layers, in addition to the permanent thermocline at about 200 - 250m (Eccles 1974; Twombly 1983), hence the nutrients in the abyssal zone are not readily available for primary production in the mixolimnion. Consequently, the algal resources change in their relative abundance, with most of them becoming less available, while others, such as *Anabaena* become quite common throughout this season (Haberyan & Mhone 1991). However, as it is also the rainy season from November to April, with a considerable amount of nutrients, such as phosphorus and nitrogen also entering the lake by means of river flooding (Bootsma 1993b), some primary production is maintained during this season as well. The rainy season in Malawi is characterised by storms, and violent winds (Torrance 1972), so shallow secondary thermoclines repeatedly form and dissipate in the mixolimnion (Eccles 1974; Twombly 1983), suggesting that some shallow mixing occurs (Lewis 1973; Twombly 1983). Such sporadic mixing induced by abrupt winds during the season when the lake is stratified renews epilimnetic nutrient supplies and stimulates some primary production (Lewis 1973; Eccles 1974; Twombly 1983; Bootsma 1993a, 1993b). But certainly the amount of food available to the fish during this season may not be as adequate as during the other seasons, as reflected by the decline in condition factors in most of the Mbuna species studied in March, or April (Fig. 2.2.1 - 2.2.3 & 2.6.4). These months mark the end of rains in Malawi, and consequently a

reduction in rainfall-based nutrient input, *e.g.*, nitrogen and phosphorus (Bootsma 1993b). Since some of the Mbuna also have a breeding peak in March or April, *e.g.*, *C. afra* (Fig. 2.7.1) and *P. tropheops* 'orange chest' (Fig. 2.7.3) at Thumbi West Island, they may certainly experience a disproportionate energetic demand as there is an elevated territorial encounter among the males (see chapter 3), while the females need extra energy for the three to four weeks oral incubation of their eggs (Fryer & Iles 1972; Marsh *et al.* 1986). In fact, all the Mbuna species studied lost their condition in the months immediately succeeding their breeding peaks (Fig 2.2.1 - 2.2.3, 2.6.4 & Fig. 2.7.1 - 2.7.4).

However, when the condition factors of males and females were compared, albeit the fact that females may experience disproportionate energy requirement for vitellogenesis (*i.e.*, provision of the eggs with yolk), and maintenance, particularly during their protracted mouth brooding period, females were significantly in better condition than males, except for *C. afra* (Fig. 2.6.1 - 2.6.4). These results are not surprising, because in the Mbuna, males exhibit both intra- and interspecific territorial aggression in defense of their usually small (30 - 140 cm diameter) territories (see chapter 3). Besides having limited space over which to feed, the male Mbuna engage in energetically demanding activities, such as courtship display, fertilizing gravid females and chasing intruders that trespass into their territories. Consequently they spend less time feeding and they lose condition (Munthali, in press *a*). Females on the other hand, have large home ranges, and even those that may defend territories, such as members of the *Pseudotropheus tropheops* species-complex (Ribbink *et al* 1983a), forage over large areas and are selectively aggressive towards females of their conspecific and congenerics (pers. obs.), hence have ample space and time to feed. Even females which are oral incubating eggs have been seen during many occasions with their ventrally bulging and enlarged mouths feeding in the water column (Pers. observ.), and food has been found in the gut of brooding

females (Fryer & Iles 1972). The mechanism used to feed while holding eggs in their mouths has not been ascertained, but if these fishes did not feed during the egg incubation period, their condition could probably be worse than that of the males.

Similarly, non-territorial males do not experience as much energetic demand as territorial males. Munthali (in press *a*) has shown that non-territorial male Mbuna forage over large areas, spend more time feeding and are in better condition than territorial males. Therefore, it is likely that biased sampling, particularly as it was much easier to catch territorial males than non-territorial males may have biased the comparison of condition factors between the males and females, in favour of females. Otherwise, in the fish that are not territorial and do not interact aggressively with their sympatric neighbours, the energetic demand for egg production and mouth brooding could be higher than the demand for foraging, gametogenesis and sperm production in males (*c.f.*, Wootton 1990).

Also, notable in this study was the disparity in condition between the introduced and native Mbuna species which overlapped in microhabitat requirements (Fig. 2.3; 2.4 & 2.5). The most likely reason for this disparity may be genetic, as the introduced and native species have different length-weight coefficients (see methods section of this chapter).

Overall, the successful population growth of the introduced species that have been studied at Thumbi West Island, Lake Malawi National Park may be attributed to their:

(i) improved condition and fecundity, particularly, by the introduced species, *P. callainos* and *P. tropheops* 'red cheek';

(ii) **production of large gonads, *e.g.*, by *P. tropheops* 'red cheek', which may probably also produce large offspring that may have high competitive abilities for essential resources;**

(iii) **starting to reproduce at relatively smaller size than the native species with which they overlap in microhabitat requirements, and probably by doing so they maximize their life-span fecundity;**

(iv) **non-synchronous breeding peaks, which precede the breeding peaks of the native species with which they overlap in microhabitat requirements. Therefore, due to priority effects (Trendall 1988b), the introduced species' offspring may be having a competitive edge in the use of essential resources, such as food and refuge over the native species whose peak recruitment is later in the year.**

Chapter 3

Microhabitat Preference and Territoriality in some Introduced and Native Mbuna, Cichlidae at Thumbi West Island, Lake Malawi National Park, Malawi

Introduction

Since the intra-lacustrine translocation of Mbuna from the northern to the southern part of Lake Malawi, more than twenty years ago, most of them have become wide spread members of the rocky shore community at Thumbi West Island, where they have been introduced (Ribbink *et al.* 1983a; Lewis *et al.* 1986; Trendall 1988a). The mechanisms through which these Mbuna have succeeded to establish themselves in the seemingly species-rich and crowded community at Thumbi West Island are not known.

From an abiotic point of view, the intra-lacustrine translocation of fish from northern to southern Lake Malawi were mere geographic redistributions, with subtle, but probably no overt implications for the introduced species. This may be the case because the physical environment of the rocky habitat and the physico-chemical aspects of the water in the donor and recipient communities are similar. Therefore, the introduced species may have easily acclimatised in their new environment. However, from an ecological point of view, the successful establishment of introduced species may imply that either the recipient community is governed by a biotic process, and that it may be at, or near equilibrium, but some essential resources may be unlimited. Hence, the introduced and native species may coexist by occupying, feeding and breeding in different microhabitats, or it may imply that introduced species are superior competitors in the use of essential environmental resources (*c.f.*, Ross 1990). The latter hypothesis is amplified by the fact that the introduced and many of the native species in the recipient community belong to the same species flock, and appear to have similar ecological requirements (Ribbink *et al.* 1983a). Consequently, it can be assumed that the introduced and native species may exclude each other, particularly if the essential ecological requirements are limited (*c.f.*, Gause 1934; Brown & Orian 1970; MacArther 1972;

Sale 1976; Pianka 1978). This seemed likely because most males of these fishes exhibit both intra- and interspecific aggression in defense of their territories to which females are attracted to spawn (Fryer & Iles 1972; Ribbink *et al.* 1983a). Sneak fertilization (kleptogamy) by non-territorial males has never been observed in the field (Chang & Ribbink 1990), and it is probable that only males defending territories propagate their genes. The demand for optimal territory sites in the Mbuna community may be exacerbated by their long territorial residence (*e.g.* Hert 1990; Kornfield *et al.* in press). Also, since the majority of the Mbuna are stenotopic and their distribution is restricted to specific habitats and depths (Ribbink *et al.* 1983a; Trendall 1988a), it can further be assumed that increases in the number of introduced species in the already crowded community may increase density-dependent aggression, probably with the consequence of decreased reproductive success in some native Mbuna species.

The goal of the study reported in this chapter was to test the hypotheses that introduced and native species either coexist by occupying and utilizing different microhabitats, or that the introduced species exclude native species from optimal microhabitats through interference competition. Interference competition in this study was considered as any activity which either directly or indirectly limit a competitor's access to an essential resource, or requirement (Miller 1967). The specific objectives were:

1. To identify the microhabitats that are preferred by the introduced and native species, and find out if they overlap, or if they are ecologically segregated;
2. To assess the diurnal activities (*e.g.*, courtship, mating, feeding, aggression, *etc*) of the introduced and native species to find out if there are diurnal, or seasonal variations that could facilitate their coexistence, or if there is a crush, with the consequence of interference competition;

3. To determine and measure territories occupied by the introduced and native species and ascertain if there are any temporal, or seasonal variations which could facilitate their coexistence;
4. To assess the spatial distribution, or pattern of territories occupied by the introduced and native species in relation to their conspecifics.
5. To find out if there is natural interspecific territory turn-over between the introduced and native species, and through a removal experiment, monitor population dynamics of the introduced and native species. The underlying assumptions were: (a) that the removal of introduced fishes from their territories would leave the space open for others to occupy. This would indicate whether conspecific supernumeraries (*i.e.*, adult, sexually active males which would hold a territory if they could), or other species, such as displaced native species would occupy territories if they became vacant. In this way an indication of the similarity of ecological requirements with regard to territoriality might be made. (b) That competition for common essential resources, such as appropriate rocky substrata, or refuge and spawning holes exists between the introduced and native Mbuna species living sympatrically. (c) That competition for space through adult male territoriality would provide the clearest indication of which species have the most similar ecological, and/or breeding space requirements.
6. To determine whether management steps, such as culling should be taken if introduced species are shown to have serious negative impacts on the native species at Thumbi West Island.

Study site

The study site was Thumbi West Island, in the Lake Malawi National Park, 15°59'S, 34°54'E, Malawi (Fig. 3.1).

Species studied

The principal focus of this study was on the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *P. tropheops* 'red cheek', and the native species, *P. zebra* and *P. tropheops* 'orange chest' (see chapter 1).

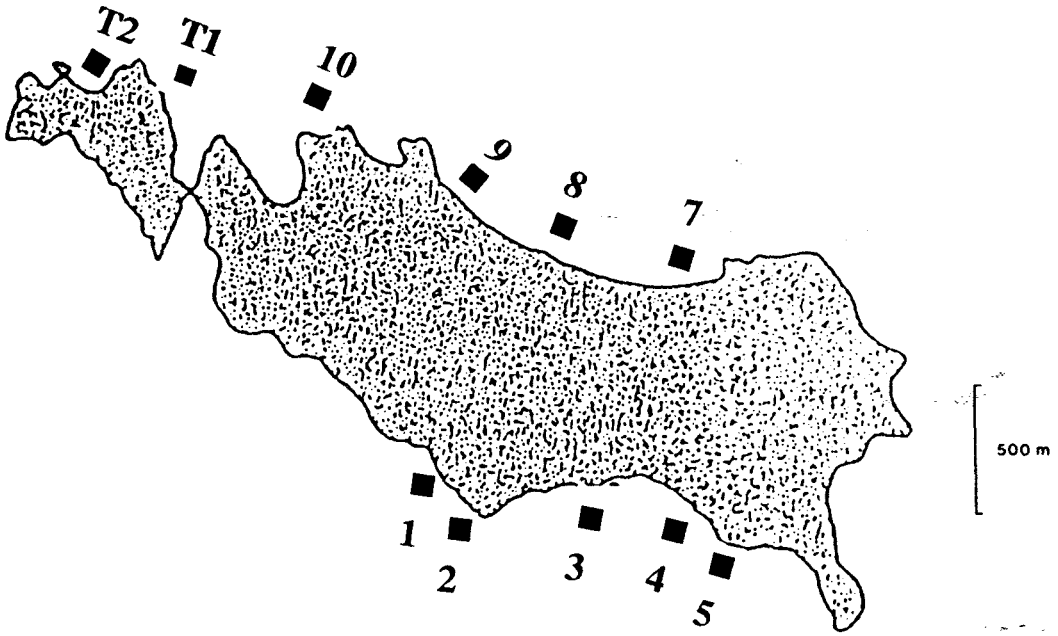


Fig. 3.1. Map of Thumbi West Island with insets of sites at which sampling was done. Note, study site 6 has not been shown because the quadrat was stolen, and no further sampling was undertaken at this site.

Methods

This study was conducted from September, 1992 to November, 1994. All measurements and observations were done in situ by means of SCUBA.

(i) Microhabitat preferences

Nine (7m x 7m) permanent quadrats, and two transects (2m x 25m) were established around Thumbi West Island (Fig. 3.1) in August 1992. Within these quadrats and transects, the following were measured:

Rocks and holes

Rocks and holes between the rocks used by the territorial males of the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' and native species, *P. zebra* and *P. tropheops* 'orange chest' were measured to determine if there are specific or overlapping requirements by these Mbuna species. Measurements were taken in different directions to circumvent biased effects of irregularities in rocks and entrances to the shelters between them.

The overlap indices in the rocks and holes preferred by the introduced and native species were calculated by using Schoener's Index formula (Linton *et al.* 1981; Reinthal 1987), as follows:

$$R_o = 1 - \tfrac{1}{2}\Sigma | P_{ij} - P_{ik} |,$$

where R_o = resource overlap, P_{ij} = the proportion of the rock or hole size category i occupied by introduced species j and P_{ik} = proportion of rock or hole category i occupied by native species k. The proportion of rock and hole size occupied by the

introduced species, *C. afra*, *P. callainos*, and *P. tropheops* 'red cheek' and native species, *P. zebra* and *P. tropheops* 'orange chest' are shown in Figures 3.2a and 3.2b. The overlap values were considered high if ≥ 0.60, intermediate if 0.40 - 0.60 or low if ≤ 0.40 (*c.f.*, Reinthal 1987).

Based on the rock size measurements, the nine quadrats and two transects around Thumbi West Island (Fig. 3.1) were classified into two microhabitat categories: (i) small rocks, *i.e.*, if > 50% of the rocks within the quadrat were ≤ 65cm in diameter, and (ii) large rocks if > 50% of the rocks within the quadrat were ≥ 65 cm in diameter. On this basis, the microhabitats at the study sites, #: T1, 3, 4 and 5 (Fig. 3.1) were classified as small rocks, while sites, #: T2, 1, 2, 7, 8, 9 and 10 were classified as large rocks. Ribbink *et al.* (1983a) also classified the rocky habitat according to rock size, but their range of rock sizes is too wide to be used in discriminating differences in the microhabitats preferred by the Mbuna of this study.

Since animals may select a habitat that guarantees food availability and reproductive success (Alcock 1979), the sites where the Mbuna of this study fed within their preferred microhabitat and their mating success were assessed *in situ* by means of SCUBA.

Four quadrats were used, *i.e.*, two representing the small-rock microhabitat (quadrats at sites, #: 4 & 5) and two representing the large-rock microhabitat (quadrats at sites, #: 1 & 10) (Fig. 3.1). This replication was adopted because behavioural studies demand a lot of time and, therefore, only four quadrats could be adequately handled.

Feeding site utilization

To obtain information on feeding site utilization by each species within its preferred microhabitat, the 7m x 7m permanent quadrats were subdivided into 1m x 1m cells, using nylon cords laid across the rocks as shown in Fig. 3.3. Individuals of the species under study that occurred in the grids were chosen at random and observed for 5 minute periods, following the method of Wootton (1972) and Altmann (1973). Since the male territorial Mbuna may spend their entire lives within their territories (Fryer & Iles 1972; Ribbink *et al.* 1983a), it was easy to make these observations over an extended period of time. During these observations, the sites where the subject fed were noted and recorded on a plastic slate. Feeding "sites" were classified into either (i) water column or (ii) rock substratum. A further two feeding "sites" were recognised on the rock substratum: on top of the rock and on the rock sides. The relative feeding frequencies by each species within each of these feeding "sites" were calculated to find out if there were diurnal and/or seasonal similarities or differences between the introduced and native species that overlap in their microhabitat requirements.

The time spent feeding both on the rock substratum and in the water column was measured by an underwater stop watch. The height at which individual Mbuna fed in the water column was measured by a graduated vertical line, supported at its base by a 10cm diameter concrete ball and a buoy was tied to its other end to make it perpendicularly vertical, while under water. These data are of value in two important ways: (i) they show the degree with which the introduced and native species utilize their microhabitats for feeding, and hence shed light on the likelihood of competition for food between those species that overlap in their microhabitat requirements, and (ii) through these data, the introduced and native species that overlap in their microhabitat requirements, but are segregated by utilizing different feeding "sites" within the same microhabitats, or feed at different heights, or feed

in the same sites with different intensity could be identified.

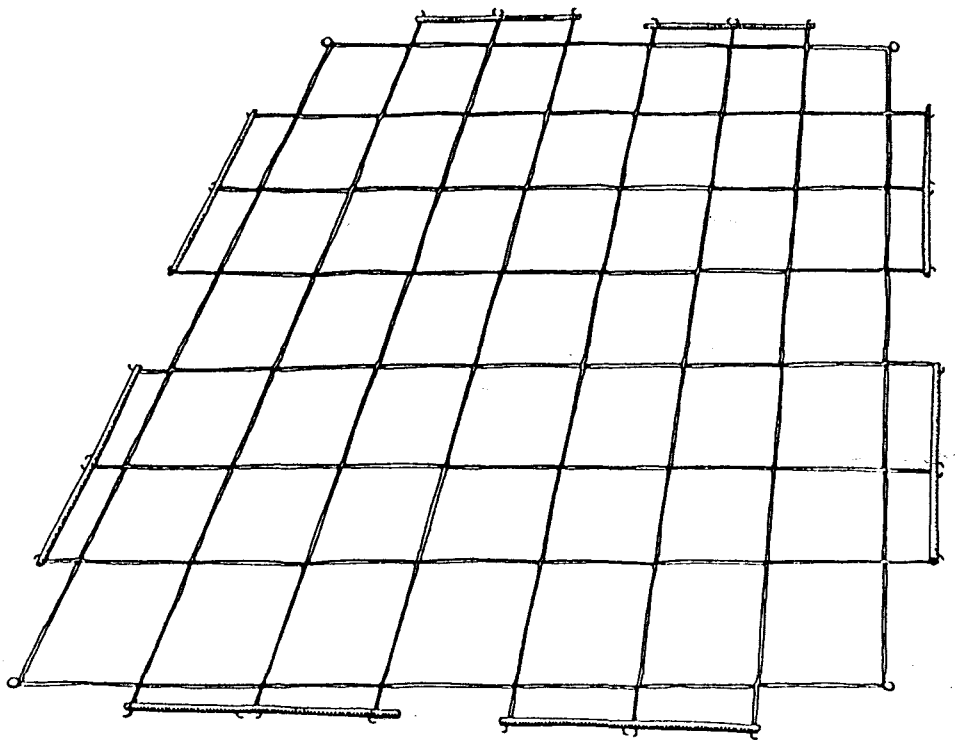


Fig. 3.3. An illustration of the 7m x 7m quadrat, subdivided into 49 x 1m squares in which behavioural studies were conducted. These divisions were easily removed and replaced as required for manipulation, measurements and mapping of territories occupied by the species under study.

Mating success

To show that the microhabitats used by introduced and native species may have significant fitness consequences, the mating success (*i.e.*, proportion of courtship displays that culminated in spawning) was quantified for each of the species under study, and the holes or crevices in which they spawned were measured in the same manner as described under the microhabitat section of the methods. Courtship involves a sequence of behaviours, which include lateral displays, quivering and leading (Fig. 3.4a & b). In a positive response, a female descends to the territory of a displaying male and enters a crevice, or hole under rocks where spawning may take place, while in a negative response, a female flees from a courting male, and there is no spawning.

The holes occupied by the individuals of species under study that did not succeed to mate were measured, and compared with those individuals that mated. The frequency of hole entering by each studied species was also quantified. These data provided opportunity to identify the microhabitats that are most critical for the reproduction of both the introduced and native species, and hence show potential conflicts between them in the acquisition of such microhabitats.

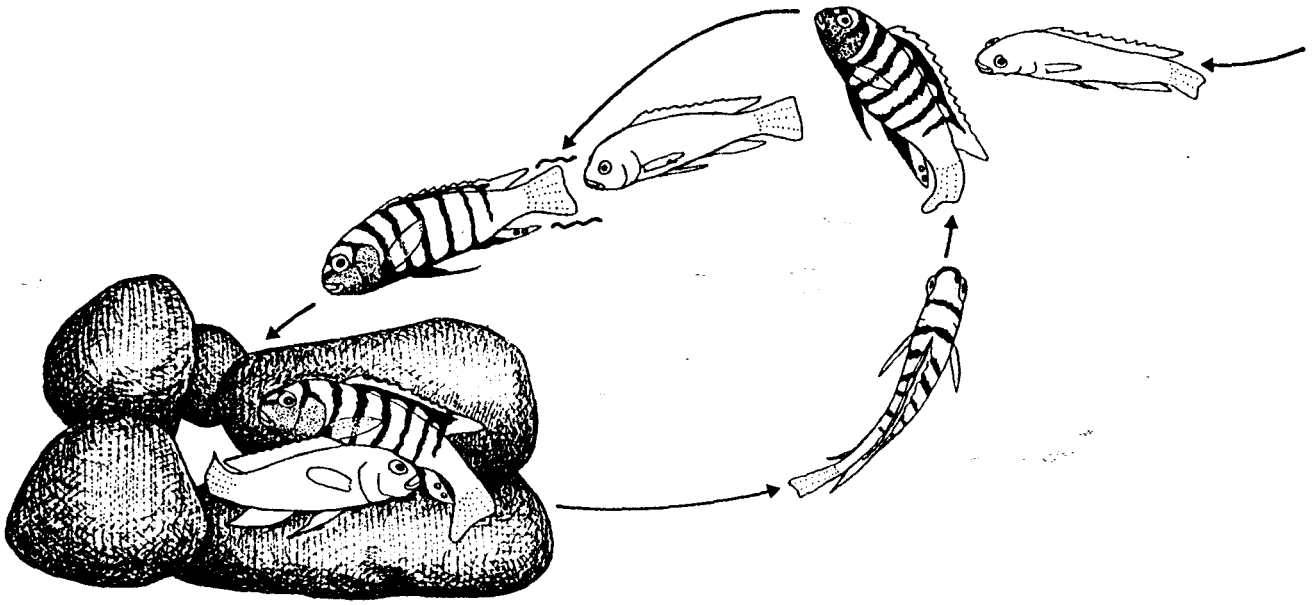


Fig. 3.4a. An illustration of the courtship sequence by the Mbuna of the small rock guild, *i.e.*, the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and native species, *P. zebra*. *A* = male (♂♂) of *C. afra* approaching a passing by conspecific female (♀♀), *B* = male courting at the female, *C* = male side shaking, *D* = female follows a courting male, *E* = male leads a female to spawning site, in a hole among rocks, *F* = male circles, and spawns with a female in a spawning site. Usually this is not seen as it is done under rocks.

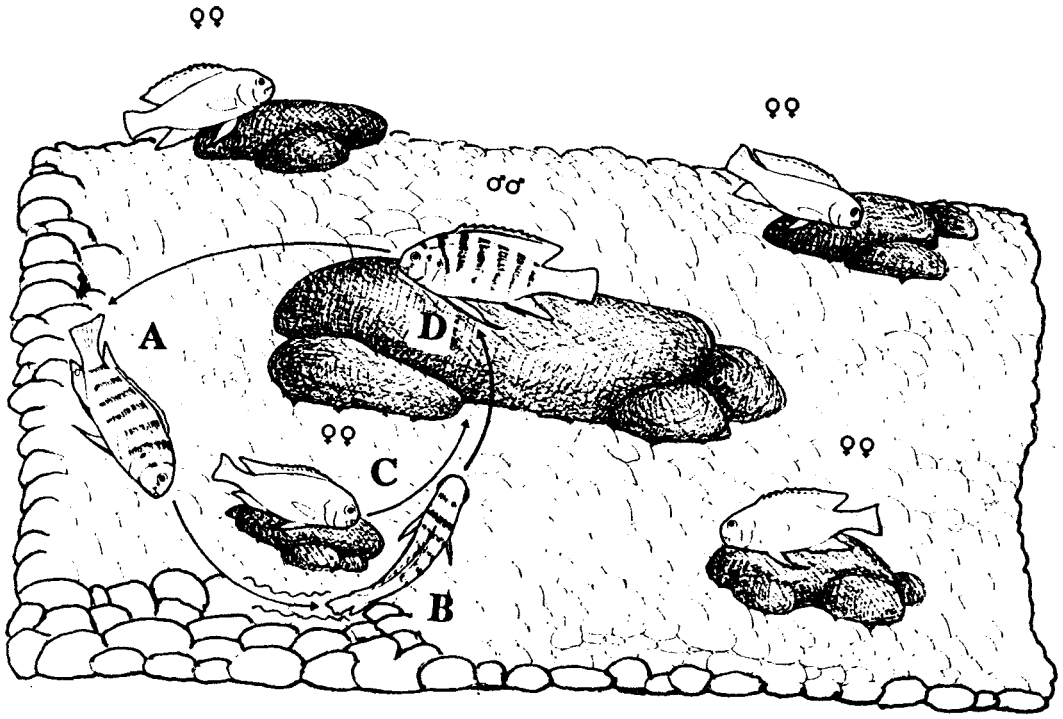


Fig. 3.4b. An illustration of the courtship sequence by the Mbuna of the large rock guild, *i.e.*, the introduced species, *Pseudotropheus tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest'. Females (♀♀) have home ranges around the territorial male (♂♂) in the centre, located on a large rock. *A* = Male approaching a female, *B* = male side shaking, inviting the female to follow him to its spawning site, *C* = follow shake, *D* = male leading a female to spawn site, which can either be in a crevice on the side of a rock, or on top of a rock.

Aggression

Aggressive behaviour was taken as any attack, or chasing by the studied species of either a conspecific or heterospecific intruder. The number of attacks by each studied species was recorded during each dive, and the species attacked were identified and recorded on an underwater slate. Finally, the relative frequency of each of the behavioural parameters observed was calculated and statistically compared between introduced and native species, particularly those that overlap in their microhabitat requirements.

To detect diurnal differences in behaviour, readings were made from first light (05h30 - 08h00), mid-morning (8h01 - 11h00), midday (11h01 - 13h00), early afternoon (13h01 - 15h00), mid-afternoon (15h01 - 17h30) and dusk (17h31 - 18h30). This intensive sampling schedule was only done from January to March, 1993. The behaviour of these fishes was also compared on seasonal basis, *i.e.*, during the upwelling, transition and stratified seasons. These seasons have been described in chapter two of this thesis.

Territory sizes

Territories defended by species under study were considered as the area occupied and defended on the rock substratum and the area used in the water column, as illustrated in Figure 3.5. The substratum area was measured by observing the chasing distance from the centre to points which were taken to represent territory boundaries. These were then marked by placing metal clips on the rock substratum. Each individual's territory was measured at different points several times and the mean diameter was calculated. The water column territories were measured by observing an individual's excursion in the water column and noting the outer-most limits. These territories were also measured at several points and a mean was taken to represent the diameter of each individual's water column territory. The territory

sizes defended by each species were compared between the small and large rock predominated microhabitats.

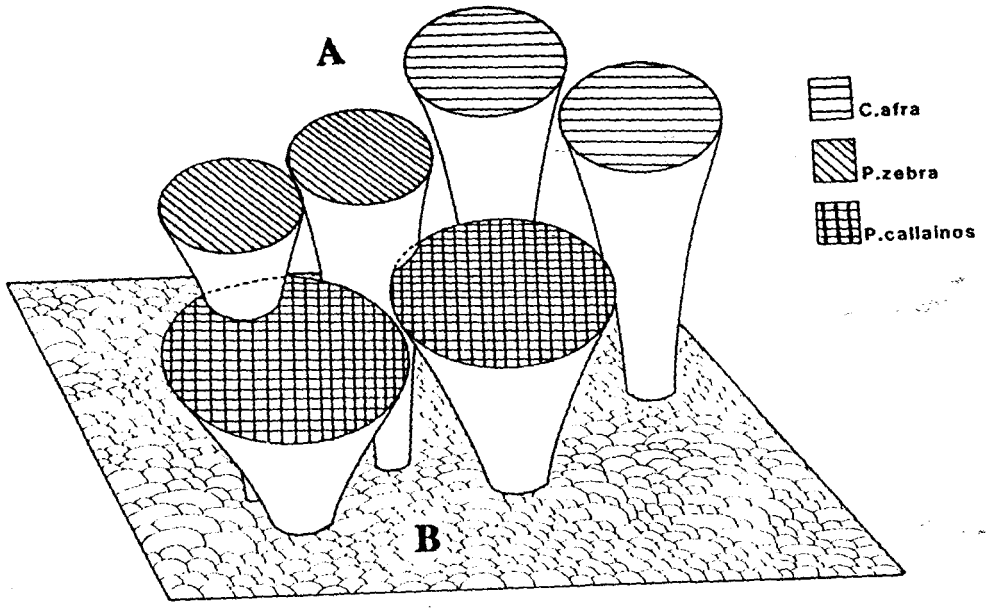


Fig. 3.5. An illustration of the territories held by the Mbuna on the rock substratum (a) and in the water column (b).

Clumping, or spatial pattern of territories held by the introduced and native species was assessed by using the Green's Index (*GI*) of dispersion formula (*e.g.*, Krebs 1989; Clarke 1994) to find out if the distribution of territorial males in relation to their conspecific significantly departed from random, as follows:

$$GI = \frac{(S^2/x) - 1}{n - 1}$$

where S^2 is the variance, x is the mean and n is the total number of individuals counted in the sample. This is a modification of the variance-to-mean ratio (index of dispersion) that is independent of the number of individuals (n) counted in the sample. Since the values were small, they were multiplied by 100. Consequently, maximum clumping gives a value of 100, randomness gives zero and uniform distribution gives a negative value (Krebs 1989; Clarke 1994).

Interspecific territory turn-over

Natural turn-over

To find out if introduced species and native species are excluding each other, the 7m x 7m quadrat at study site, #: 5 (Fig. 3.1) was permanently subdivided into forty-nine $1m^2$ square grids (as in Fig. 3.3). Within these grids, the central position of each territorial fish was marked on the grid map drawn on an underwater slate. Territory sites occupied by the introduced species *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' and native species, *P. zebra* and *P. tropheops* 'orange chest' were permanently marked by numbered plastic discs so that new-comers to their territories could easily be identified.

The marked territories were monitored once every four months throughout the study period, and the following were recorded: (i) the central position of all territorial Mbuna occurring in each grid, and (ii) the population of all territorial and non-territorial fish occurring in the quadrat. The natural turn-over experiment, described here, also acted as a control for the removal experiment described below.

(b) ***Territory turn-over due to removal of territory tenants***

A removal experiment was undertaken in a 7m x 7m quadrat, at study site, #: 3 (Fig. 3.1), as follows:

(i) The movable 49 x 1m square grids were constituted, as in Figure 3.3, and the central position of all territorial Mbuna were recorded on an underwater slate, and prescribed data forms.

(ii) All territorial and non-territorial fish occurring in the quadrat were counted, and their numbers were recorded on an underwater slate, and prescribed data forms.

(iii) Territories occupied by the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' were permanently marked, as described under natural territory turn-over.

(iv) The lines making up the $1m^2$ grids were taken out (Fig. 3.6).

(v) Territorial males of the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' were removed by catching them with a 6mm mesh size nylon multifilament net (6 meter long x 1,5 meter deep). These removals were done twice every month for sixteen months. However, at the beginning of the experiment, in September, 1992 territorial individuals of the introduced species were removed nine times in three weeks.

The effect of removals on population dynamics of introduced and native species was also monitored. This was done by counting the number of all territorial fishes in

the quadrat where removals were undertaken before and after each removal, twice every month throughout the study period.

The removal of territorial males of the introduced species provided an opportunity to test whether culling might be a viable management option for solving the problem of introduced species in the park.

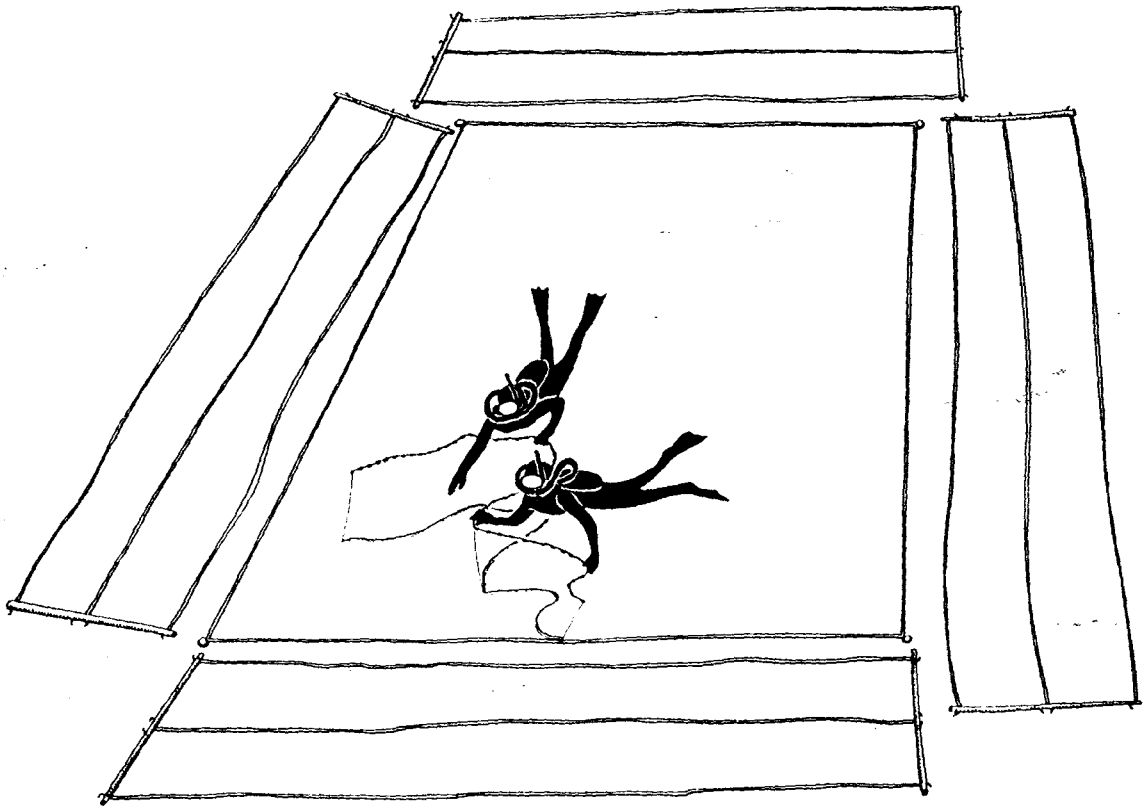


Fig. 3.6. An illustration of the 7m x 7m quadrat after removal of the $1m^2$ grids during the removal of the territorial males of the introduced species.

Results

Rocks and holes

The introduced species, *C. afra*, *P. callainos* and native species, *P. zebra* most occupied the rocks that measured between 36 - 40cm, and holes that measured between 4 - 12cm in diameter (Fig. 3.2a). On the other hand, the introduced species, P. tropheops 'red cheek' and its sibling native species, P. tropheops 'orange chest' mostly occupied the rocks that measured between 40 - 100cm and holes that measured between 8 - 19cm in diameter (Fig. 3.2b).

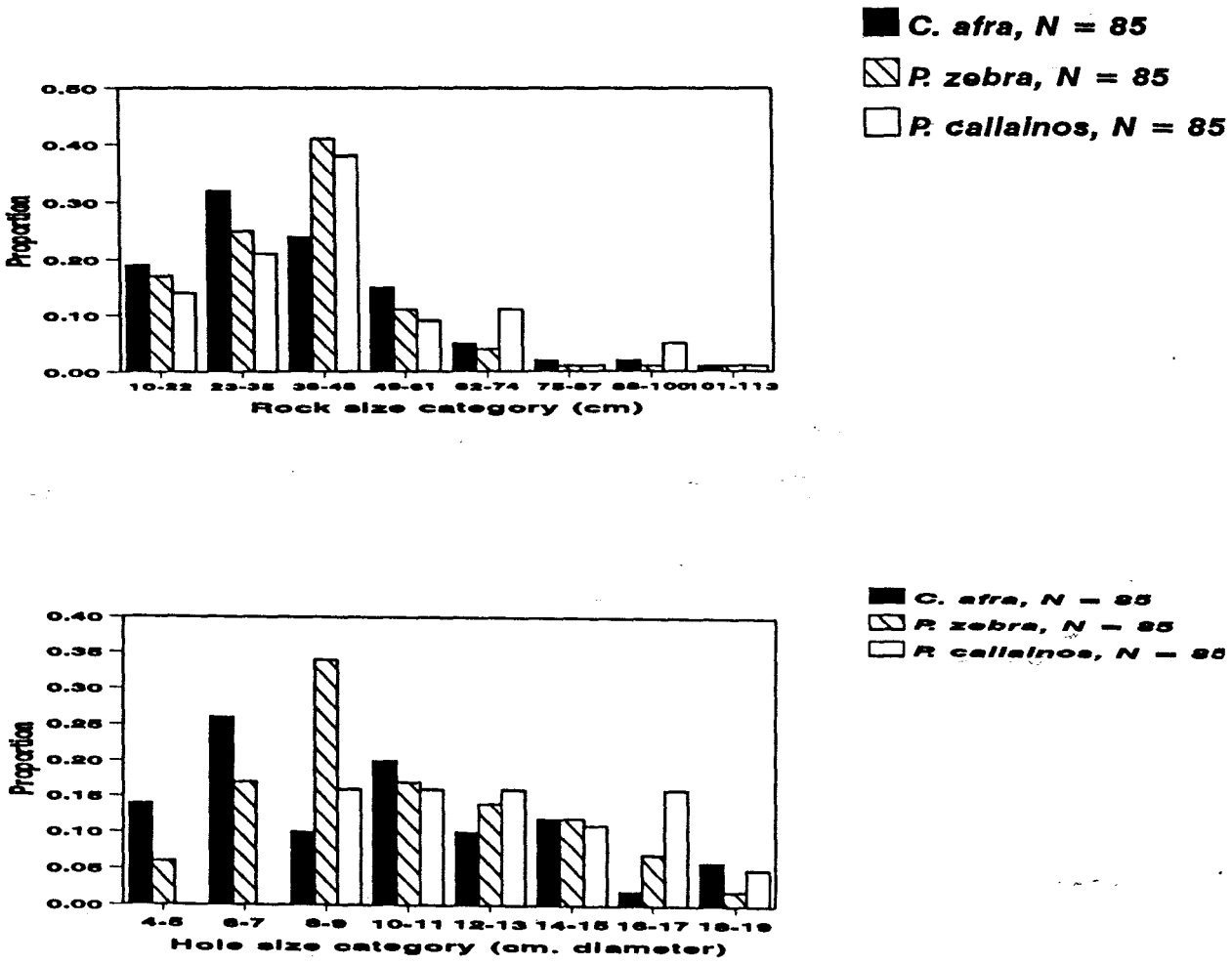


Fig. 3.2a. The proportion of the rock and hole size occupied by the Mbuna of the small rock guild, *i.e.*, *Cynotilapia afra*, *Pseudotropheus callainos* and *P. zebra*.

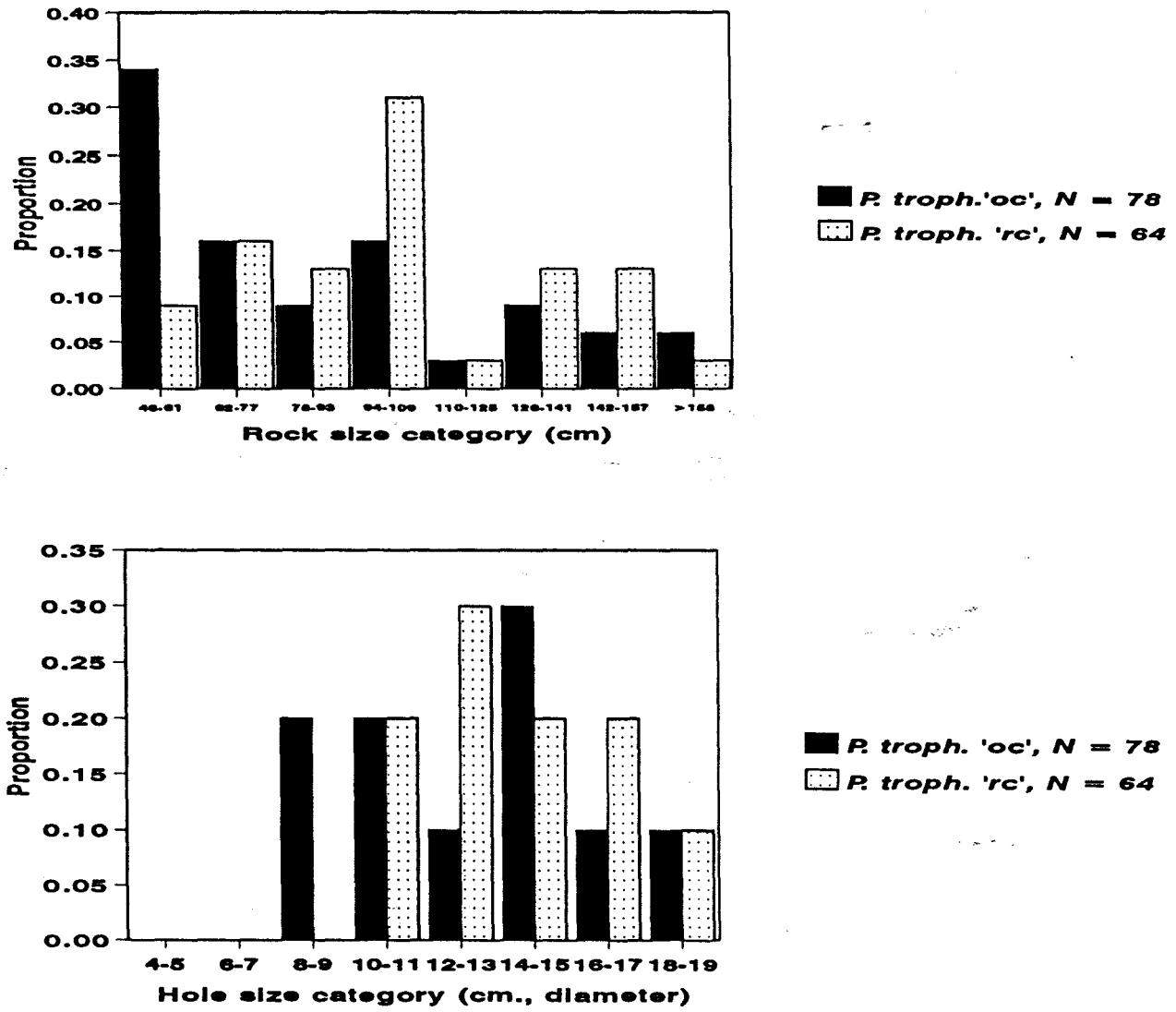


Fig. 3.2b. The proportion of the rock and hole size occupied by the Mbuna of the large rock guild, *i.e.*, the introduced species, *Pseudotropheus tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest'.

Table 3.1. The degree of overlap (calculated using Schoener's Index formula) in the rocks occupied and defended by the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek', and the native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest' at Thumbi West Island. The abbreviation oc = orange chest, rc = red cheek.

	Introduced species		
Native species	*C. afra*	*P. callainos*	*P. troph.*'rc'
P. zebra	0.81	0.87	0.27
P. troph. 'oc'	0.15	0.28	0.71

Table 3.2. The degree of overlap (calculated using Schoener's Index formula) in the holes occupied by the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' and native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest' at Thumbi West Island. The abbreviation, oc = orange chest, rc = red cheek.

	Introduced species		
	C. afra	*P. callainos*	*P. troph.*'rc'
Native species			
P. zebra	0.82	0.40	0.40
P. troph.'oc'	0.30	0.55	0.70

Table 3.3. Categorization of study sites

	Quadrat/ transect number
Small rock predominated areas:	3 4 5 T1
Large rock predominated areas:	1 2 7 8 9 10 T2

Microhabitat preference

The introduced and native species overlap in the microhabitats they occupy. Among these, the introduced species, *Cynotilapia afra* and *Pseudotropheus tropheops* 'red cheek' strongly overlap with the native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest', respectively, both in the preferred rocks (Table 3.1) and holes (Table 3.2) they occupy and defend. Similarly, another introduced species, *Pseudotropheus callainos* overlaps with its sibling native species, *P. zebra* in the rocks it occupies and it also overlaps, although not strongly with another native species, *P. tropheops* 'orange chest' in the holes, or crevices it occupies.

Based on the microhabitat preference, two main guilds were recognised: (i) those species that occupy and defend rocks that are ≤ 65cm and holes that are ≤ 10cm in diameter, *e.g.*, the introduced species, *C. afra*, *P. callainos* and the native species, *P. zebra* (hereafter referred to as the small rock guild), and (ii) those species that occupy and defend rocks that are > 65cm and holes, or crevices that are > 10cm in diameter, *e.g.*, the introduced species, *P. tropheops* 'red cheek' and the native species, *P. tropheops* 'orange chest' (hereafter referred to as the large rock guild).

Feeding and feeding site preference

(i) *The small rock guild*

The Mbuna that prefer small rocks feed both on the rock substratum and in the water column. However, there were some differences in the intensity with which each species utilized the two sites. *Cynotilapia afra*, for instance, almost exclusively fed in the water column, except during the transition season (September-October), when it browsed on the epilithic algae, spending on average, about 0.01 ± 0.005 minute of the 5 minutes observation period. *Pseudotropheus callainos* and *P. zebra*, on the other hand frequently fed on Aufwuchs on the rock substratum and on phytoplankton in the water column (Fig. 3.7).

These Mbuna swim and hover above their territories, while feeding in the water column, and during such feeding bouts, there is a high degree of interspecific overlap. Conspecific males are, however, antagonistic towards each other when they overlap during feeding.

During the upwelling season, particularly, in May and June, territorial males of the small rock guild, *i.e.*, the introduced species, *C. afra*, *P. callainos* and native species, *P. zebra* often feed far from their territories and are out of sight several times a day. This behaviour was particularly common when the lake was rough and the phytoplankton bloom was evident in the water column. During such out of sight feeding forays, other fishes, notably juveniles, females and non-territorial males of different species fed in the vacated substratum territories. Consequently, there is a positive relationship between the height at which the territorial *C. afra* ($r = 0.95$; $t = 7.59$; $P < 0.05$), *P. callainos* ($r = 0.81$; $t = 3.43$; $P < 0.05$) and *P. zebra* ($r = 0.89$; $t = 4.66$; $P < 0.05$) fed and the number of other fish that fed in the temporarily vacated territories (Fig. 3.8). Similarly, among the species of the small

rock guild, there was no apparent interference between the introduced and native species that overlap in their microhabitat requirements when they were feeding in the water column. For instance, the introduced species *C. afra* and native species, *P. zebra* which overlap in the rocks (Table 3.1) and holes (Table 3.2) they occupy, fed on the phytoplankton in the water column with different frequencies (X^2 = 16.16, $P < 0.05$; Fig. 3.7a), and they fed at different heights in the water column ($X^2 = 20.52$, $P < 0.01$; Fig. 3.7b). *Pseudotropheus callainos* and *P. zebra*, besides feeding on the phytoplankton in the water column in a similar manner (Fig. 3.7c), also feed on the rock substratum. Both brush the Aufwuchs from the rocks within their preferred microhabitats. To find out if there was a preference for specific sites on the rock substratum where these Mbuna grazed, the relative frequency with which they fed on different sites of the rock, *e.g.*, rock top or rock sides were noted, quantified and compared. Results in Table 3.4 show that both *P. callainos* and *P. zebra* preferentially brush the Aufwuch from the rock sides. But, they do so with different frequencies ($X^2 = 52.86$, $P < 0.01$; Fig. 3.7d).

Table 3.4. Comparison of feeding frequency, expressed as proportion of the total feeding bouts that the introduced species, *Pseudotropheus callainos*, *Pseudotropheus tropheops* 'red cheek' and a native species, *Pseudotropheus zebra* and *Pseudotroheus tropheops* 'orange chest' fed on algae growing on the rock sides and rock top.

		Feeding site	
Species	***N***	**Rock top**	**Rock side**
P. callainos	45	0.36	0.64
P. zebra	73	0.25	0.75
P. tropheops 'rc'	52	0.19	0.81
P. tropheops 'oc'	64	0.30	0.71

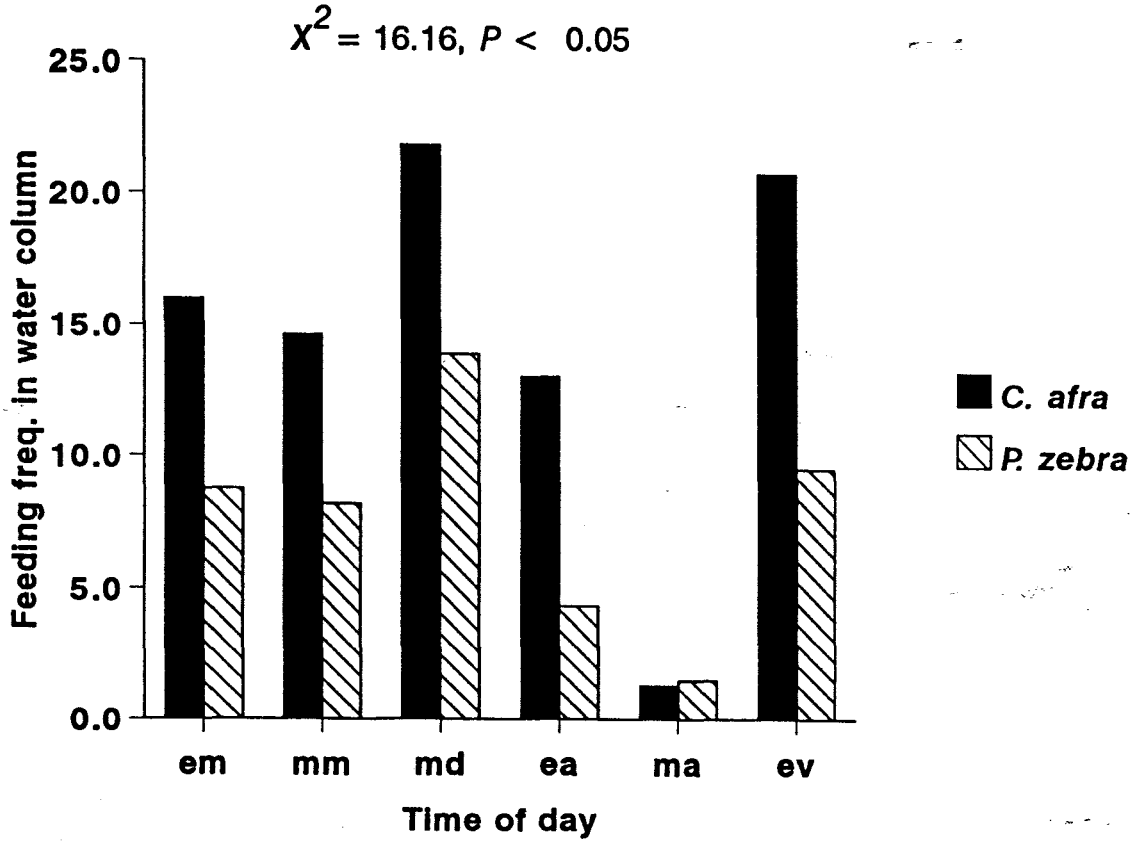


Fig. 3.7a. The feeding frequency on the phytoplankton in the water column by *C. afra* and *P. zebra*.

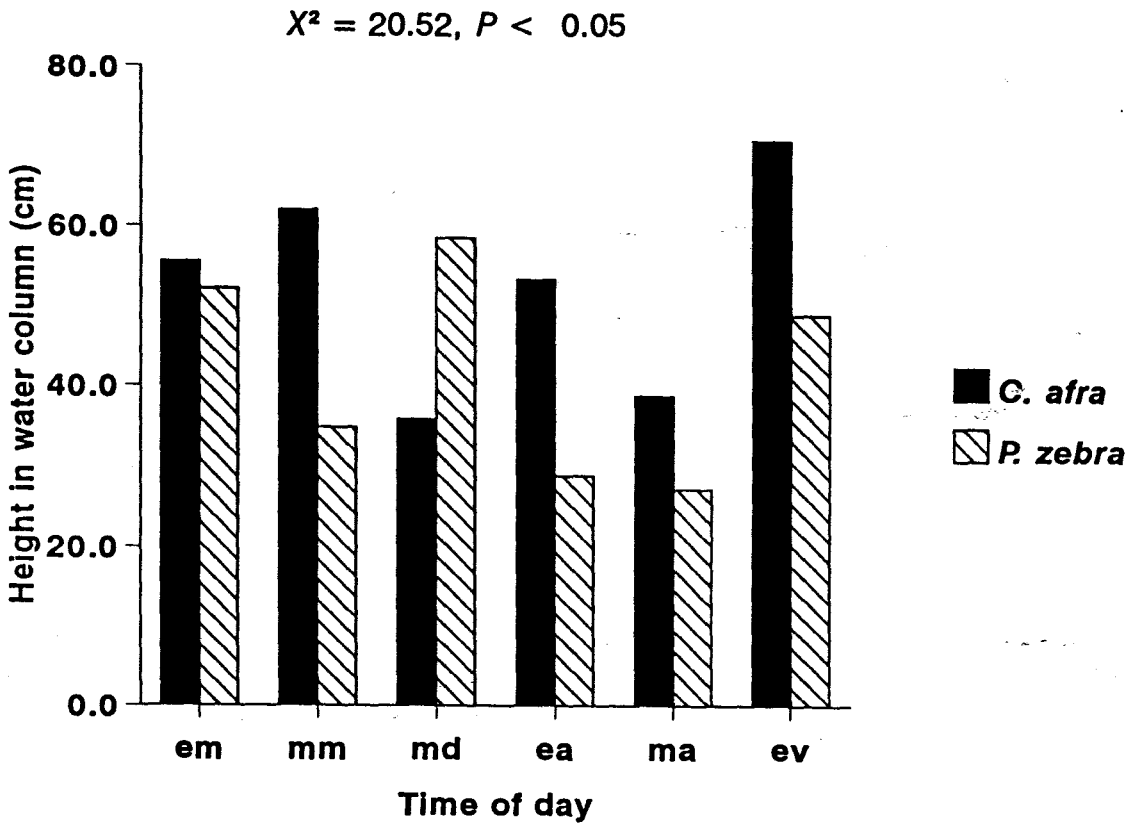


Fig. 3.7b. The height at which the introduced species, *C. afra* and native species, *P. zebra* ascended while feeding on the phytoplankton in the water column.

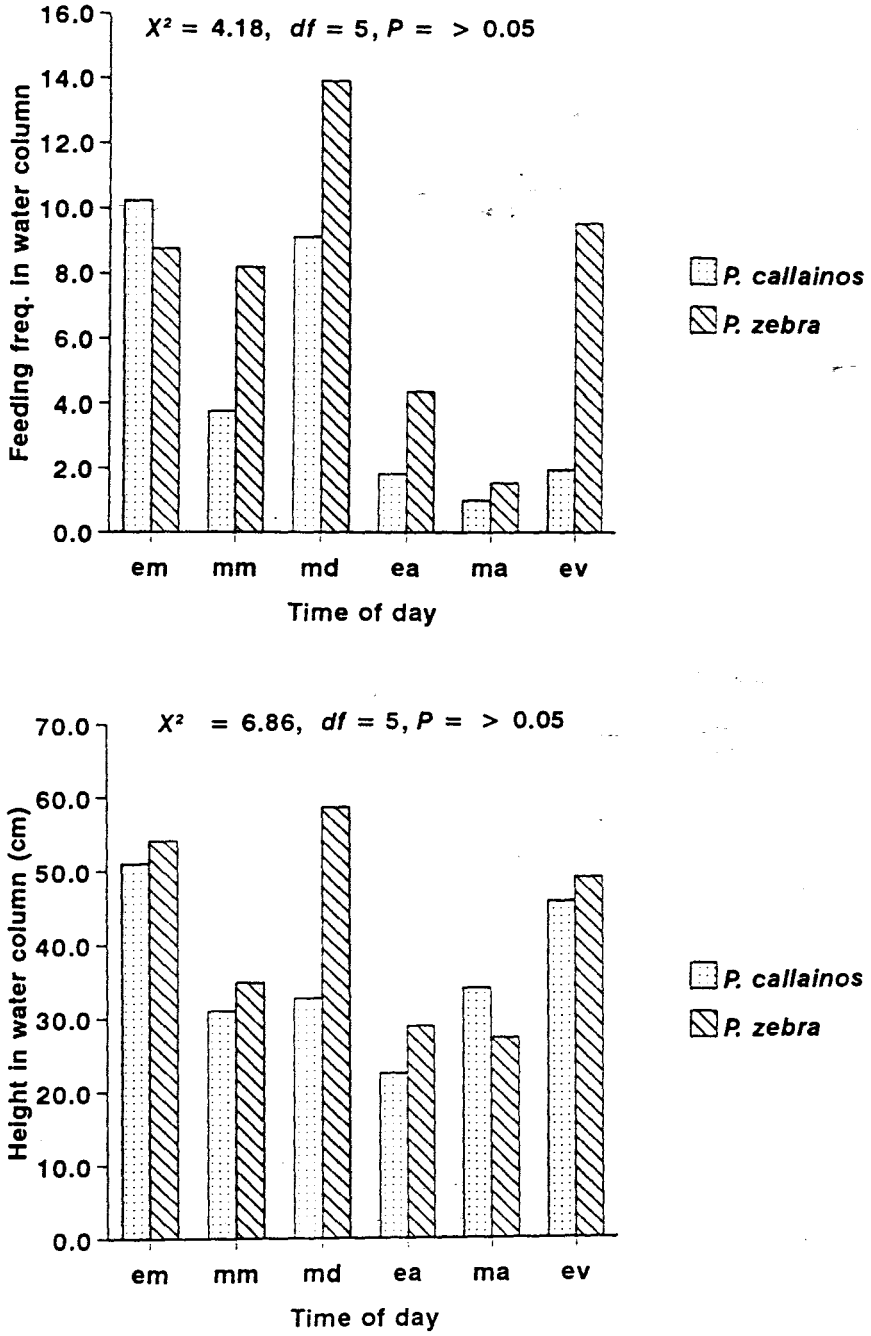


Fig. 3.7c. The feeding frequency on the phytoplankton in the water column and and height ascended in the water column by the introduced species, *P. callainos* and its native sibling species, *P. zebra*.

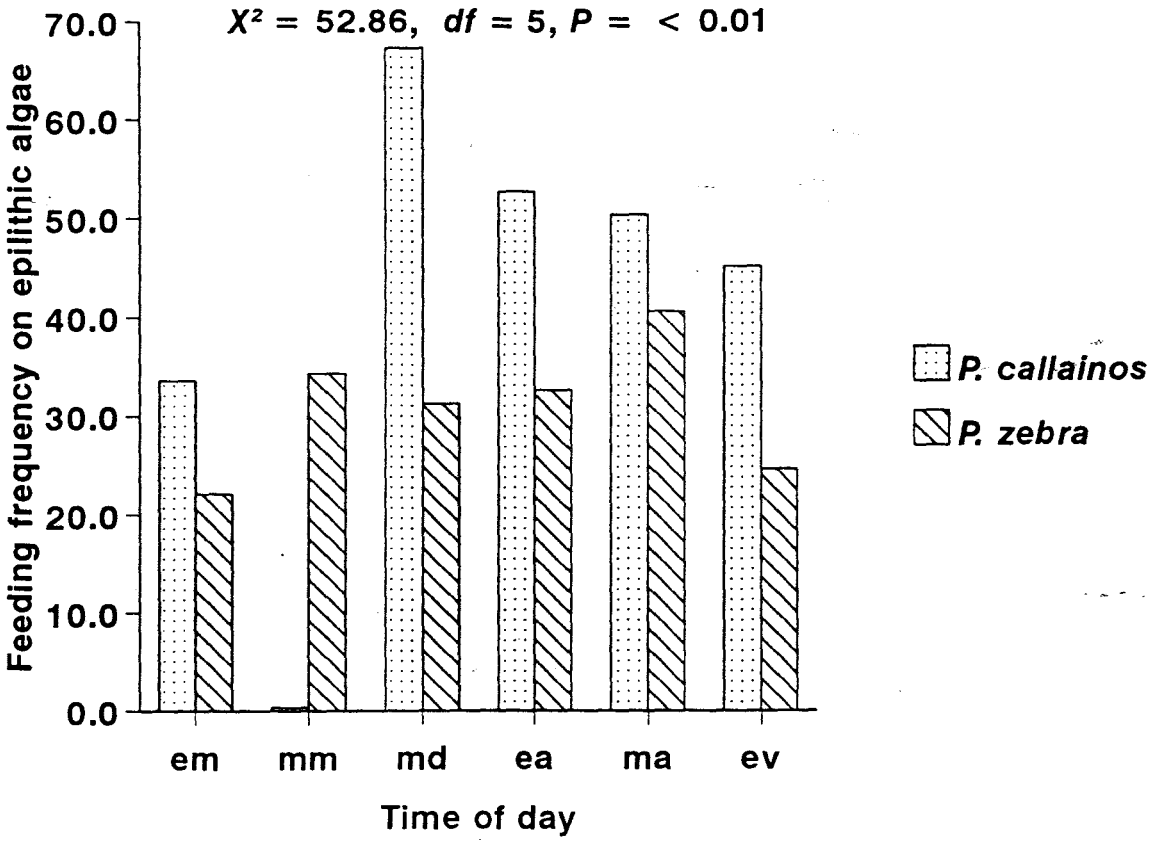


Fig. 3.7d. The feeding frequency on epilithic algae by the introduced species, *P. callainos* and its sibling native species, *P. zebra*.

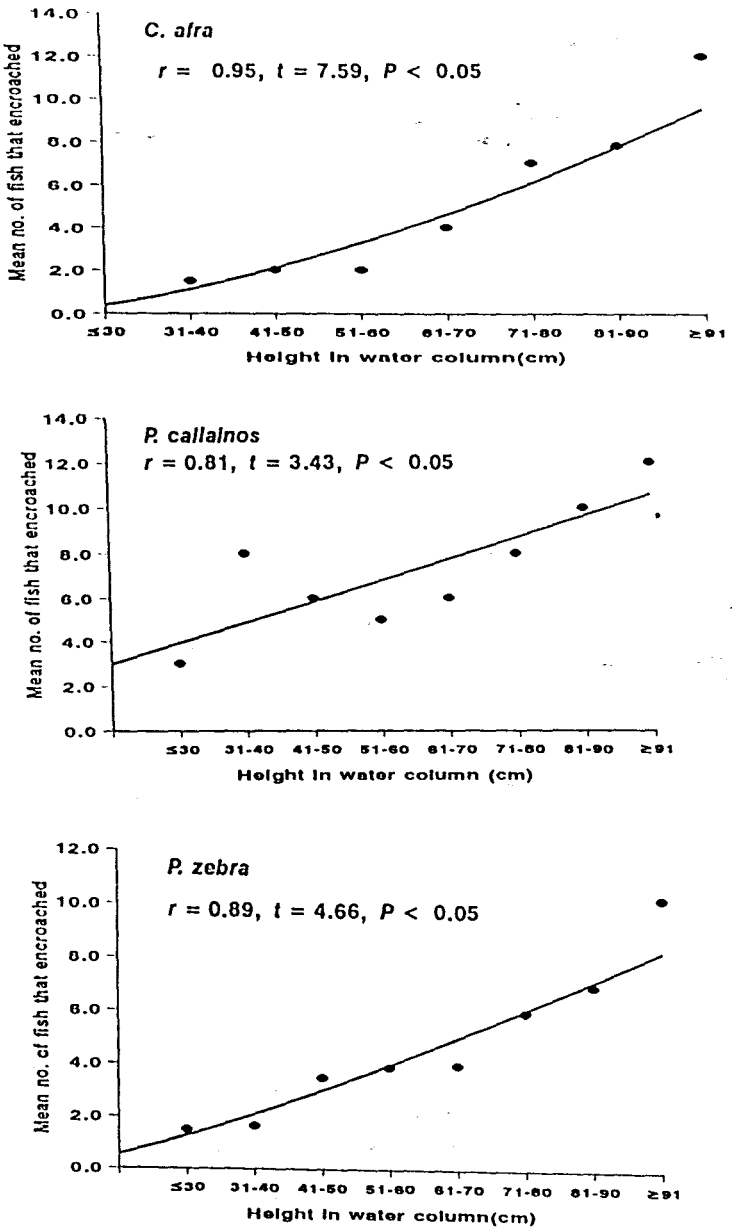


Fig. 3.8. The relationship between the height ascended in the water column by the territorial male Mbuna of the small rock guild and the number of fish that encroached in the temporarily vacated territories.

(ii) *The large rock guild*

The Mbuna of this guild, *i.e.*, the introduced species, *P. tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest' preferentially feed on the large rocks, and in many instances, individuals defend and feed on more than one rock within their territories. Both browse selectively on epilithic algae. They also preferentially browse on the algae growing on the rock sides (Table 3.4), and they do not exhibit significant variation in the frequencies with which they feed on the epilithic algae ($X^2 = 6.08$, $P > 0.05$; Fig. 3.9a). They spend almost identical time feeding on the rock substratum ($X^2 = 9.62$; $P = 0.05$; Fig. 3.9). Only, *P. tropheops* 'red cheek' fed on the phytoplankton in the water column during the transition (September - October) and upwelling seasons (May - August), spending on average about 0.60 $\pm$ 0.49 and 0.15 $\pm$ 0.13 minute, respectively of the five minutes observation period. Otherwise, during much of the year, both *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' feed exclusively on epilithic algae, but briefly venture into the water column to patrol their expansive territories. Both ascend into the water column to almost the same heights ($X^2 = 5.48$, $P > 0.05$; Fig. 3.9c). Therefore, in terms of feeding, conflicts between *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' are apparent because they feed in similar manner and both prefer algae growing on the rock sides. However, direct conflicts between them seem to be ameliorated by defending territories far apart from each other (mean $\pm$ *Sd* = 92.67 $\pm$ 4.62 cm).

Both *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' staunchly defend the food resources within their territories, and since both hardly leave their territories for a long time, encroachments by other fishes into their territories are rare. The only exception was the sharing of territories between territorial males of the introduced species, *P. tropheops* 'red cheek' and females of the native rock-dwelling cichlid, *Protomelas taeniolatus*. Both selectively browse on the epilithic algae. Their

feeding association index (*sensu*, Martin & Bateson 1993) (Fig. 3.10) was however, lower in August, when *P. tropheops* 'red cheek' was at its peak breeding season (see chapter 2), but it was relatively higher during the rest of the year, with a peak of 0.60 in November. This was also the month when most females of *P. taeniolatus* were seen guarding their fry. However, only 8% of the fifty-one *P. taeniolatus* observed guarded their fry within the territories of *P. tropheops* 'red cheek'. Guarding of fry in *P. tropheops* 'red cheeks's territories certainly consolidates the defence of territorial resources, while at the same time the fry of *P. taeniolatus* are protected from both specialised and opportunistic predators as a result of joint territorial defence by the two species.

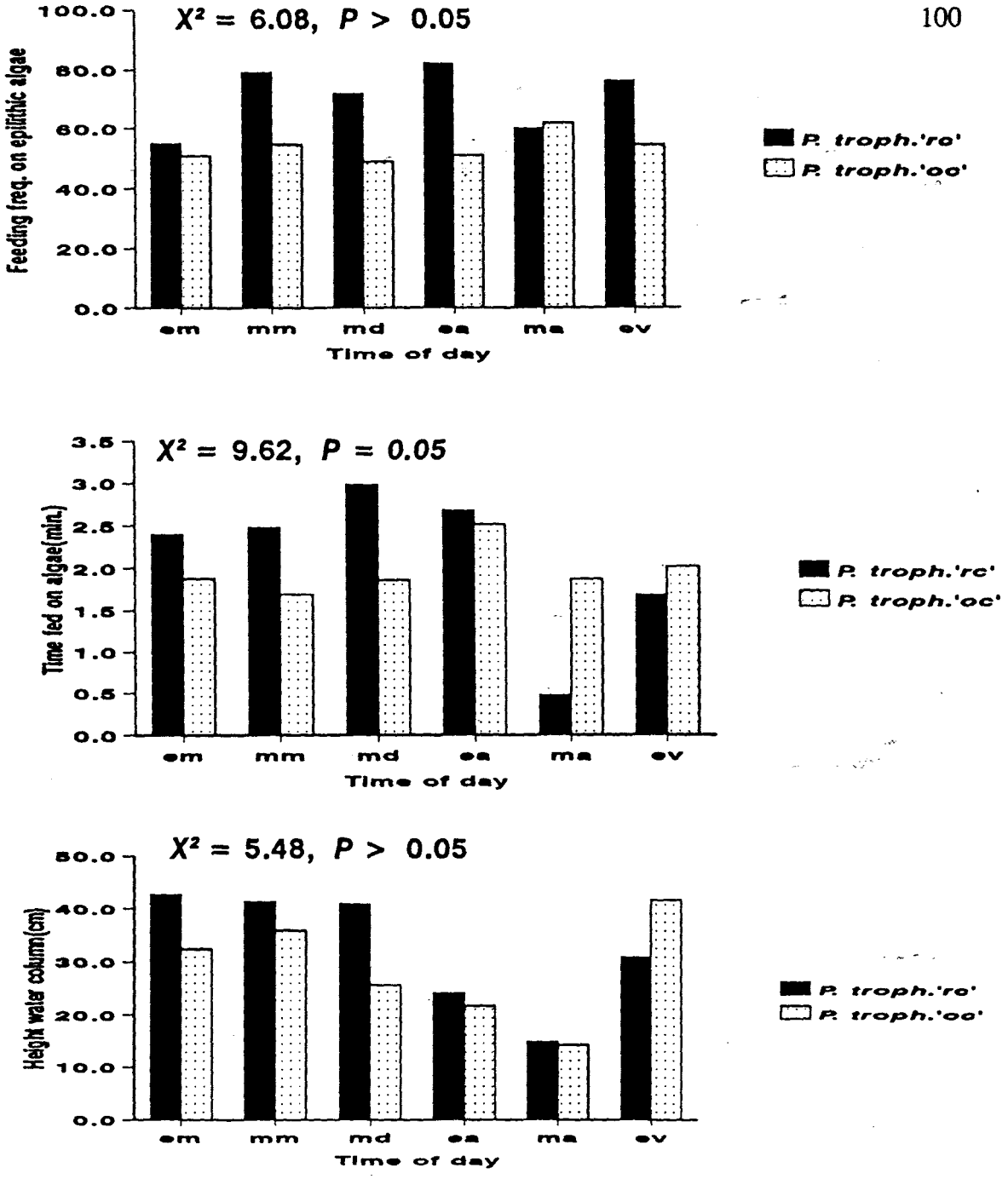


Fig. 3.9. The feeding frequency, time spent feeding on epilithic algae and height ascended in the water column by the Mbuna of the large rock guild, *i.e.*, *Pseudotropheus tropheops* 'red cheek' and *P. tropheops* 'orange chest', during the 5 minutes observation time.

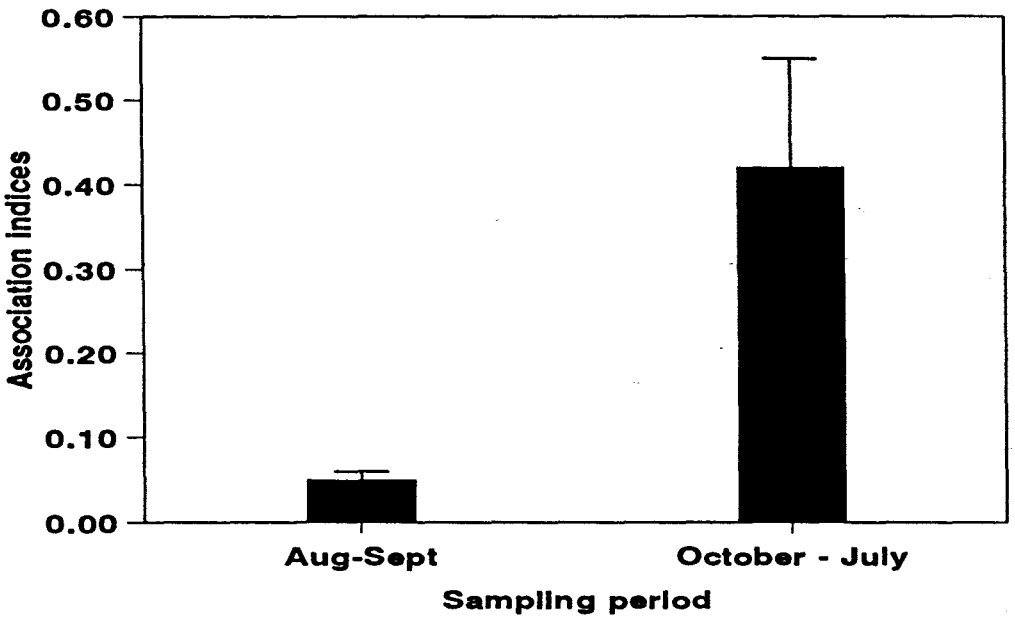


Fig. 3.10. The feeding association indices between the territorial males of the introduced species, *Pseudotropheus tropheops* 'red cheek' and females of the native rock-dwelling cichlid species, *Protomelas taeniolatus*. Association indices were calculated using Martin & Bateson's (1993) formula: $IA = N_{rt} /(N_r + N_t + N_{rt})$, where *IA* is the Index of association, N_{rt} is the number of occasions *P. tropheops* 'red cheek' and *P. taeniolatus* were seen together, N_r is the number of occasions *P. tropheops* 'red cheek' was seen alone and N_t is the number of occasions *P. taeniolatus* was seen alone.

To find out if sharing of the same territories by males of *P. tropheops* 'red cheek' and females of *P. taeniolatus* was facilitated by their selecting different food items, the stomach contents of fifteen individuals of *P. tropheops* 'red cheek' and *P. taeniolatus* (see Table 3.5) were examined during the months of April, May, August and November. The volume of each food item, expressed as percentage of the total volume of food in the stomach (*e.g.*, Reinthal 1987; 1990), and the overlap index were calculated using Schoener's Index formula (Linton *et al.* 1981; Reinthal 1987). Results in Table 3.5, show that the volume of food items taken by *P. tropheops* 'red cheek' and *P. taeniolatus* differs significantly between them ($X^2 = 182.95$; $P < 0,05$). The diet overlap between these species is only 0.28, suggesting that their association may also be partly facilitated by their selecting different food items, or they may coincidentally be having similar rock preferences.

Table 3.5. Comparison of the percent volume of the algal food items found in the stomach of an introduced species, *Pseudotropheus tropheops* 'red cheek' and a native species, *Protomelas taeniolatus* that often fed in the same territories. A total of fifteen *P. tropheops* 'red cheek' and fifteen *P. taeniolata* were sampled. The algae were identified only to the genus level (*e.g.*, Reinthal 1987).

	% Volume found in the stomachs of	
Algal food item	*P. troph.* 'rc'	*P. taeniolatus*
Calathrix	0.00	7.44
Cladophora	47.11	10.55
Cymbella	7.18	17.67
Lyngbya	42.22	12.78
Mougeolia	0.00	7.44
Nitzschia	0.00	1.00
Navicula	4.50	3.78
Oscillatoria	55.00	0.00
Rhapalodia	5.67	24.58
Stephanodiscus	0.00	2.33
Dietary breadth[1]	1.40	7.89

[1] $D_b = 1/\Sigma p_i^2$, where D_b is the dietary breadth and P_i is the percent volume of food item i to a species (*c.f.*, Levin 1968; Reinthal 1987).

Mating success

(a) *The small rock guild*

Territorial males of this guild often hover in the water column, where besides feeding, they attract females by courting them. Usually the passing-by of a gravid female ignites intensive courtship competition among the sympatric conspecific males. Each male zig-zags towards a female, displaying at her, sometimes outside the male's territory. These courtship displays are punctuated by frequent hole entering by the males (Fig. 3.11). Hole entering is like an advertisement to the females for the hole, or spawning site quality each male defends against intruders and, indeed females were seen inspecting the spawning sites, or holes before they spawned with the tenant males.

The female's response to the courting male was to either flee immediately after being approached by the courting male, or to follow the male to its spawning site and enter a hole among rocks where spawning took place (Fig. 3.4). Often such pairs were out of sight, hence it could only be assumed that spawning had taken place under the rocks. Sometimes a female simply nosed at the spawning hole, and subsequently fled. In such circumstances, the male wrathfully chased the female, but if she re-adopted a courtship attitude, the male sometimes started to court her again. There were also instances when a courtship sequence ended abruptly because the female entered a male's hole 'under its own will'. In such cases, females themselves seem to have searched for optimal spawning sites, and males holding such territories benefited by mating without investing much effort in courtship display. Overall, positive responses by females towards the courting males represented about 16.94% of the total 923 courtship attempts observed in all the species studied during the entire study period.

Among the small rock guild, *C. afra* was the only species that had a higher mating success in its preferred microhabitat (Table 3.6), *P. callainos* mated more successfully in the microhabitat with large rocks, while the native species, *P. zebra* which overlaps with *C. afra* in the microhabitat requirements mated with almost equal magnitude in microhabitats predominated by small and large rocks. However, in either microhabitat, individual males of *C. afra*, *P. callainos* and *P. zebra* that spawned were those defending significantly smaller holes (Table 3.7).

To find out if the mating success was influenced by the number of females available at the study sites, the population of females was assessed during the peak breeding season (March-April) and (August-September), and the sex ratio of each species, *i.e.*, number of females per male was calculated for each microhabitat type. Results in Table 3.8 show that the number of females may not have been the only key factor influencing the mating success because *C. afra*, *P. callainos*, *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' performed better at sites where the sex ratio was lower (Table 3.8). Similarly, to find out if territory size had any influence in the mating success of these Mbuna species, territories held by individuals that successfully spawned were compared with those that did not spawn. Results shown in Table 3.9 indicate no significant difference between the territory sizes held by spawners and non-spawners. This suggests that territory size *per se* may not have influenced the mating success of these Mbuna species. Many factors, *e.g.*, number of females, time of year, activities of males, territory size, spawning hole size, *etc*, may interact in influencing the mating success of these Mbuna species. However, it appears the size of spawning hole defended by territorial males has significant implications on their mating success (Table 3.6).

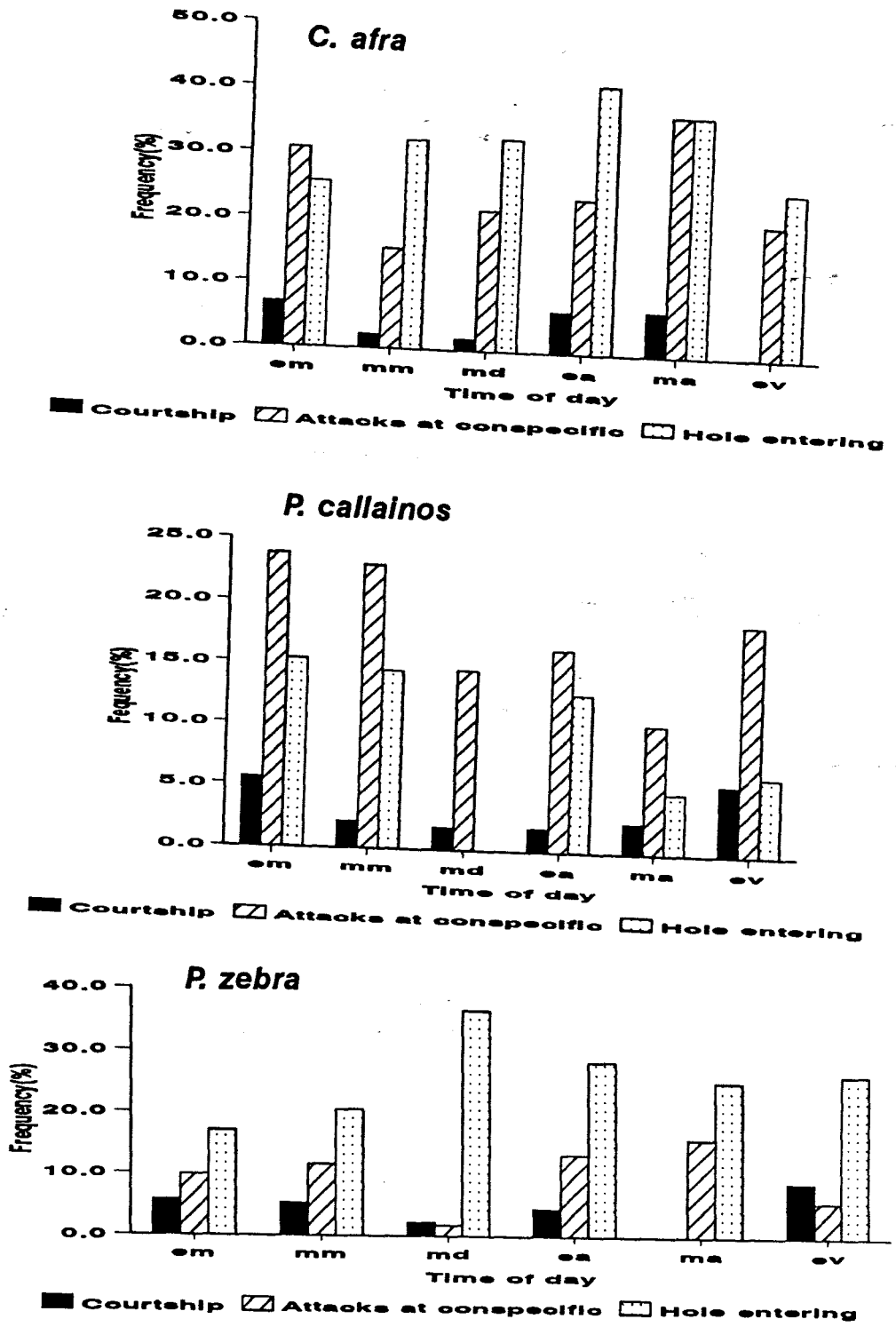


Fig. 3.11. The frequency in courtship displays, attacks at conspecific intruders and hole entering by the males of territorial Mbuna of the small rock guild, *i.e.*, the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and the native species, *P. zebra*. em = early morning, mm = mid morning, md = mid day, ea = early afternoon, ma = mid afternoon and ev = evening (see methods).

Table 3.6. Comparison of the number of courtship displays by the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' and native species, *Pseudotropheus zebra* and *Pesudotropheus tropheops* 'orange chest' that culminated into spawning (mating success) between two microhabitats; the small and large rocks predominated areas during 30 months.

	Microhabitat type	
	Small rocks	Large rocks
Introduced species		
C. afra's number m^{-2}	24.30	12.90
No. of courtship displays by *C. afra*	240.00	42.00
% Mating success	13.75	4.76
P. callainos's number m^{-2}	26.80	10.60
No. of courtship displays by *P. callainos*	86.00	144.00
% Mating success	13.95	20.00
P. tropheops 'red cheek's' number m^{-2}	5.50	2.90
No. of courtship displays by *P. tropheops* 'red cheek'	105.00	79.00
% Mating success	15.39	26.58
Native species		
P. zebra's number m^{-2}	28.30	39.00
No. of courtship displays by *P. zebra*	87.00	36.00
% Mating succes	11.50	13.89
P. tropheops 'orange chest's' number m^{-2}	10.80	14.29
No. of courtship displays by *P. tropheops* 'orange chest'	47.00	57.00
% Mating success	27.66	38.60

Table 3.7. Comparison of hole size, in cm diameter occupied by territorial males of *Cynotilapia afra*, *Pseudotropheus callainos*, *Pseudotropheus zebra*, *Pseudotropheus tropheops* 'red cheek' and *Pseudotropheus tropheops* 'orange chest' that spawned and those that did not spawn. The significant difference in the hole sizes was evaluated by the Mann-Whitney *U*-test.

Species	*N*	Spawners	*N*	Non-spawners	*U* value	*P* value
C. afra	24	7.8	72	12.8	21.0	< 0.05
P. callainos	19	9.4	40	22.7	15.0	< 0.05
P. zebra	22	8.6	72	13.4	102.5	< 0.05
P. troph.'rc'	10	13.5	28	20.5	40.0	< 0.05
P. troph.'oc'	19	14.1	69	22.7	103.0	< 0.05

Table 3.8. Comparison of sex ratio, *i.e*, number of females per male of *Cynotilapia afra*, *Pseudotropheus zebra*, *Pseudotropheus callainos*, *Pseudotropheus tropheops* 'red cheek' and *Pseudotropheus tropheops* 'orange chest' at study sites predominated by small and large rocks.

	Microhabitat type	
Species	**Small rocks**	**Large rocks**
C. afra	0.77	0.81
P. zebra	0.62	0.60
P. callainos	0.89	0.44
P. tropheops 'rc'	1.07	0.59
P. tropheops 'oc'	1.36	1.00

Table 3.9. Comparison of territory sizes, in centimetre diameter held by individuals of *Cynotilapia afra*, *Pseudotropheus callainos*, *Pseudotropheus zebra*, *Pseudotropheus tropheops* 'red cheek' and *Pseudotropheus tropheops* 'orange chest' that spawned and those that did not spawn.

Species	*N*	Spawners	*N*	Non-spawners	*U* value	*P* value
C. afra	24	47.7	72	43.8	54.5	> 0.05
P. zebra	22	50.5	72	41.8	46.0	> 0.05
P. callainos	19	65.0	40	64.3	47.5	> 0.05
P. troph. 'rc'	10	93.5	28	91.1	41.5	> 0.05
P. troph. 'oc'	19	91.3	69	92.7	57.0	> 0.05

(b) *The large rock guild*

Unlike the Mbuna that prefer small rocks, which usually courted conspecific females when they swam past the male's territories, females of *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' establish permanent home ranges around conspecific males. Home range as used here, denotes an area traversed by an individual in its normal activities of foraging and mating (Burt 1943). Each female of the large rock guild during its foraging activities overlaps with more than one male of its species. However, males tolerated the presence of conspecific females within their territories only when the females were gravid and ready to spawn. The males seemed capable of detecting gravid females, which they courted from their home ranges, and in a positive response, the female was lead to the male's territory where spawning took place, usually in a crevice among the rocks (Fig. 3.4b). In most negative responses, females followed the courting males to their territories, but instead of spawning with the male, they fed on the often abundant algal resources that grew in the male's territory. Under such circumstances, females were promptly chased by the territorial males.

Both *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' spawned more successfully in their preferred microhabitat, *i.e*, areas predominated by large rocks (Table 3.6). However, just like the Mbuna that prefer small rocks, individual males that spawned successfully were those that defended significantly smaller crevices (Table 3.7).

Territory sizes

(a) *The small rock guild*

The Mbuna that prefer small rocks defend both substratum and water column territories which are three dimensional (Fig. 3.5). The water column territories are

primarily used for feeding and courting females that pass through, while the substratum territories are used for mating and as feeding ground, particularly by the introduced species, *P. callainos* and its sibling native species, *P. zebra*.

The water column territories held by *C. afra* and *P. zebra* were significantly larger than their substratum territories (Table 3.10). *P. callainos* on the other hand, held water column and substratum territories that did not differ significantly in size ($t = 1.63$, $P > 0.05$; Table 3.10).

Territories held by *P. zebra* and *P. callainos* significantly fluctuated seasonally (Table 3.11), but these fluctuations did not differ significantly between them (Fig. 3.12). Consequently, their coexistence in the same microhabitats can not be attributed to seasonal fluctuations in their territory sizes.

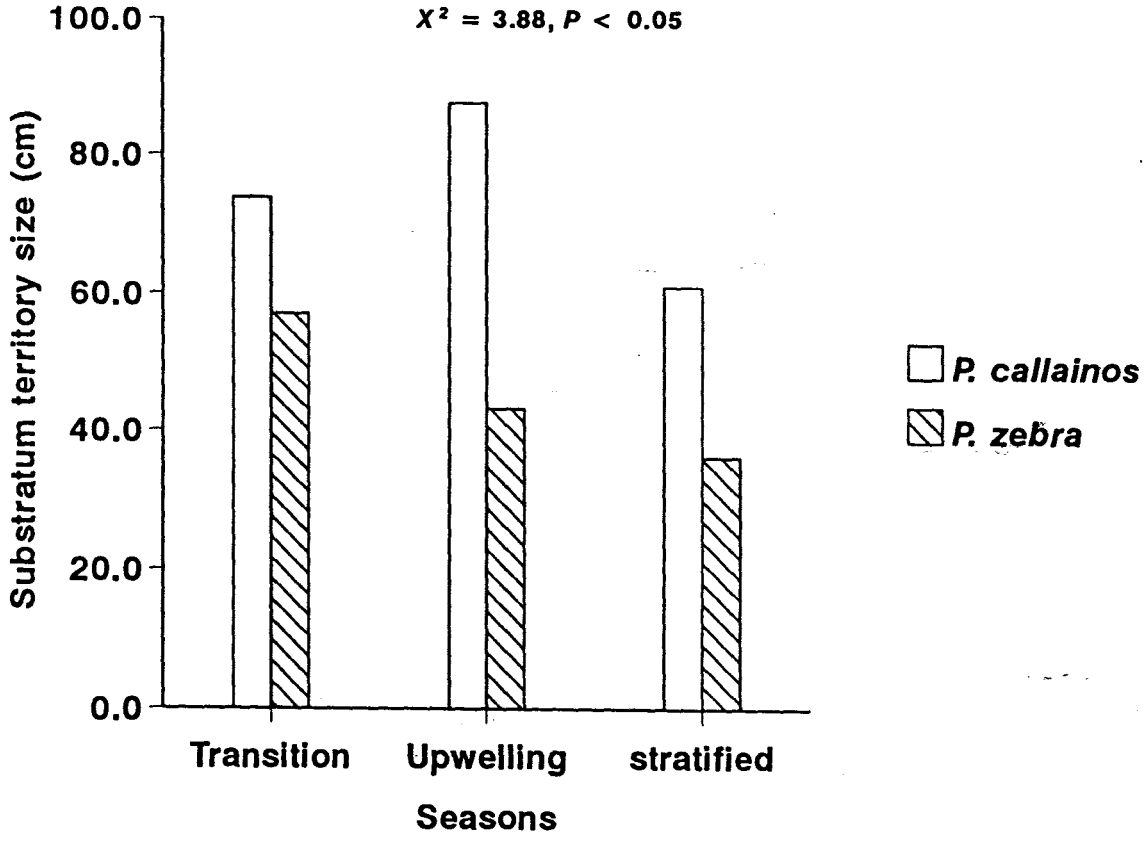


Fig. 3.12. Territories, in centimetre diameter seasonally defended by the introduced species, *Pseudotropheus callainos* and its sibling native species, *Pseudotropheus zebra*. The seasons are transition (September - October), upwelling (May - August) and stratified (November - April).

Table 3.10. Comparison of territory sizes, in centimetre diameter, presented as mean ± standard deviation defended on the substratum and in the water column by *Cynotilapia afra*, *Pseudotropheus zebra* and *Pseudotropheus callainos*.

Species	*N*	Substratum	*N*	Water column	*t* value	*P* value
C. afra	72	43.6 ± 2.75	72	49.9 ± 3.28	2.23	< 0.05
P. zebra	72	41.3 ± 3.07	72	48.2 ± 3.65	2.11	< 0.05
P. callainos	40	67.8 ± 6.45	40	75.6 ± 6.42	1.63	> 0.05

Spatially, *C. afra* and *P. zebra* in relation to their conspecific territorial males were uniformly distributed, both in areas predominated by small and large rocks (Table 3.12). The distance between the centre of territories held by *C. afra* and *P. zebra* was small (mean ± *Sd* = 59.94 ± 21.10cm, n = 62), and although in most cases they occurred as sympatric neighbours, their territories did not overlap. *Pseudotropheus callainos* was uniformly distributed in the microhabitats predominated by small rocks, but was randomly distributed at sites with predominantly large rocks (Table 3.12). The distance between territories held by *P. callainos* and its congeneric native species, *P. zebra* was also small (mean ± *Sd* = 45.73 ± 14.62 cm, n = 46), and often these species had overlapping territories. Intraspecifically, none of the Mbuna of the small rock guild had overlapping territories.

***Cynotilapia afra* and *P. callainos* at Thumbi West Island held territories that were significantly smaller in size than the territories defended by the same species at sites of their origin, in the northern part of Lake Malawi (Table 3.13).**

Table 3.11. Comparison of territories, in centimetre diameter defended during the upwelling (May - August), transition (September - October) and stratified (November - April) seasons by *Cynotilapia afra*, *Pseudotropeus zebra*, *Pseudotropheus callainos*, *Pseudotropheus trophops* 'red cheek' and *Pseudotropheus tropheops* 'orange chest' at Thumbi West Island. Kruskall-Wallis (K) test was used in analysing significant differences in the territory sizes.

	Seasons							
Species	*N*	Upwell	*N*	Trans	*N*	Strat	*K*	*P* value
(a) Substratum								
C. afra	72	45.8	40	52.0	72	40.2	5.2	> 0.05
P. zebra	72	43.2	40	57.0	72	36.2	12.6	< 0.05
P. callainos	72	87.6	40	73.8	72	60.9	10.5	< 0.05
P. troph. 'rc'	28	91.3	28	99.6	28	91.3	1.5	> 0.05
P. troph. 'oc'	69	93.7	40	100.8	69	87.3	3.1	> 0.05
(b) Water column								
C. afra	72	56.2	40	46.0	72	54.0	3.6	> 0.05
P. zebra	72	56.9	40	59.2	72	44.0	4.6	> 0.05
P. callainos	72	89.2	40	76.0	72	66.3	8.4	< 0.05
P. troph. 'rc'	-	-	-	-	-	-	-	-
P. troph. 'oc'	-	-	-	-	-	-	-	-

Table 3.12. Coefficients of dispersion (Green's indices) of the territorial *Cynotilapia afra*, *Pseudotropheus zebra*, *Pseudotropheus callainos*, *Pseudotropheus tropheops* 'red cheek' and *Pseudotropheus tropheops* 'orange chest' at sites dominated by small and large rocks.

Species	Small rocks	Large rocks
C. afra	- 8.0	- 2.0
P. zebra	- 12.0	- 0.4
P. callainos	- 37.0	0.0
P. tropheops 'rc'	0.0	0.0
P. tropheops 'oc'	- 21.0	0.0

Note: negative value indicates uniform distribution, and zero a random distribution (see Krebs 1989).

Table 3.13. Comparison of territory sizes, in centimetre diameter held by the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' at their site of origin, in the northern Lake Malawi and at Thumbi West Island where they have been introduced. Significant differences were evaluated by Mann-Whitney *U*-test.

	Seasons							
Species	***N***	**Upwell**	***N***	**Trans**	***N***	**Strat**	***K***	***P*** **value**
(a) Substratum								
C. afra	72	45.8	40	52.0	72	40.2	5.2	> 0.05
P. zebra	72	43.2	40	57.0	72	36.2	12.6	< 0.05
P. callainos	72	87.6	40	73.8	72	60.9	10.5	< 0.05
P. troph.'rc'	28	91.3	28	99.6	28	91.3	1.5	> 0.05
P. troph.'oc'	69	93.7	40	100.8	69	87.3	3.1	> 0.05
(b) Water column								
C. afra	72	56.2	40	46.0	72	54.0	3.6	> 0.05
P. zebra	72	56.9	40	59.2	72	44.0	4.6	> 0.05
P. callainos	72	89.2	40	76.0	72	66.3	8.4	< 0.05
P. troph.'rc'	-	-	-	-	-	-	-	-
P. troph.'oc'	-	-	-	-	-	-	-	-

Females of the Mbuna that prefer small rocks did not establish permanent territories. When they were observed at ten minute periods, *C. afra* females were found to forage over a mean ± *Sd* distance of 486.70 ± 128.85cm (n = 30), *P. zebra* females foraged over a mean ± *Sd* distance of 800.00 ± 141.84 cm (n = 30), while *P. callainos* females fed over a mean ± *Sd* distance of 902.50 ± 88.42 cm (n = 30). Tagging of females to find out if they used specific home ranges (*i.e.*, area traversed by an individual in its normal activities of foraging and mating (Burt 1943)) was also done in May 1993 and February 1994. During both occasions, the tagged fish disappeared without trace within a week, hence nothing of value was inferred from the tagging experiment. Mouth-brooding females were however sedentary, often seen on rock slabs churning their eggs, but when disturbed they sought shelter in holes among the rocks.

(b) ***The large rock guild***

Pseudotropheus tropheops 'red cheek' and its sibling native species, *P. tropheops 'orange* chest' hold substratum territories only, which are extensive (Table 3.11), and do not significantly fluctuate seasonally in size (Table 3.11). Territories held by *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' were far apart (mean ± *Sd* = 92.67 ± 4.62cm, n = 30) and did not overlap. Spatially, *P. tropheops* 'red cheek' was randomly distributed both in microhabitats predominated by small and large rocks, while *P. tropheops* 'orange chest' was randomly distributed at sites with predominantly small rocks and it was uniformly distributed at sites with predominantly large rocks (Table 3.12). The distribution of Mbuna of the large rock guild seems to be primarily influenced by the availability of large rocks, on which they feed, and on the crevices among these rocks in which spawning takes place (Table 3.7). Intraspecifically, territories held by the Mbuna of the large rock guild do not overlap.

Females of *P. tropheops* 'red cheek' had home ranges that measured about 150 ± 24.83cm in diameter (n = 26), while females of *P. tropheops* 'orange chest' had home ranges of about 186 ± 27.80cm in diameter (n = 26). Their home ranges overlapped, and also during their daily foraging activities, they overlapped with many sympatric heterospecific territorial males and non-territorial males and females, including juveniles of various species.

Males of *P. tropheops* 'red cheek' also held smaller territories at Thumbi West Island than at their site of origin, Likoma Island in the northern part of Lake Malawi (Table 3.13).

Aggression

(a) *The small rock guild*

Intraspecifically, the degree of aggression in these Mbuna species varied diurnally (Fig. 3.11). For instance, *C. afra* was aggressive throughout the morning hours until about mid afternoon, *P. callainos* was more aggressive during early morning, mid morning and evening, while *P. zebra* was most aggressive during early morning and evening. These were also the times when these Mbuna actively engaged in courtship behaviour (Fig. 3.11). The frequency of hole entering was also high during active courtship (Fig. 3.11), probably as means of advertising to conspecific females the quality of spawning hole each male defended, preventing sneak fertilization by conspecific non-territorial males, and preventing egg predation during spawning. Also, the Mbuna that prefer small rocks exhibited elevated aggression towards conspecific intruders during the months preceding their breeding peak, and or the months when they were at a breeding peak (Fig. 3.13a & b). The breeding peaks of these Mbuna species have been shown in chapter 2 of this thesis.

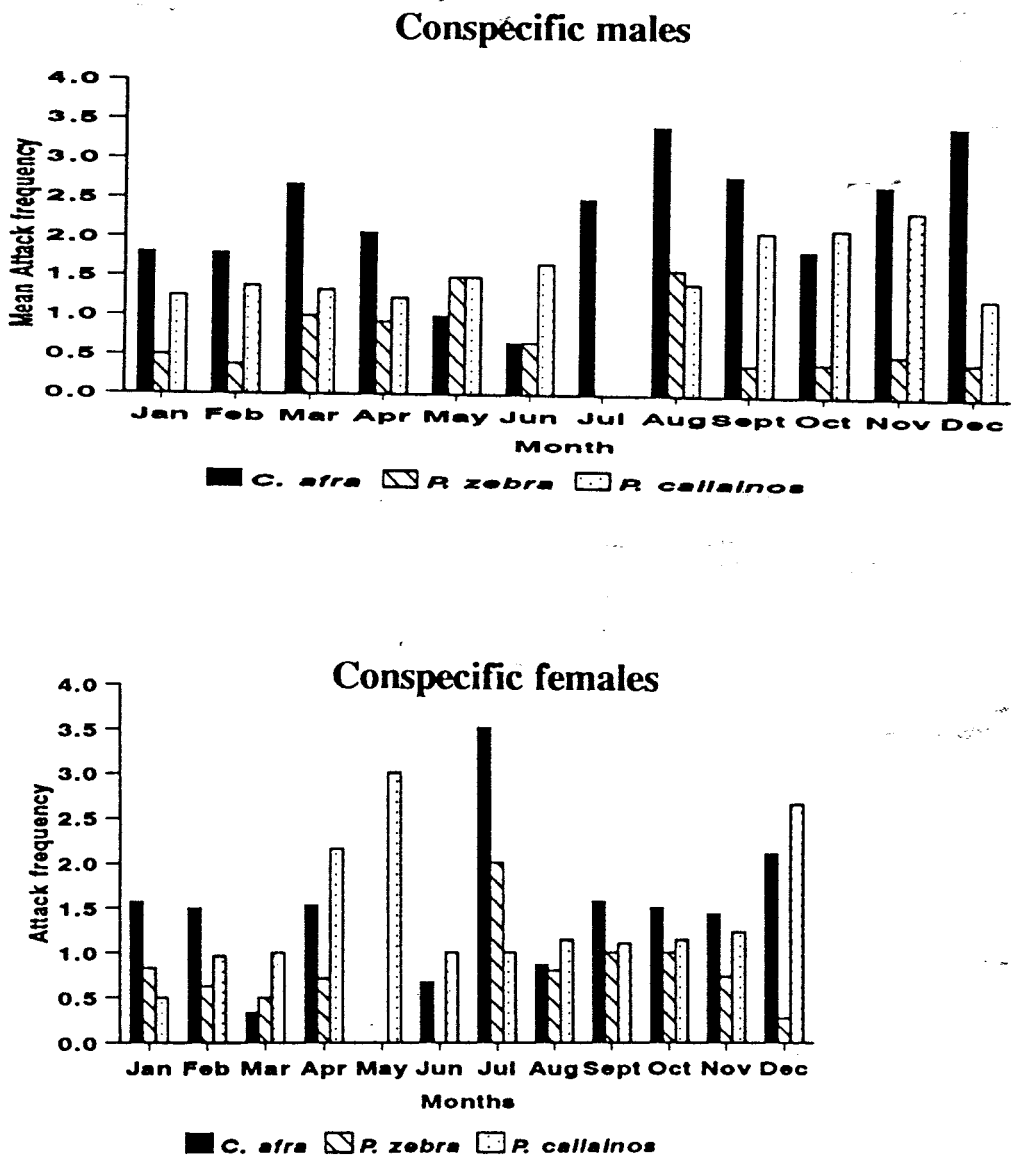
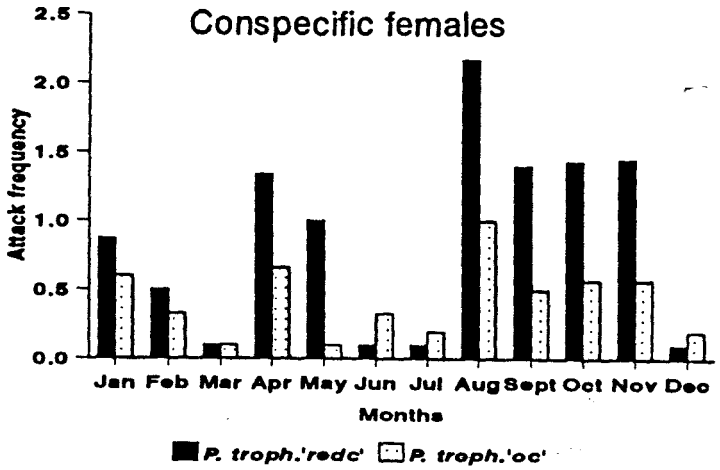


Fig. 3.13a. Mean monthly attack frequency by the Mbuna of the small rock guild, *i.e.*, the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and native species, *P. zebra*.



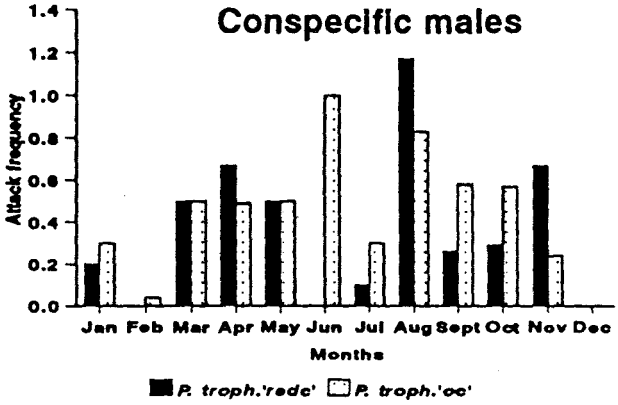


Fig. 3.13b. Mean monthly attack frequency by the Mbuna of the large rock guild, *i.e.*, the introduced species, *Pseudotropheus tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest'.

Diurnally, *C. afra* and *P. zebra* exhibited significant variation in their aggression towards heterospecific intruders ($X^2 = 14.89$, $df = 5$, $P < 0.05$; Fig. 3.14a), while *P. callainos* did not ($X^2 = 10.22$, $df = 5$; $P > 0.05$; Fig. 3.14b). *Cynotilapia afra* exhibited the highest interspecific aggression during the mid morning, while *P. zebra* did so in the early morning. Overall, *C. afra*, *P. zebra* and *P. callainos* mostly attacked heterospecifics which overlapped with them in the microhabitat requirements (Table 3.1, 3.2). They also mostly attacked the species that were most abundant at the study sites (Fig. 3.15a-c).

The Mbuna that prefer small rocks were highly antagonistic towards each other. More particularly, the introduced species, *C. afra* and native species, *P. zebra* were the most aggressive towards each other (Fig. 3.15a & c). On the other hand, an introduced species, *P. callainos* was more aggressive towards its sibling native species, *P. zebra*, in the small rock predominated areas than in areas predominated by large rocks (Fig. 3.15b & c).

Seasonally, *C. afra*, *P. callainos* and *P. zebra* were most aggressive during the stratified season (Fig. 3.16a-c), when food is generally limited in Lake Malawi (Eccles 1974; Twombly 1983; Haberyan & Mhone 1992; Bootsma 1993a). During this season, *C. afra* attacked twenty-three heterospecifics (Fig. 3.16a), while *P. callainos* and *P. zebra* attacked only ten and thirteen heterospecific intruders, respectively (Fig. 3.16b & c). *Cynotilapia afra* and *P. zebra* attacked Mbuna and other cichlid species, while *P. callainos* only attacked Mbuna species. The least number of attacks was recorded during the transition season, when *C. afra*, *P. callainos* and *P. zebra* attacked only five, two and four heterospecific intruders, respectively (Fig. 3.16a-c). However, territorial defence against conspecifics by *C. afra*, *P. callainos* and *P. zebra* was fairly constant throughout the year (Fig. 3.13a).

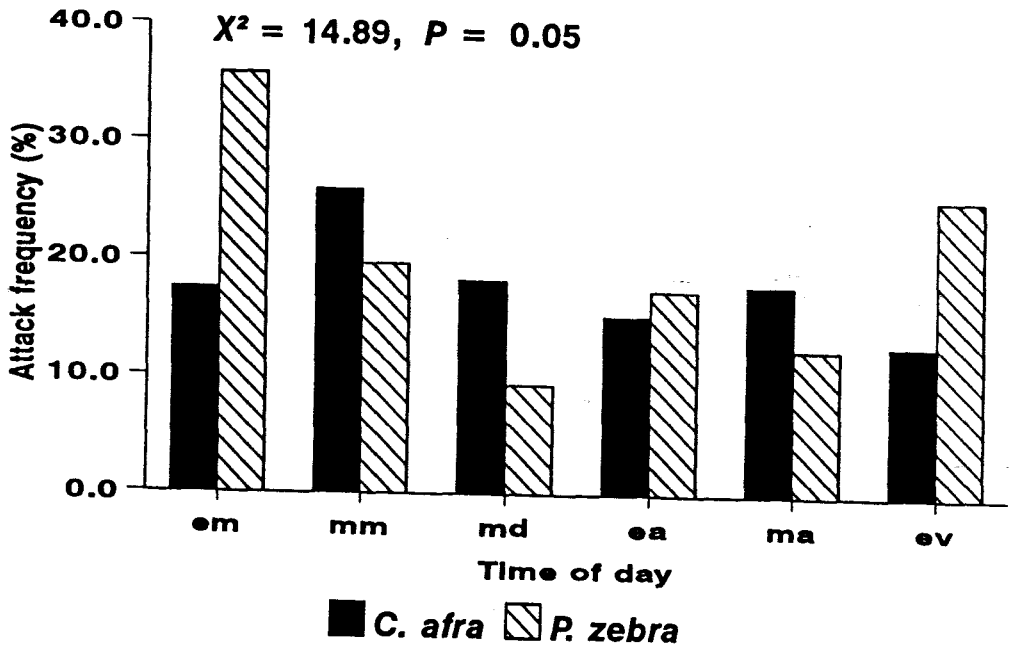


Fig. 3.14a. Diurnal attack frequency, presented as proportion of the total number of attacks that were directed at heterospecific intruders by the introduced species, *Cynotilapia afra* and native species *Pseudotropheus zebra*. The times of day, em = early morning (05h30 - 08h00), mm = mid morning (08h01 - 11h00), md = mid day (11h01 - 13h00), ea = early afternoon (13h01 - 15h00), ma = mid afternoon (15h01-17h30) and ev = dusk (17h31 - 18h30).

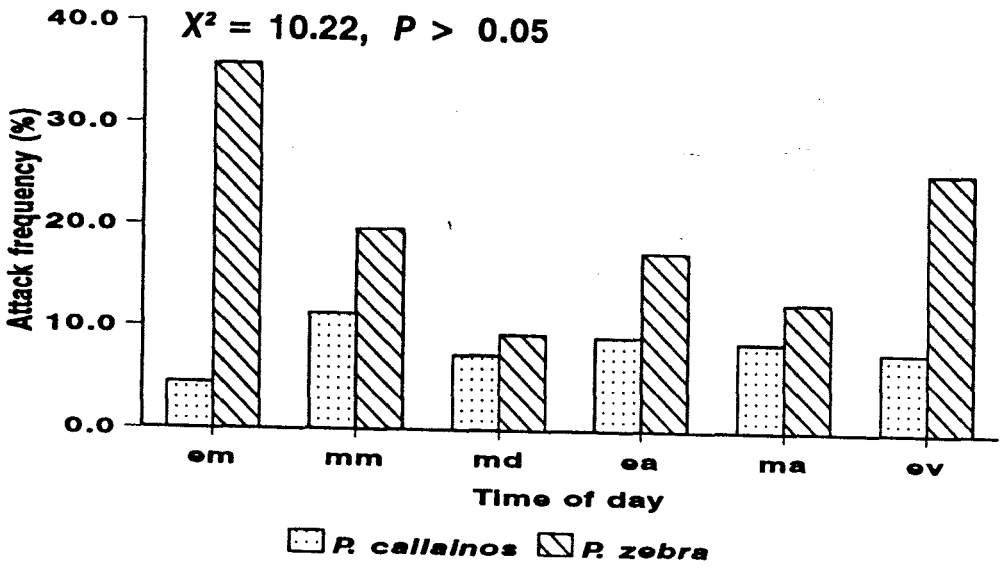


Fig. 3.14b. Diurnal attack frequency, presented as proportion of the total number of attacks that were directed at heterospecific intruders by the introduced species, *Pseudotropheus callainos* and native species, *Pseudotropheus zebra*. The times of day are the same as specified in Figure 3.14a above.

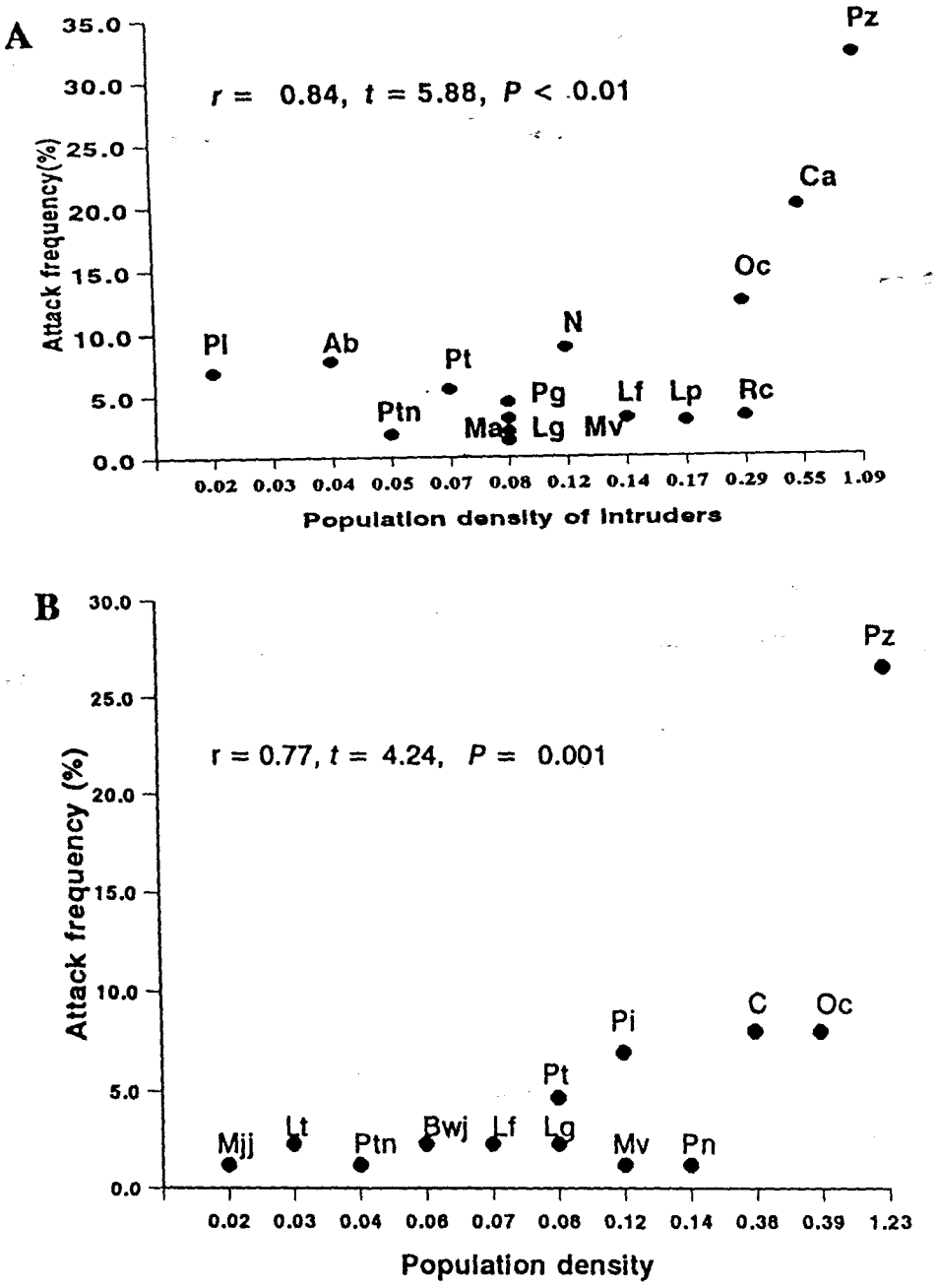


Fig. 3.15a. Correlation between the population density (number m^{-2}) of the intruders and the attack frequency by the introduced species, *Cynotilapia afra* in areas predominated by small (A) and large rocks (B). Mjj = *Melanochromis joanjohnsonae*, Lt = *Labeotropheus trewavasae*, Lf = *Labeotropheus fuelleborni*, Lg = *Labidochromis gigas*, Ls = *Labidochromis strigatus*, Ptn = *Protomelas taeniolatus*, Bwj = *Melanochromis* 'black-white' *johanni*, Ma = *Melanochromis auratus*, Mv = *Melanochromis vermivorus*, N = *Petrotilapia nigra*, Pg = *Petrotilapia genalutea*, C = *Pseudotropheus callainos*, Ca = *Cynotilapia afra*, Oc = *Pseudotropheus tropheops* 'orange chest', Rc = *Pseudotropheus tropheops* 'red cheek', Pz = *Pseudotropheus zebra*, Pi = *Pseudotropheus tropheops* 'intermediate', Pt = *P.* 'tiny', Ab = *Aulonacara* 'blue'.

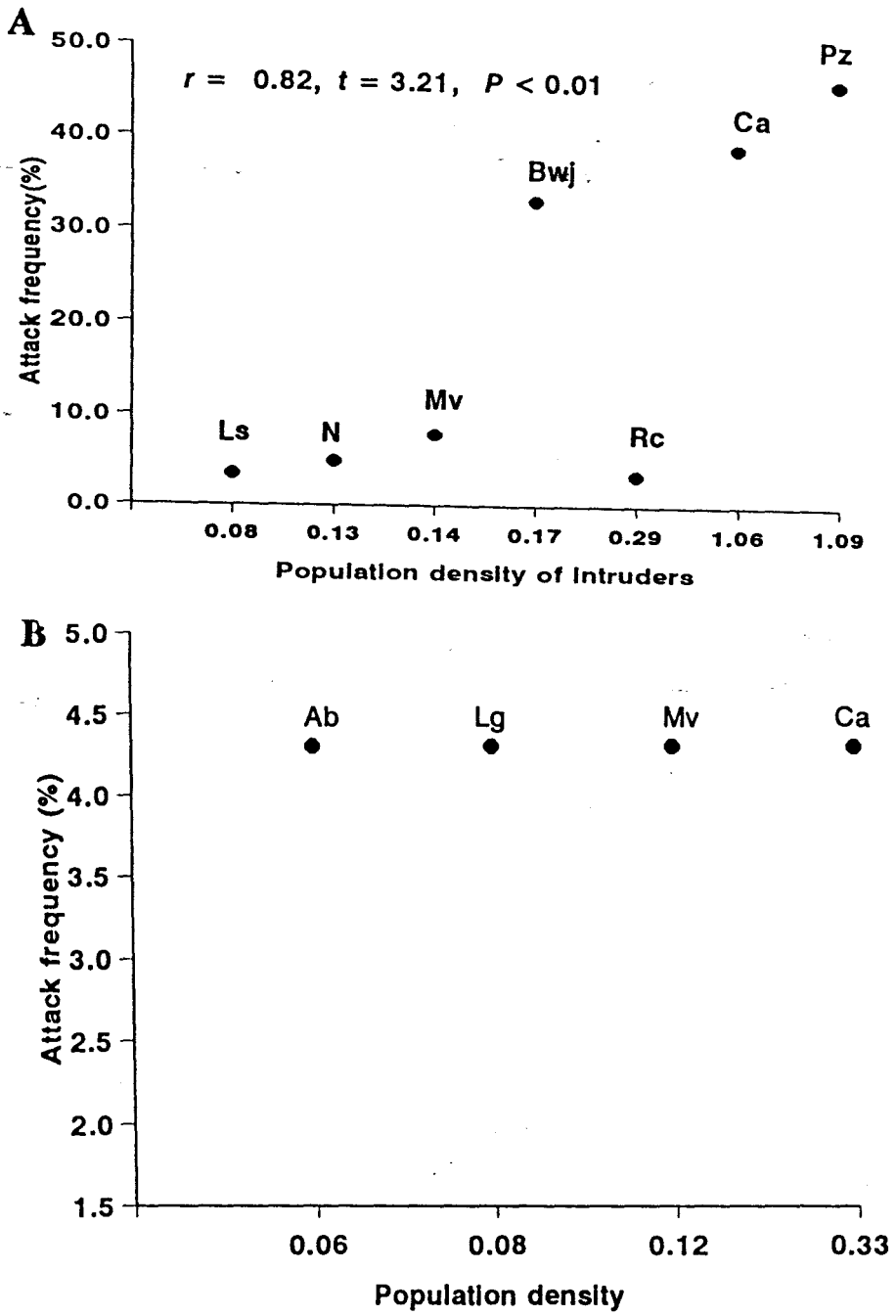


Fig. 3.15b. Correlation between the population density (number m^{-2}) of the heterospecific intruders and the attack frequency by the introduced species, *Pseudotropheus callainos* in areas predominated by the small (A) and large rocks (B). Ca = *Cynotilapia afra*, Mjj = *Melanochromis joanjohnsonae*, Lt = *Labeotropheus trewavasae*, Ptn = *Protomelas taeniolatus*, Bwj = *Melanochromis* 'black-white' *johanni*, Ma = *M. auratus*, Lf = *Labeotropheus fuelleborni*, Pt = *Pseudotropheus* 'tiny', Lg = *Labidochromis gigas*, Mv = *Melanochromis vermivorus*, N = *Petrotilapia nigra*, Pg = *P. genalutea*, C = *Pseudotropheus callainos*, Oc = *Pseudotropheus tropheops* 'orange chest', Rc = *P. tropheops* 'red cheek', Pi = *P. tropheops* 'intermediate', Pz = *P. zebra* and Ab = *Aulonacara* 'blue'

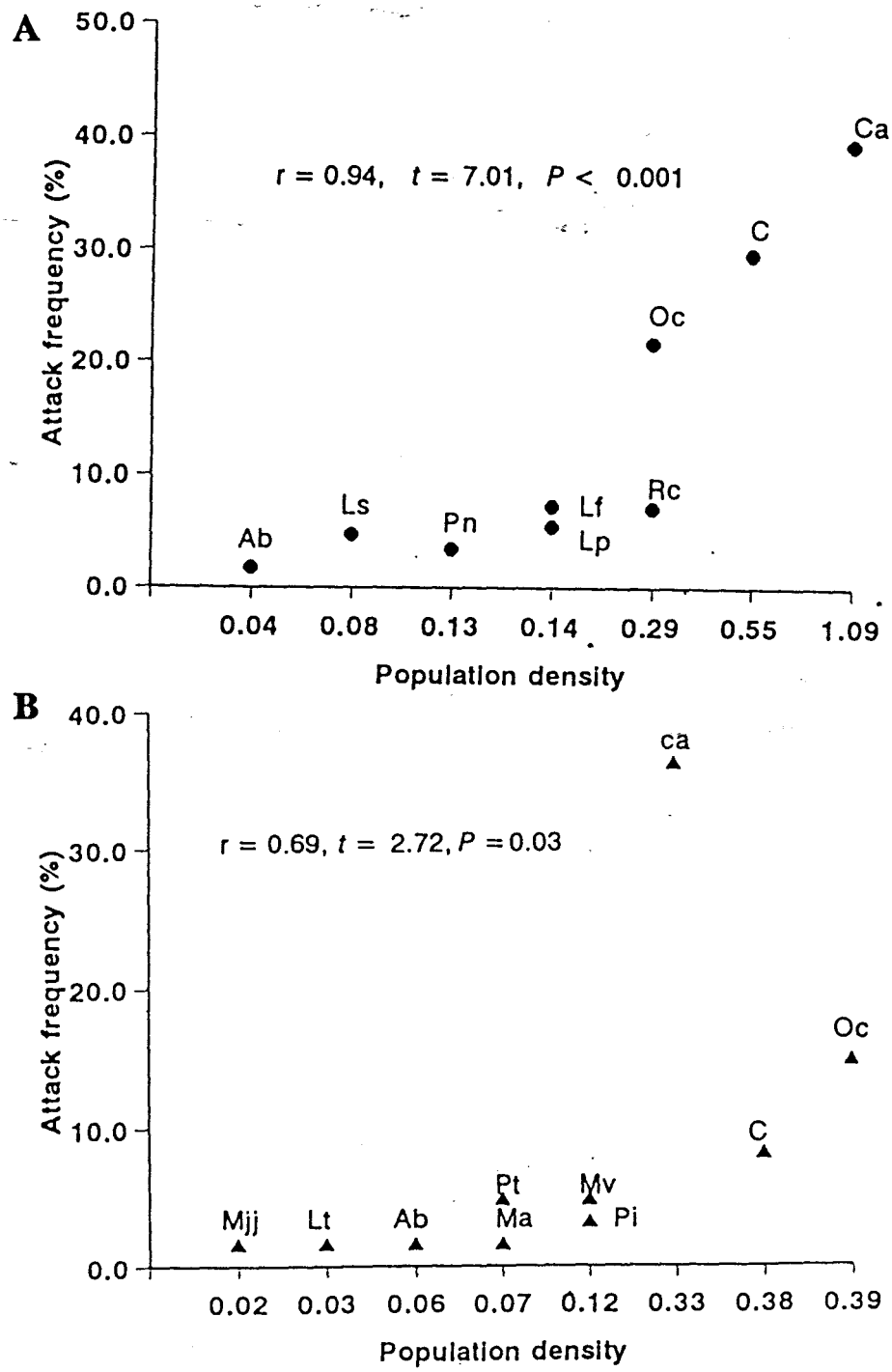


Fig. 3.15c. Correlation between the population density (number m^{-2}) of the heterospecific intruders and the attack frequency by the native species, *Pseudotropheus zebra* in areas predominated by the small (A) and large rocks (B). Ca = *Cynotilapia afra*, Mjj = *Melanochromis joanjohnsonae*, Lt = *Labeotropheus trewavasae*, Ptn = *Protomelas taeniolatus*, Bwj = *Melanochromis* 'black-white' *johanni*, Ma = *M. auratus*, Lf = *Labeotropheus fuelleborni*, Pt = *Pseudotropheus* 'tiny', Lg = *Labidochromis gigas*, Mv = *Melanochromis vermivorus*, N = *Petrotilapia nigra*, Pg = *P. genalutea*, C = *Pseudotropheus callainos*, Oc = *Pseudotropheus tropheops* 'orange chest', Rc = *P. tropheops* 'red cheek', Pi = *P. tropheops* 'intermediate', Pz = *P. zebra* and Ab = *Aulonacara* 'blue'

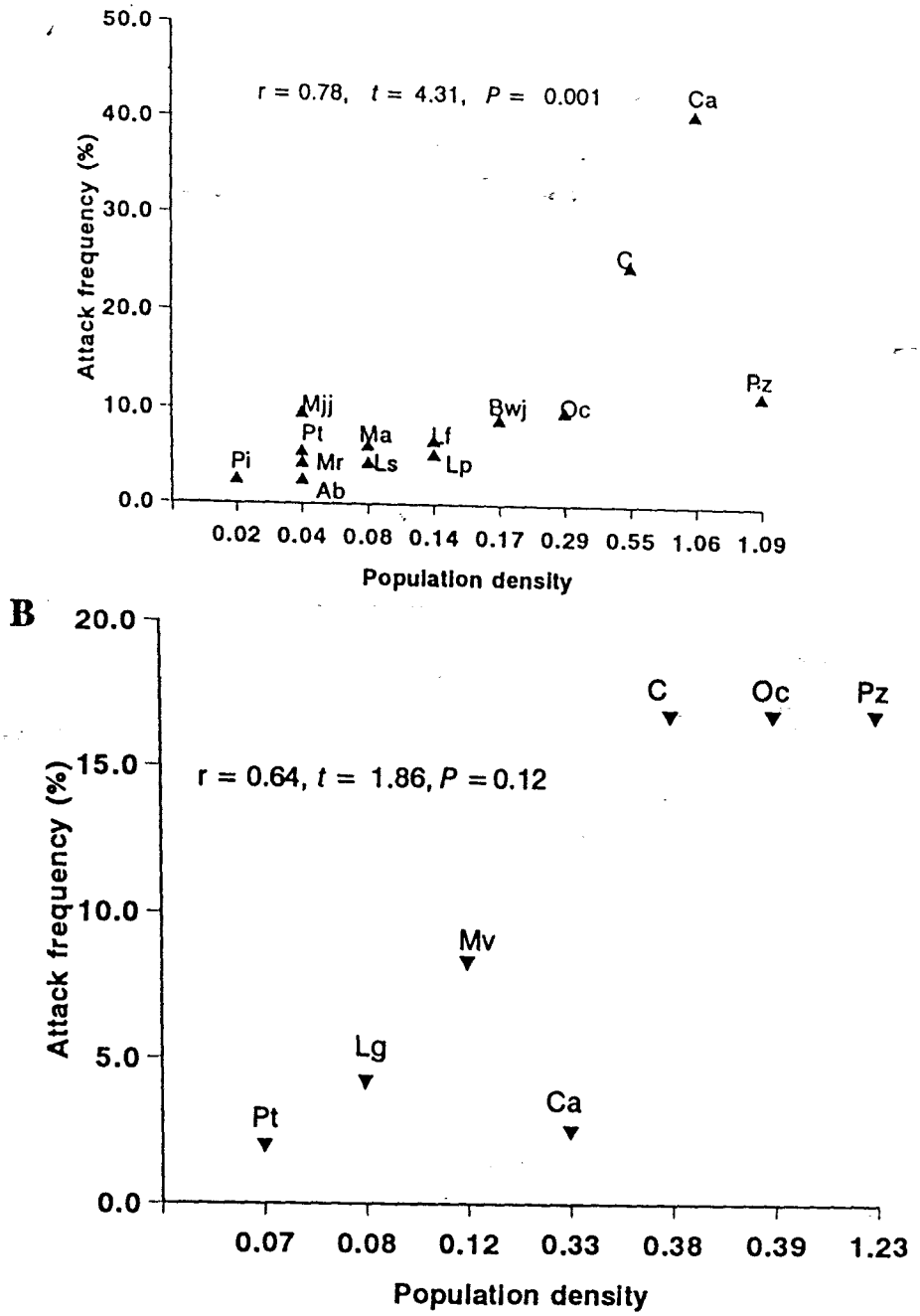


Fig. 3.15d. Correlation between the population density (number m^{-2}) of the heterospecific intruders and the attack frequency by the introduced species, *Pseudotropheus tropheops* 'red cheek' in areas predominated by small (A) and large rocks (B). *Cynotilapia afra* in areas predominated by small (A) and large rocks (B). *Cynotilapia afra*, Mjj = *Melanochromis joanjohnsonae*, Lt = *Labeotropheus trewavasae*, Ptn = *Protomelas taeniolatus*, Bwj = *Melanochromis* 'black-white' *johanni*, Ma = *M. auratus*, Lf = *Labeotropheus fuelleborni*, Pt = *Pseudotropheus* 'tiny', Lg = *Labidochromis gigas*, Mv = *Melanochromis vermivorus*, N = *Petrotilapia nigra*, Pg = *P. genalutea*, C = *Pseudotropheus callainos*, Oc = *Pseudotropheus tropheops* 'orange chest', Rc = *P. tropheops* 'red cheek', Pi = *P. tropheops* 'intermediate', Pz = *P. zebra* and Ab = *Aulonacara* 'blue'

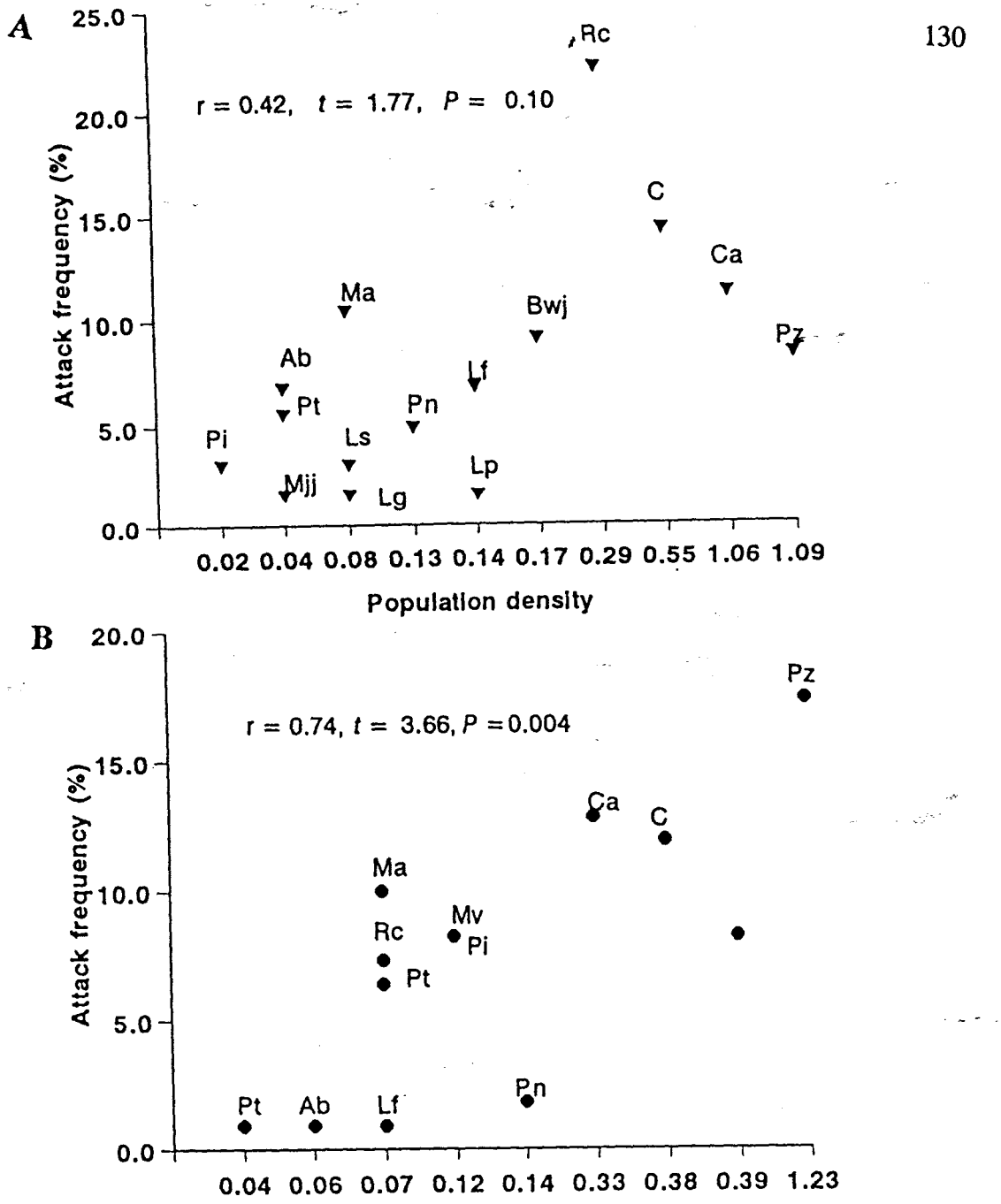


Fig. 3.15e. Correlation of the population density (number m^{-2}) of the heterospecific intruders and the attack frequency by the native species, *Pseudotropheus tropheops* 'orange chest' in areas dominated by the small rocks (A) and large rocks (B). Mjj = *Melanochromis joanjohnsonae*, Lt = *Labeotropheus trewavasae*, Lf = *Labeotropheus fuelleborni*, Lg = *Labidochromis gigas*, Ls = *Labidochromis strigatus*, Ptn = *Protomelas taeniolatus*, Bwj = *Melanochromis* 'black-white' *johanni*, Ma = *Melanochromis auratus*, Mv = *Melanochromis vermivorus*, N = *Petrotilapia nigra*, Pg = *Petrotilapia genalutea*, C = *Pseudotropheus callainos*, Ca = *Cynotilapia afra*, Oc = *Pseudotropheus tropheops* 'orange chest', Rc = *Pseudotropheus tropheops* 'red cheek', Pz = *Pseudotropheus zebra*, Pi = *Pseudotropheus tropheops* 'intermediate', Pt = *P.* 'tiny', Ab = *Aulonacara* 'blue'.

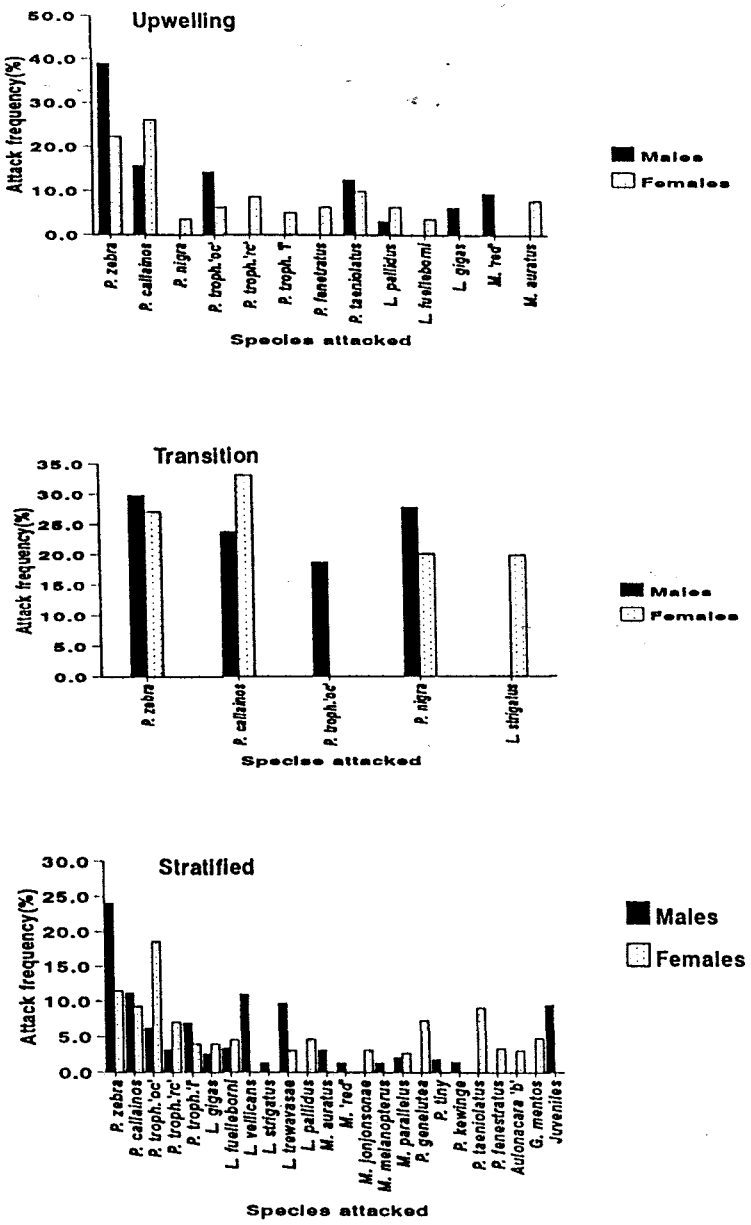


Fig. 3.16a. Seasonal attack frequency at heterospecific intruders by the introduced species, *Cynotilapia afra*. See appendix 1 for full species names. The season are upwelling (May - August), transition (September - October) and stratified (November - April).

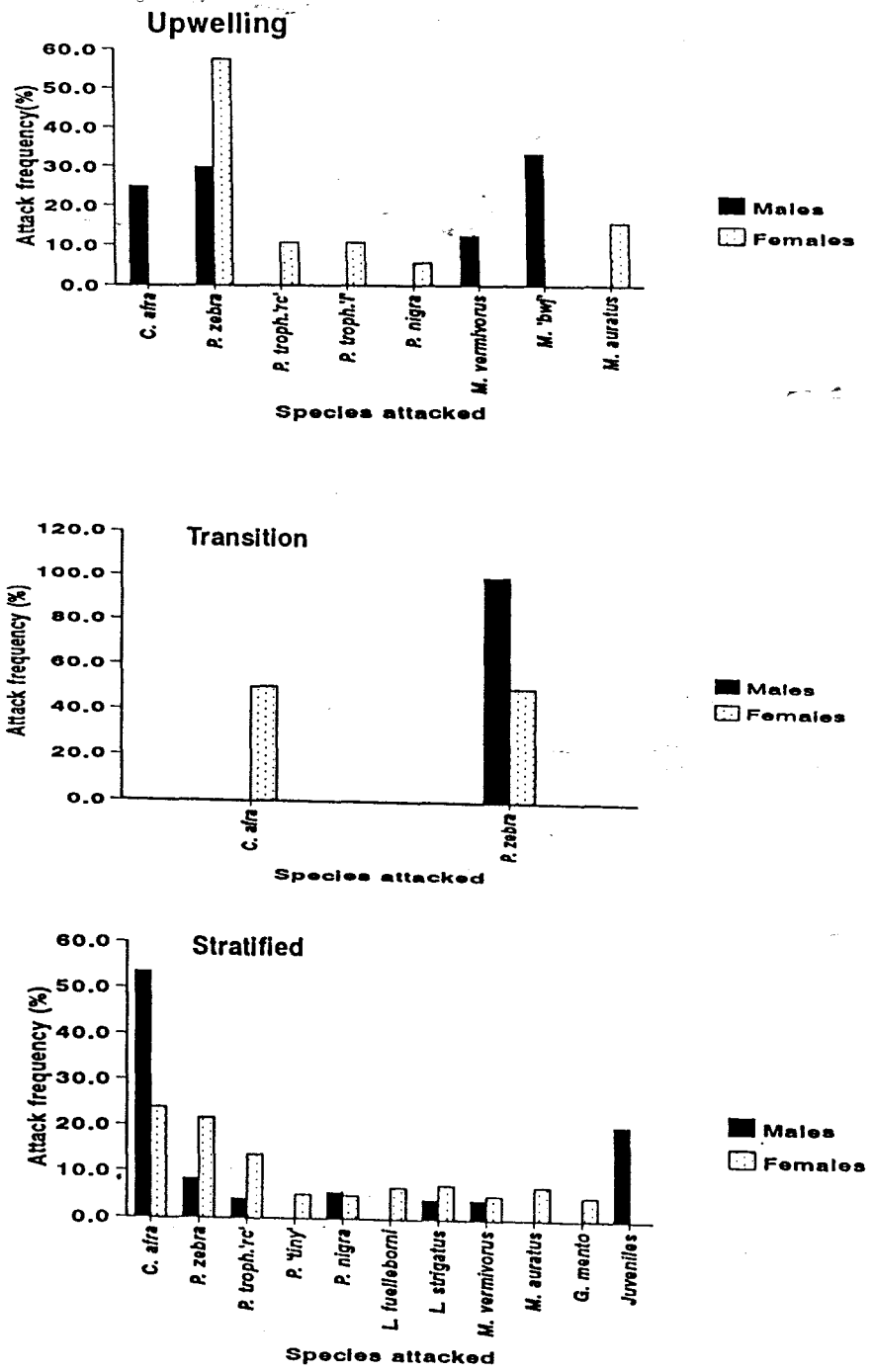


Fig. 3.16b. Seasonal attack frequency at heterospecific intruders by the introduced species, *Pseudotropheus callainos*. See appendix 1 for full species names. The seasons are upwelling (May - August), transition (September - October) and stratified (November - April).

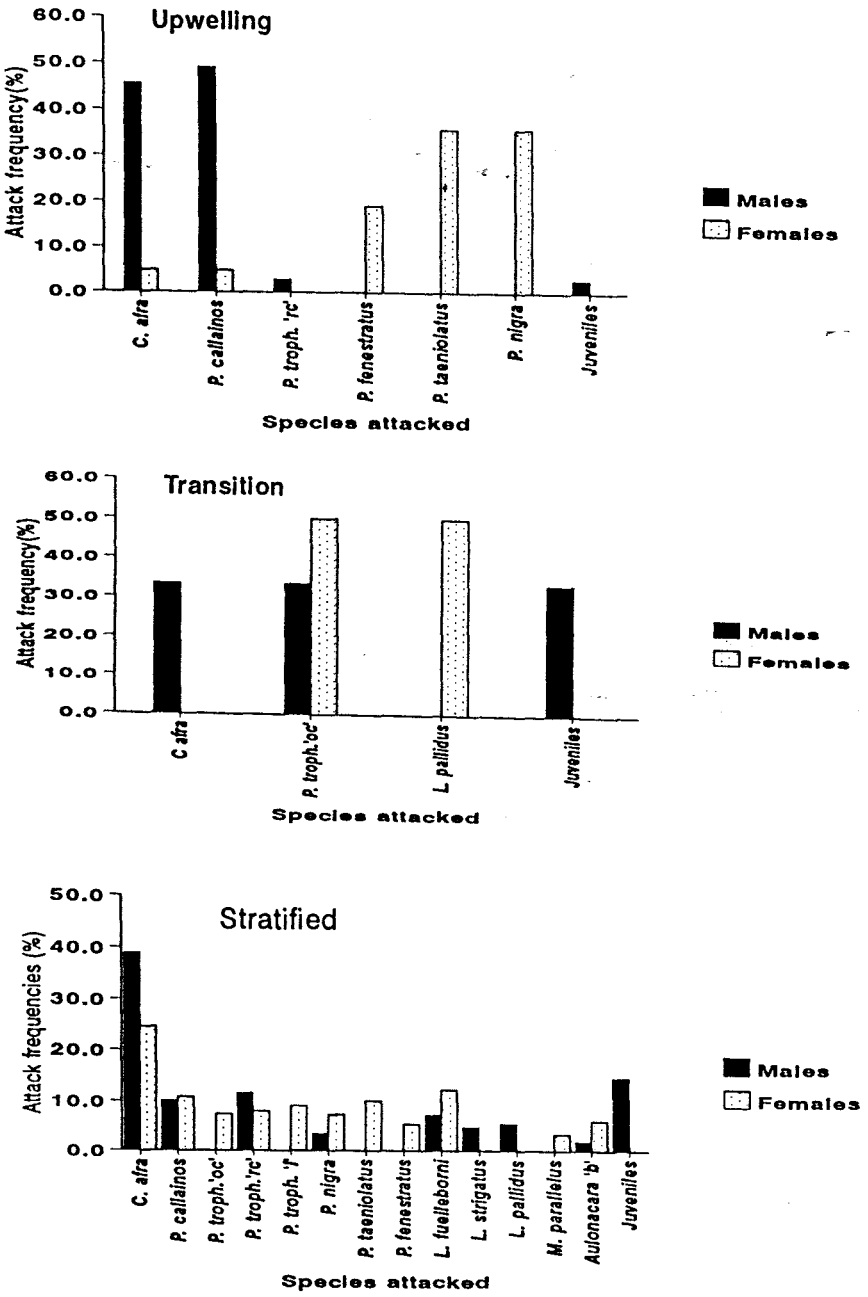


Fig. 3.16c. Seasonal attack frequency at heterospecific intruders by the native species, *Pseudotropheus zebra*. See appendix 1 for full species names. The seasons are upwelling (May - August), transition (September - October) and stratified (November - April).

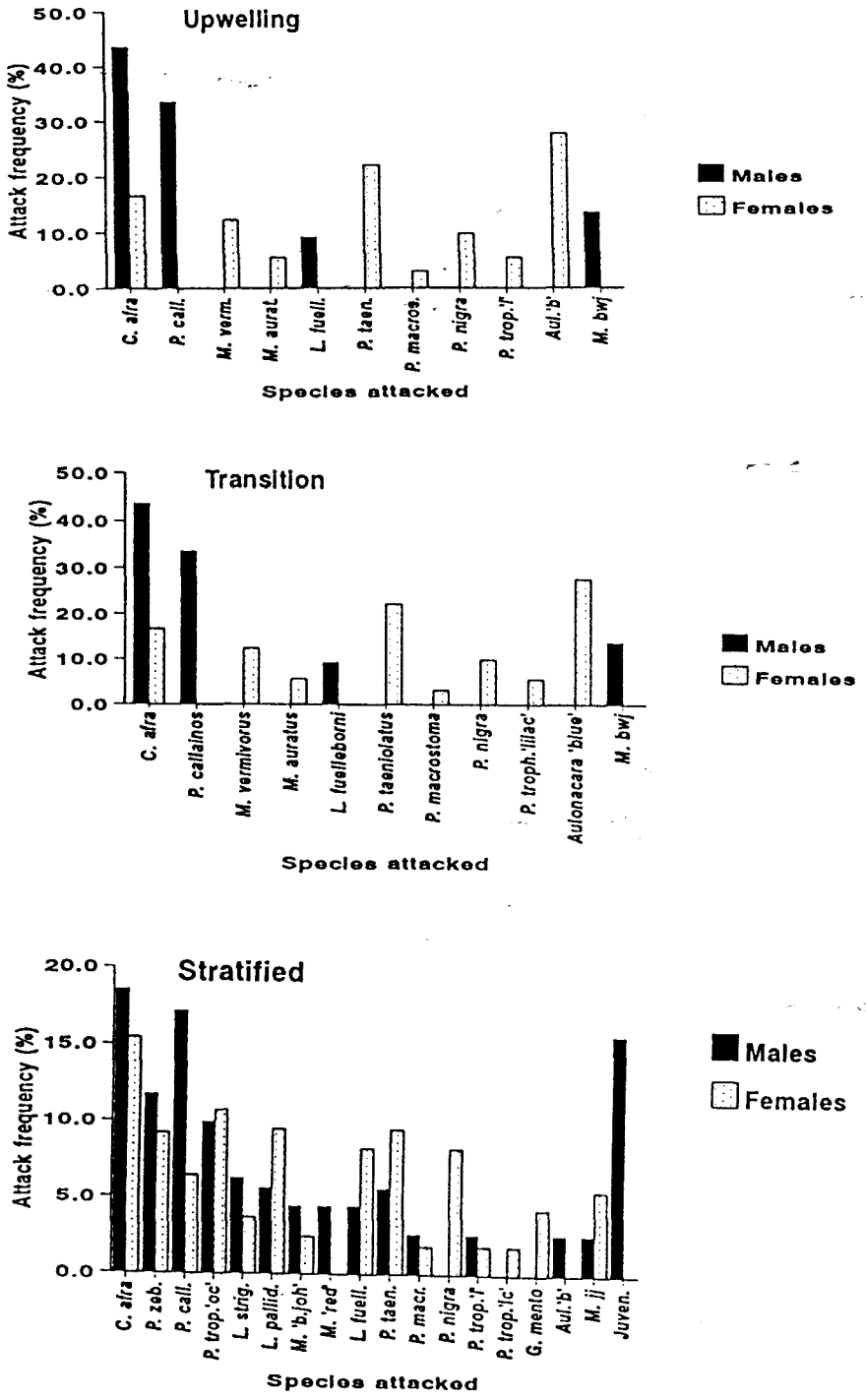


Fig. 3.16d. Seasonal attack frequency at heterospecific intruders by the introduced species, *Pseudotropheus tropheops* 'red cheek'. See appendix 1 for full species names. The seasons are upwelling (May - August), transition (September - October) and stratified (November - April).

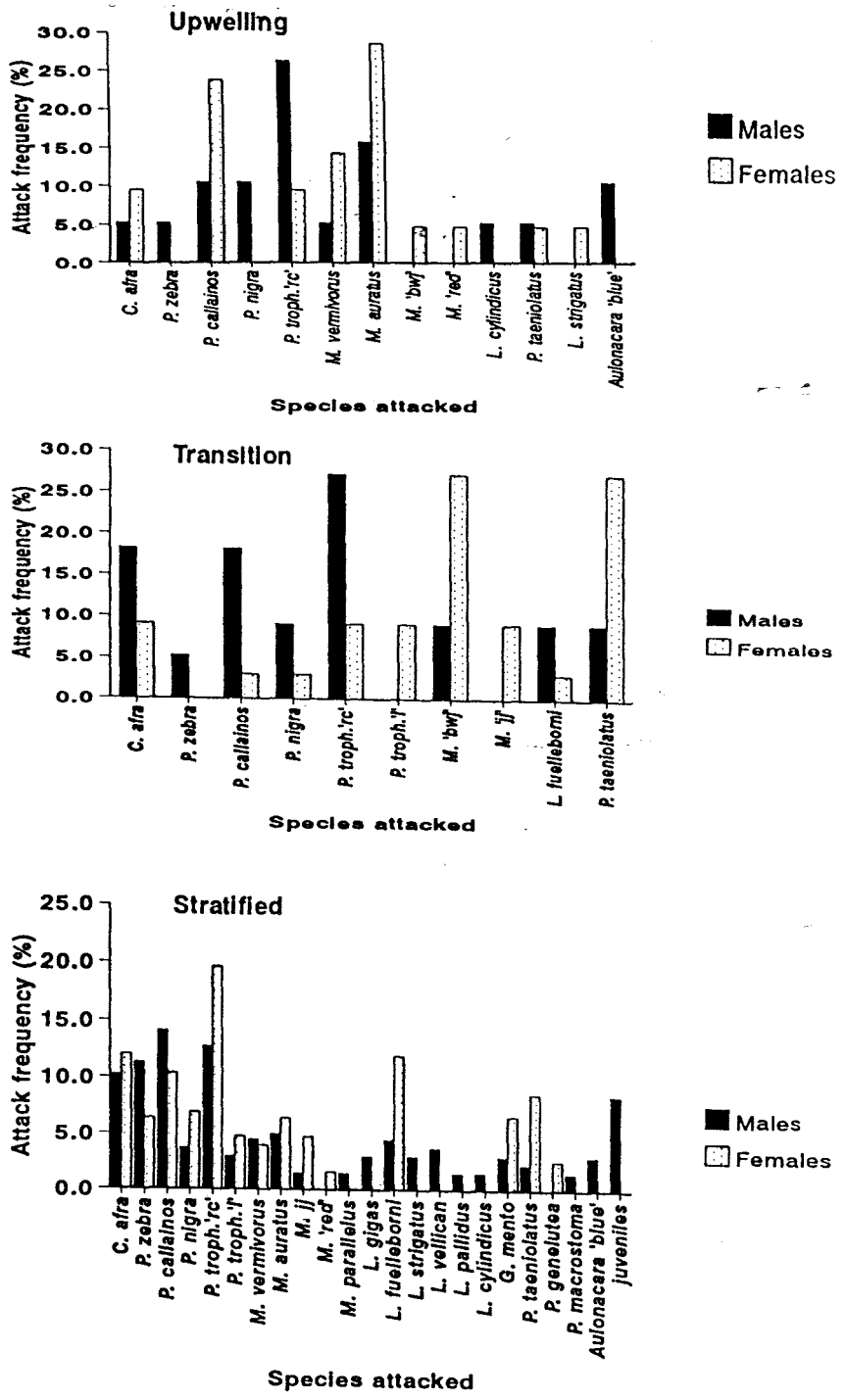


Fig. 3.16e. Seasonal attack frequency at heterospecific intruders by the native species, *Pseudotropheus tropheops* 'orange chest'. See appendix 1 for full species names. The seasons are upwelling (May - August), transition (September - October) and stratified (November - April).

Territorial contests by the Mbuna of the small rock guild, in the form of fights between the territory tenants and non-territorial males were fairly common between conspecifics and rare between heterospecifics. During the entire study period twenty-seven fights were observed, *i.e.*, four between territorial *C. afra* and *P. zebra* that trespassed into each others territories, two between territorial *C. afra* and non-territorial *P. zebra* males, twelve between territorial and non-territorial *C. afra* males and nine between territorial and non-territorial *P. zebra*. Non-territorial males often attempted to take over territories when the residents were away feeding in the water column, but in all cases, territorial males won the contests. However, conspecific males sometimes fought ferociously, locking their mouths and chewing each other's lips, consequently, some of *C. afra* territorial males were seen with broken teeth and/or chewed lips. Such individuals were also common among the non-territorial males, suggesting that they were once territorial, or their lips and/or teeth may have been damaged in a fight.

Females of *C. afra*, *P. zebra* and *P. callainos*, on the other hand often fed in large schools and were neither intraspecifically nor interspecifically antagonistic towards intruders. However, brooding females sometimes chased conspecific females if they came too close to their shelter, *i.e.*, either a flat rock, or a hole among the rocks.

(b) *The large rock guild*

The Mbuna that prefer large rocks consistently defended their expansive territories against conspecific and other fishes, irrespective of their trophic specialization. The native species, *P. tropheops* 'orange chest' was more aggressive in defending its territories than its sibling introduced species, *P. tropheops* 'red cheek' (Fig. 3.16d & e).

Diurnally, *P. tropheops* 'orange chest' was both intra- and interspecifically most aggressive during the early and mid afternoon, while *P. tropheops* 'red cheek' was most aggressive towards its conspecifics in the evening and mid day, respectively (Fig. 3.11b). These were also the times when these Mbuna engaged in active feeding (Fig. 3.9a). Territorial disputes, in terms of physical fights between *P. tropheops* 'orange chest' and *P. tropheops* 'red cheek' were rare, partly because their territories were often far apart (mean $\pm$ *Sd* = 92.67 $\pm$ 4.62cm, n = 30). But when the two species crossed paths, the territorial tenants always dominated over the intruders. However, judging from the frequency of chases *P. tropheops* 'red cheek' received from *P. tropheops* 'orange chest' (Fig. 3.16d & e), it appears *P. tropheops* 'orange chest' was dominant over *P. tropheops* 'red cheek'. The evidence of *P. tropheops* 'orange chest' domination was more obvious at study site # 1 (Fig. 3.1), where there were twenty territorial *P. tropheops* 'orange chest' males, and only six *P. tropheops* 'red cheek' males, of which three defended territories comprised of small rocks ($\leq$ 65cm in diameter), and interspaced by sand. These territories were sub-optimal for this species, which prefers sediment free large rocks ($\geq$ 65cm in diameter; also see Ribbink *et al.* 1983a)

The degree of attacks of intruders by both *P. tropheops* 'orange chest' and *P. tropheops* 'red cheek' was highest during the stratified season (Fig. 3.16d & e). During this season, *P. tropheops* 'orange chest' attacked as many as twenty-three different species, while it attacked only thirteen and ten different species during the upwelling and transition seasons, respectively. *Pseudotropheus tropheops* 'red cheek' on the other hand, attacked nineteen, eleven and only five different species, during the stratified, upwelling and transition seasons, respectively (Fig. 3.16d). *P. tropheops* 'orange chest' during the stratified season most frequently chased females of its sibling species, *P. tropheops* 'red cheek' and males of *P. callainos*, which overlaps with it in the hole preference (Table 3.2). During the upwelling and

transition seasons, it mostly attacked males of *P. tropheops* 'red cheek'. The relationship between the population density of intruding fish species and the number of attacks by *P. tropheops* 'orange chest' was positive, but it was significant only in its preferred microhabitat, *i.e.*, areas predominated by large rocks (Fig. 3.15e). *Pseudotropheus tropheops* 'red cheek' on the other hand, attacked *C. afra* most frequently throughout the three seasons (Fig. 3.16d), and it appears the most abundant fish species were the ones most frequently attacked by *P. tropheops* 'red cheek' (Fig. 3.15d).

Contests, in terms of physical fights between the territorial and non-territorial males of both *P. tropheops* 'orange chest' and *P. tropheops* 'red cheek' were rare. During the entire study period, only eleven fights, involving lateral display-circling-butting and chasing (*e.g.*, Baerends & Baerends-van Roon 1950) were observed. Four of these were between the *P. tropheops* 'orange chest' males and seven between *P. tropheops* 'red cheek' males. Territorial *P. tropheops* 'orange chest' males won all the fights, while *P. tropheops* 'red cheek' territorial tenants won six and lost one to a supernumerary male. Besides this, at study site # 5, one territory occupied by a male *P. tropheops* 'red cheek' was reoccupied by three different conspecific males during 30 months of observation. The exact fate of the previous tenants was not ascertained, but it is probable that they were overthrown by conspecific males. The size of individuals that won or lost the fights was not measured.

Among *P. tropheops* 'orange chest' males, it appears there is some dominance hierarchy, as smaller males occupy smaller rocks, and the bigger males occupy larger rocks (Fig. 3.17). This is also the case with *P. tropheops* 'red cheek', but the relationship is not significant (Fig. 3.17). Therefore, it is probable that the observed territorial turn-overs among the males of *P. tropheops* 'red cheek' may be partly

due to the weak dominance hierarchy in its rock occupation.

Females of *P. tropheops* 'red cheek' and *P. tropheops* 'orange chest' are also antagonistic towards each other (Fig. 3.18). Most particularly, *P. tropheops* 'orange chest' females often chased females of *P. tropheops* 'red cheek', because they regularly crossed paths while foraging in their large home ranges. *Pseudotropheus tropheops* 'orange chest' females interspecifically chased females of *Labidochromis pallidus*, but did not attack any males. Whereas, females of *P. tropheops* 'red cheek' were interspecifically aggressive towards females of *Melanochromis vermivorus*, *P. zebra* and the supernumerary juvenile males of its own species. The level of aggression between females of *P. tropheops* 'orange chest' and *P. tropheops* 'red cheek', however, was not so serious, as to negatively affect each other's feeding, or reproductive success.

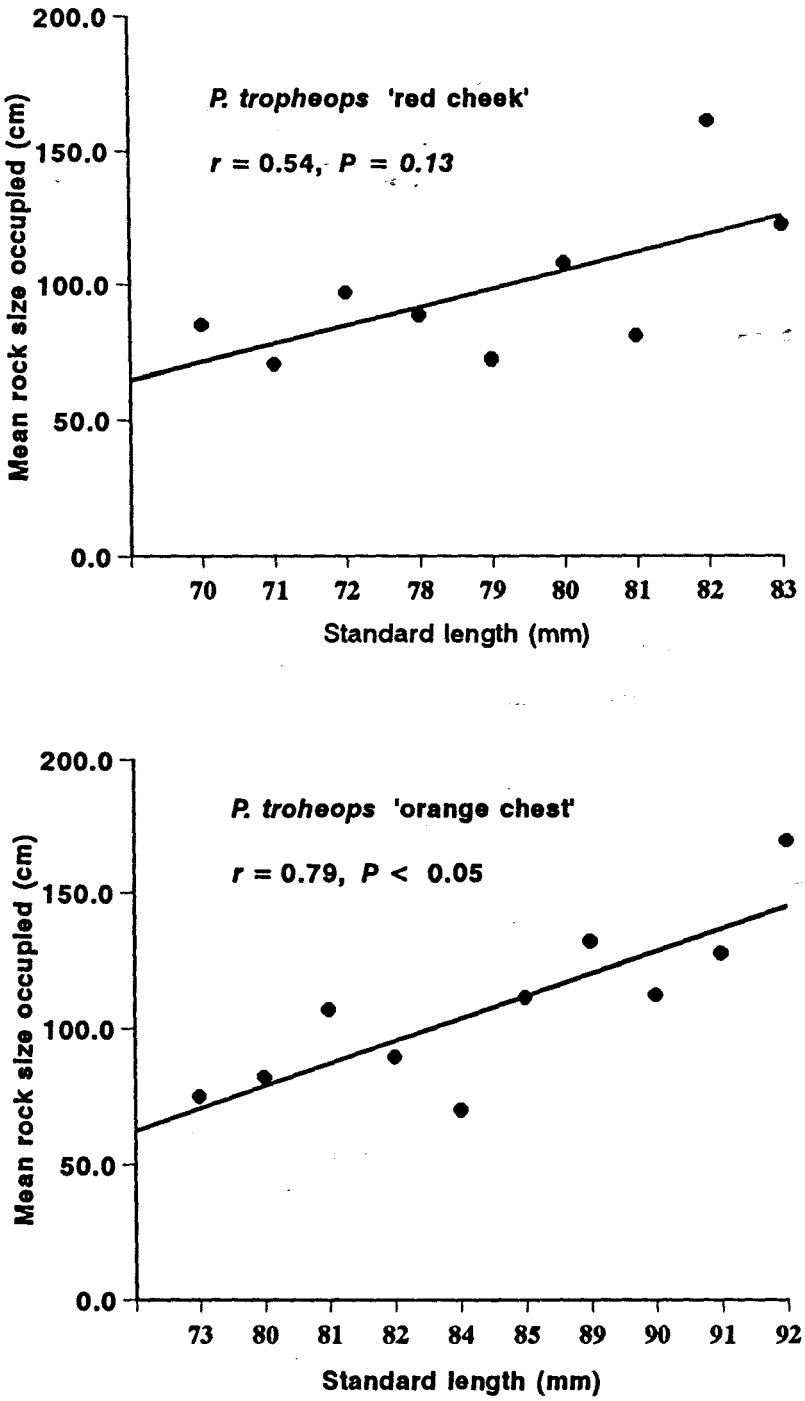


Fig. 3.17. The relationship between the size (Standard length in millimetres) and the rock size occupied by the introduced species *Pseudotropheus tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest' at Thumbi West Island.

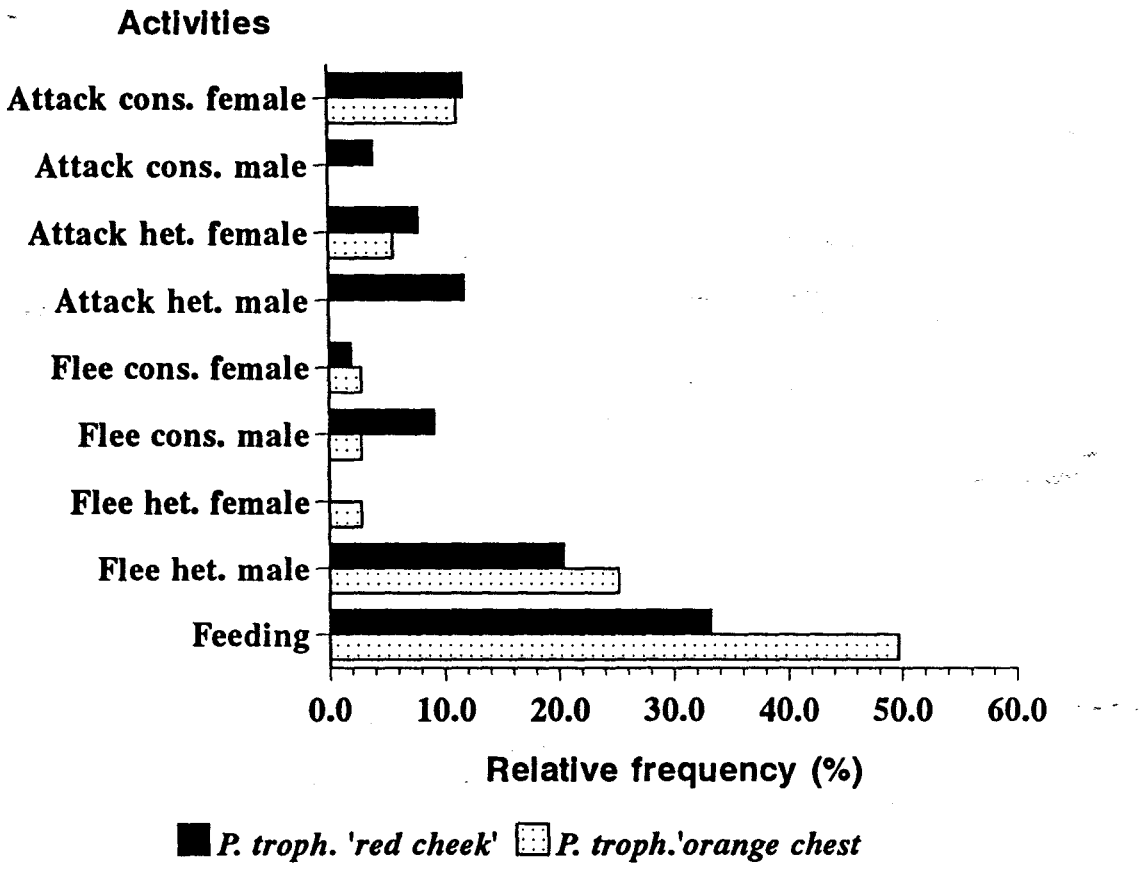


Fig. 3.18. The commonest activities engaged in by the females of the introduced species, *Pseudotropheops tropheops* 'red cheek' and females of the native species, *P. tropheops* 'orange chest', during ten minutes observation periods.

Interspecific territory turn-over

Interspecific territory turn-over occurred under natural conditions (control) and experimental removal of territorial males of the introduced Mbuna species.

(a) *Natural turn-over, control*

At site # 5, *C. afra* lost twelve (12.12%) territories of its ninety-nine territories established in thirty months, as a consequence of natural displacement by other species. Six (50%) of these were taken over by *P. zebra*, three (25%) by *P. callainos* and three (25%) were abandoned, but used by adjacent *P. zebra* and *P. callainos* (Table 3.14).

***Pseudotropheus callainos* lost twenty territories (16.81%) of its 119 territories established in thirty months. Eight (40%) of these were taken over by *C. afra*, six (30%) by *P. zebra*, two (10%) by *P. tropheops* 'red cheek', three (15%) by *P. tropheops* 'orange chest' and one (5%) by *P. tropheops* 'lilac'.**

***Pseudotropheus zebra* lost twenty-one (19.10%) of its 110 territories established in 30 months. Seventeen (80.95%) of these were taken by *C. afra*, three (14.29%) by *P. callainos* and one (4.76%) of its territories was abandoned, but was used by non-territorial fishes, *e.g.*, juveniles and females of various Mbuna.**

***Pseudotropheus tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest' had the highest rate of territory turn-over (25%) (Table 3.14). Six (60%) of *P. tropheops* 'red cheek's' territories were recolonised by *P. tropheops* 'orange chest', and four (40%) remained vacant, but were used by non-territorial fishes. Similarly, three (42.86%) of *P. tropheops* 'orange chest's' territories were taken by *P. tropheops* 'red cheek', two (28.57%) by *P. tropheops* 'lilac' and two (28.57%) remained vacant, but were used by non-territorial fishes (Table 3.14).**

(b) *Territory turn-over due to removals*

The number of territorial individuals removed from the quadrat at site # 3 (Fig. 3.1) was variable. More were removed during the early months because of increased removal effort. After forty-one removals in eighteen months, a total of 806 *C. afra*, 601 *P. callainos* and 129 *P. tropheops* 'red cheek' territorial males were removed from the quadrat. Despite the high number being removed, *C. afra* males still retained fifteen (54%) of the 28 territories originally occupied because the individuals removed were replaced by conspecifics. The standard length of the conspecific males reoccupying the vacated territories was almost constant throughout the study period (Fig. 3.19). The other thirteen territories, held by *C. afra* were all lost to other species, principally to native species, *P. zebra* (84.62%), and *P. tropheops* 'orange chest' (15.38%), which were shared with an adjacent *P. callainos*.

The replacement by conspecifics of those *P. callainos* which had been removed resulted in this species retaining twenty-six (62%) of its forty-two original territories, and losing sixteen territories (38%). However, the size (standard length) of the conspecific males reoccupying the vacated territories declined significantly with repeated removals (Fig. 3.19). Fifteen (57.69%) of the twenty-six territories retained by *P. callainos* overlapped with those of *P. zebra*. These species also naturally overlap their territories, as noted earlier in this chapter (also see Holzberg 1978). Therefore, the removal experiment may not have precipitated this behaviour. Eight (50%) of the sixteen territories lost by *P. callainos* were taken over by the native species, *P. zebra*, six (37.50%) were reoccupied by *P. tropheops* 'orange chest', one (6.25%) was taken over by *Pseudotropheus* 'aggressive brown' and one (6.25%) was taken over by *Melanochromis vermivorous* (Table 3.15).

Territorial males of *P. tropheops* 'red cheek' stabilized at five individuals, and very few new territorial tenants were removed after November, 1992. Conspecific males that reoccupied *P. tropheops* 'red cheek' territories also declined significantly in size with repeated removals (Fig. 3.19). Six (60%) of its ten lost territories were taken by *P. tropheops* 'orange chest', two (20%) were shared by adjacent *P. zebra* and *Petrotilapia nigra* and one (20%) remained vacant, but was used by non-territorial fishes.

The non-territorial native species which fed in undefended vacated territories were females of *P. tropheops* 'orange chest', *Protomelas taeniolatus*, *P. zebra* and *Labidochromis vellicans*. Juveniles of various species also fed in the territories where males of introduced species had been removed.

Overall, the number of territorial individuals belonging to introduced species declined, but not significantly with repeated removals over time (Fig. 3.20). Nonetheless, their reduction in numbers was followed by an increase in the number of territorial males of some native species. The species whose number increased significantly were *P. zebra* ($r_s = 0.89$, $P < 0.05$) and *P. tropheops* 'orange chest' ($r_s = 0.95$, $P < 0.05$, Fig. 3.21). These species increased in numbers by both taking over vacated territories, and establishing new territories within open spaces. Therefore, removal of introduced species created more opportunities for these native species to increase in numbers.

Table 3.14. Natural interspecific territory turn-over between the introduced and native species in a 7m x 7m quadrat, subdivided into $1m^2$ grids, at site # 5 (Fig. 3.1).

	Species				
	C. afra	*P. callainos*	*P. troh.*'rc'	*P. zebra*	*P.troph.*'oc'
No. of territories established in 30 months	99.00	119.00	40.00	110.00	40.00
No. of territories taken by other species	12.00	20.00	10.00	21.00	10.00
% Of lost territories taken by *C. afra*	-	40.00	0.00	85.95	0.00
% Of lost territories taken by *P. callainos*	25.00	-	14.29	0.00	0.00
% Of lost territories taken by *P. tropheops* 'red cheek'	0.00	10.00	-	0.00	42.86
% Of lost territories taken by *P. zebra*	50.00	30.00	0.00	-	0.00
% Of lost territories taken by *P. tropheops* 'orange chest'	0.00	15.00	60.00	0.00	-
% Of lost territories taken by *P. tropheops* 'lilac'	0.00	5.00	0.00	0.00	28.57
% Of abandoned territories remained vacant	0.00	0.00	40.00	4.76	28.57

Table 3.15. Territory turn-over due to sixteen months removal of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' from a 7m x 7m quadrat at site # 3 (Fig. 3.1).

	Removed species		
	Cynotilapia afra	*Pseudotropheus callainos*	*P. troph.*'red cheek'
No. of territories occupied originally	28.00	42.00	12.00
No. of territories retained after removals	15.00	26.00	5.00
No. of territories lost after removals	13.00	16.00	7.00
% Of lost territories taken by *C. afra*	-	0.00	0.00
% Of lost territories taken by *P. callainos*	0.00	-	0.00
% Of lost territories taken by *P. tropheops* 'red cheek'	0.00	0.00	-
% Of lost territories taken by *P. zebra*	84.62	50.00	0.00
% Of lost territories taken by *P. tropheops* 'orange chest'	0.00	37.50	60.00
% Of lost territories taken by *P.* 'aggressive brown'	0.00	6.25	0.00
% Of lost territories shared by *P. troph.* 'orange chest' and *P. callainos*	15.38	0.00	0.00
% Of lost territories shared by *P. zebra* and *Petrotilapia nigra*	0.00	0.00	20.00
% Of lost territories remained vacant, used by non-territorial fish	0.00	0.00	20.00

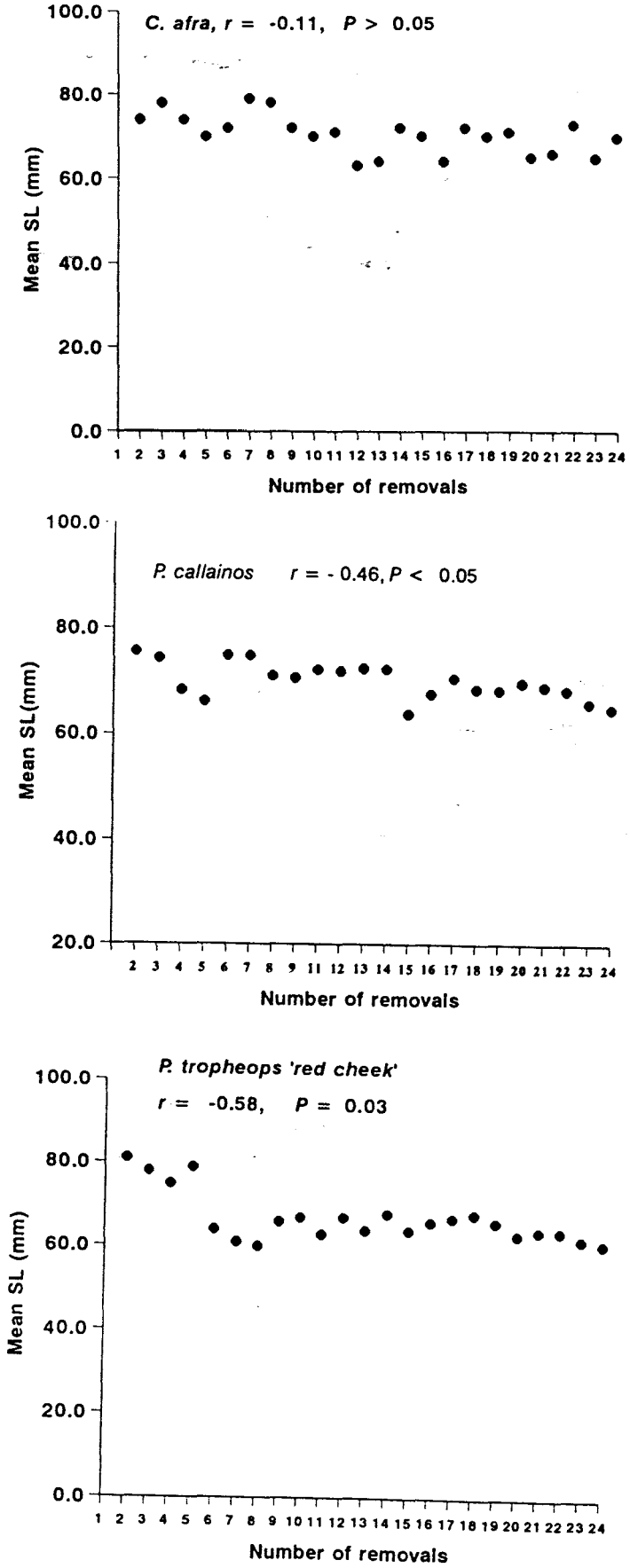


Fig. 3.19. The standard length of conspecific males that took over territories vacated by the introduced species that had been experimentally removed at Thumbi West Island, at site # 3.

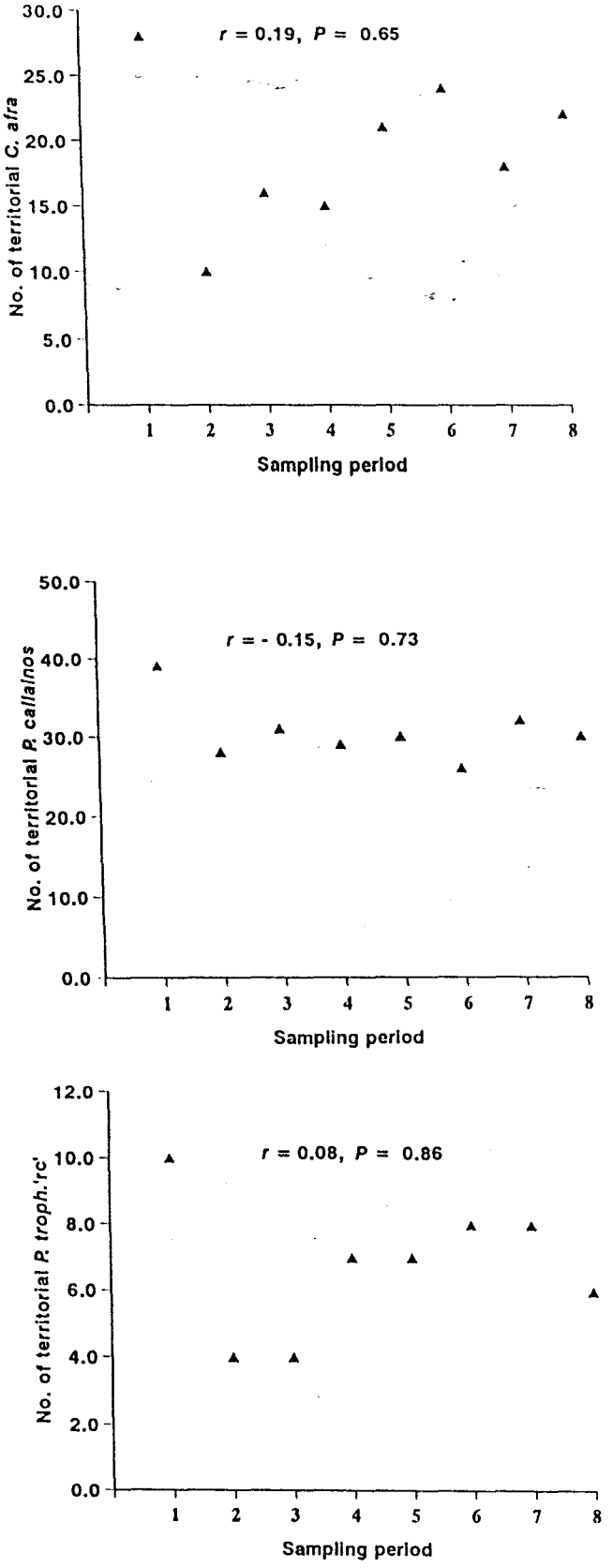


Fig. 3.20. Population trends of the remaining territorial males of the introduced species, *Cynotilapia afra*, *Pseudotropheops callainos* and *Pseudotropheus tropheops* 'red cheek' during the sixteen months period when they were being experimentally removed in a 7m x 7m quadrat at Thumbi West Island, site # 3. Sampling of the population of territorial males was done every four months.

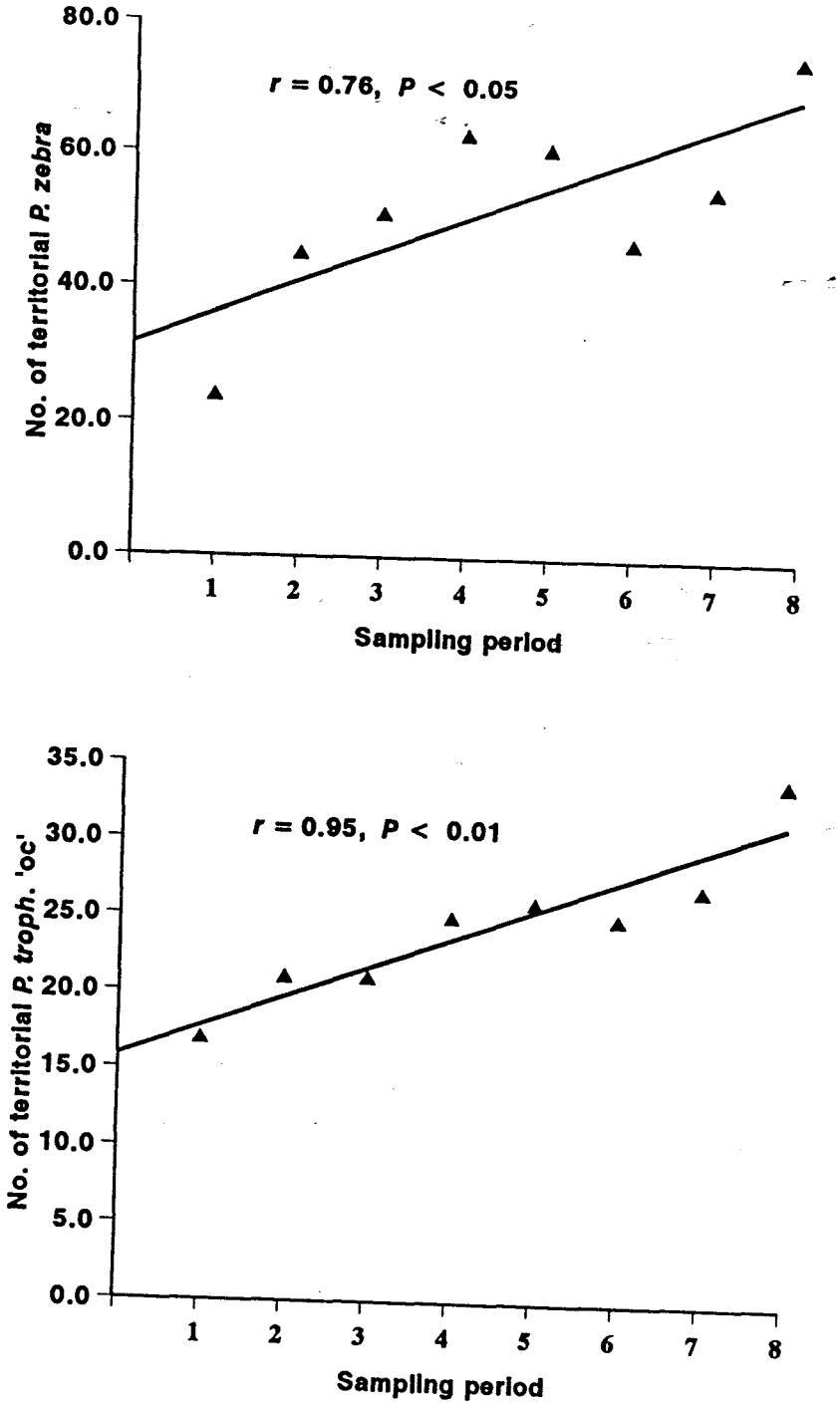


Fig. 3.21. Change in the population of territorial males of the native species, *Pseudotropheus zebra* and *Pseudotropheus tropheops* 'orange chest' after the removal of the introduced species, *Cynotilapia afra*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' in a 7m x 7m quadrat at Thumbi West Island, site # 3. Sampling was done every four months.

Discussion

Microhabitat preference

The Mbuna species of this study exhibit preferences for specific rocks and holes, or crevices among the rocks (Table 3.1, 3.2). Preference for specific microhabitats has also been observed in other fish families (Partridge 1978), marine invertebrates (Thorson 1950; Jones 1970), birds (Klopfer & Hailman 1965) and small mammals (Wecker 1963).

As with any phenotypic character, microhabitat preference could be transmitted from parents to offspring in a number of ways. For instance, it could be through inheritance which can be reinforced by exposure to particular microhabitats early in life (Wecker 1963; Alcock 1979; Partridge 1978), or particular microhabitats may be preferred because of food availability, or because such microhabitats confer higher reproductive success upon the occupants (Partridge 1978).

Every animal, or plant has a normal species-specific habitat tolerance range, and this defines the habitats occupied by the organism. In the case of Mbuna, which are mouth-brooders, inheritance and imprinted recognition of features of the areas in which they are bred and reared may partly contribute to their microhabitat preferences. For instance, in the Mbuna, once the young are released from the mother's mouth, they remain hidden in rock crevices, or holes within their mother's territories until they are large enough to avoid predators (Fryer & Iles 1972; Ribbink *et al.* 1983a). In achieving this, they probably become habituated to their mother's territories, and presumably that is why their microhabitat preferences remain identical to their parents.

Food availability, as a proximate factor influencing microhabitat preference may not be applicable to all Mbuna species. For instance, some of the Mbuna species of this study, *e.g.*, *C. afra, P. zebra* and *P. callainos* often feed away from their

territories (Fig. 3.8). Robinson (1995) also reports that some of the Mbuna species she studied at Thumbi East Island foraged outside their territories. This suggests that food resources within territories of these Mbuna species may be inadequate to sustain their requirements. Therefore, it is unlikely that their microhabitat choice could depend on food availability. However, the *Pseudotropheus tropheops* species, which selectively browse on epilithic algae, and have narrow dietary breadth (Table 3.5; Reinthal 1987) prefer large rocks probably because such rocks support higher food biomass. Indeed, as large rocks were occupied by large territorial males (Fig. 3.18), whose food requirements for maintenance may be high, it seems likely that the microhabitat choice by the *Pseudotropheus tropheops* species may be partly dependent on food availability.

The adaptive significance of microhabitat choice in relation to reproductive success was, however, seen in all the Mbuna that were studied, for which a hole or crevice among the rocks was an essential requirement for territories in which all spawnings took place. Also, since each species tends to be restricted within its preferred habitat in which mating partners are co-adapted (*sensu*, Paterson 1985; Ribbink 1988; Lambert 1984), aspects of the Mbuna's preferred microhabitats may be important components of their specific mate recognition system (SMRS). However, with regards to microhabitat choice based on reproductive success, males that occupied smaller holes or crevices mated more than those defending larger holes (Table 3.7). Among the sand-dwelling cichlids of Lake Malawi, females of *Cyrtocara eucinostomus* also preferentially mate with conspecific males that build the largest bowers (Mckaye *et al.* 1990). This suggests that females of these fish species discriminate among potential mates and base their choice of a mate at least partly on characteristics of the spawning site it defends. In other taxa, a number of studies have also shown that males with high quality territories, have access to more females, *e.g.*, in insects (Alcock 1987; Koenig 1990), birds (Armitage 1974; Lenington 1980; Carey & Nolan 1975; Johnson & Searcy 1993; Searcy & Yasukawa 1989) and mammals

(Dunbar & Roberts 1990; Carey 1991). The consensus in these studies is that the physical characteristics of the territory are of primary importance in female choice (*e.g.*, Bartholomew 1970; Miller 1975; Raugh 1985; Warner 1987).

In the Mbuna of this study, the reason for female's preference of males defending smaller holes, or crevices (Table 3.7) may be for safety against egg predation during spawning because specialised egg predators are ubiquitous over rocky areas in Lake Malawi (Ribbink *et al.* 1983a; Mckaye 1984) and egg predation by non-specialized Mbuna is common (Ribbink *et al.* 1983a). Therefore, by restricting spawning activities to smaller territorial holes, the female Mbuna minimise the risk of egg predation, and consequently, maximise their reproductive success. Similarly, males holding territories with small holes, or crevices maximise their fitness. Therefore, in terms of the Mbuna's microhabitat preference, the rocky substrate with smaller holes, or crevices, can be considered to be of high quality, or optimal, *i.e.*, areas in which individuals have the highest probability of propagating their genes.

The issue of territory quality can however, be clouded by the problem that in many species, it is the larger (and presumably, older) males which occupy the territories of high quality (*e.g.*, Davis 1978; Downhower & Brown 1980; Thornhill 1981). In the Mbuna species, *C. afra* and *P. zebra* Munthali (in press *a*) has shown that size *per se* may not influence the acquisition of a territory. He has suggested that priority residence effect, *i.e.*, dominance by the resident (Braddock 1949), aggressiveness, experience and motivation may be more important in the maintenance of high quality territories by Mbuna. Even among the *P. tropheops* species, whose larger males occupy larger rocks (Fig.3.17), the larger rocks were not necessarily associated with the smaller crevices which females preferred. What is probably happening is that the male Mbuna seeking territory sites initially have equal opportunities. However, for those that acquire optimal sites, the benefits of mating with gravid females, and/or access to exclusive food resources may create a strong incentive for them to exclude all

subsequent territory seekers, irrespective of size. Thus, knowledge of the resource value within the territory and prior residence may confer upon the territorial tenant a greater potential for dominance over intruders (*e.g.*, Krebs 1982).

Priority residence effect is a common phenomenon that has been documented in cichlids (Turner 1994) and other fish families (*e.g.*, Braddock 1949; De Boer & Heuts 1973; Brown & Green 1976; Figler & Einhorn 1983; Figler *et al.* 1986; Buchheim & Hixon 1992), amphibians (Wells 1977; Stewart & Rand 1991; Baugh & Forester 1994), birds (Sandwell & Smith 1991) and insects (Davies 1978; Hoffman 1987; Waage 1988; Englund & Otto 1991).

Overlapping microhabitat preferences

Some introduced and native Mbuna species overlap in the microhabitats they occupy (Table 3.1, 3.2). However, despite their identical microhabitat preferences, direct interference between them, in terms of trophic ecology, was not apparent. For instance, the introduced and native Mbuna species of the small rock guild, *i.e.*, *C. afra*, *P. zebra* and *P. callainos* are ecologically separated by feeding at different heights in the water column and they feed at different sites with different intensity (Fig. 3.7a-d). Even when they interspecifically overlap while feeding in the water column, they do so without being antagonistic towards one another. Similarly, the introduced species, *P. tropheops* 'red cheek' and native species, *P. tropheops* 'orange chest', which occupy large rocks scarcely interfered with one another's feeding activities because their territories were often far apart.

Also, *P. tropheops* 'orange chest' predominantly feeds on the epilithic algae, Calothrix (Reinthal 1987), while *P. tropheops* 'red cheek' predominantly feeds on Oscillatoria and Cladophora (Table 3.5). Therefore, direct competition between these Mbuna species may also be ameliorated by preferentially feeding on different food items.

However, despite the apparent segregation with respect to feeding, all the Mbuna species of this study exhibited intra- and interspecific aggression towards their territorial intruders.

Intraspecific aggression

The functional significance of intraspecific territorial aggression has been the subject of considerable reviews (*e.g.*, Noble 1939; Orians & Willson 1964; van den Assem 1967; Murray 1971; Rice 1978). The concensus in these reviews is that intraspecific aggression serves to increase reproductive success and access to food resources by the territorial owner. In the Mbuna species of this study, the link between intraspecific aggression and reproductive success was seen in all of them. These Mbuna species exhibited the highest level of aggression towards conspecific intruders during the peak breeding months, and/or during the months preceding their breeding peaks (Fig. 3.13a & b; also see chapter 2 for these fishes breeding peaks). Diurnally, *C. afra*, *P. zebra* and *P. callainos* were also most aggressive towards conspecific when they engaged in active courtship behaviour (Fig. 3.11a). The conspecific intruders attacked included females, sympatric territorial neighbours when they were competing for gravid females and supernumerary adult sexually active males which did not hold any territory. Since in Mbuna only males holding territories are capable of breeding (Fryer & Iles 1972; Ribbink *et al.* 1983a), and as the key to a male's genetic success generally lies in securing opportunities to fertilize a female's eggs (Alcock 1979), by excluding conspecific males from breeding, territorial owners increase their potential to contribution to their population gene pools of the future.

Securing food as suggested by Orians & Willson (1964), and others is however, unlikely to be the primary function of intraspecific territorial aggression. In the case of Mbuna, *C. afra*, *P. zebra* and *P. callainos* often feed outside their territory holdings (*c.f.*, Robinson 1995), implying that food in the territories of these Mbuna species may not be adequate at all times. Also when they

temporarily abandon their territories, other fishes, including conspecific, feed in the temporarily vacated territories (Fig. 3.8). Furthermore, Munthali (in press *a*) has shown that territorial *C. afra* and *P. zebra* were nutritionally in worse condition than conspecific non-territorial males. He has suggested that the biological significance of territoriality in some Mbuna species may be mate attraction and reproductive success for which they may trade-off their nutritional condition. Nevertheless, in other Mbuna, particularly those that prefer large rocks, the role of intraspecific aggression in securing food resources was quite apparent, as discussed earlier in this chapter. Both sub-adult and adult males of *P. tropheops* 'orange chest and *P. tropheops* 'red cheek' were seen defending territories (*c.f.*, Sharp 1981), and since they hardly leave their territories, all their food requirements have to be met within these territories. Therefore, it would be advantageous for these Mbuna to defend food resources against intruders in order to meet their own nutritional needs.

Intraspecific territorial aggression may also facilitate the species range expansion (Immelmann 1980; Branch 1984; Robinson 1985). The argument presented is that intraspecific aggression may facilitate dispersion of surplus individuals of a species when population density in a particular habitat has increased to the point where pressure is placed on its carrying capacity. At Thumbi West Island, optimal territory sites seem to be limited, as evidenced by the frequent replacement of vacated territories by conspecific males in the removal experiment (Table 3.15). For supernumerary males to reproduce, they have to either wait for territory vacancies when the occupants die, or when occupants vacate their territories due to other reasons. However, such opportunities may be rare, therefore, the best option available to the floating males may be to seek alternative sites, irrespective of whether such sites are optimal or not. This may be one of the ways introduced species have spread around Thumbi West Island (chapter 4). There are also instances where some individuals of the introduced Mbuna species have occupied marginal microhabitats because optimal sites are either taken by conspecific males, or by native species with similar microhabitat

requirements.

Immelmann (1980) suggested that intraspecific territorial aggression may also promote sexual selection in which the strongest and "healthiest" individuals may be selected for reproduction. In Mbuna of this study, this aspect was not assessed, but it is probable that the individuals that mated successfully (Table 3.6) were the strongest as they were capable of sustaining intensive competition for optimal territory sites.

Interspecific aggression

The evolutionary significance of interspecific territorial aggression has been subjected to controversial debate, particularly among the avian ecologists (*e.g.*, Orians & Willson 1964; Murray 1971; Rice 1978). One of the popular arguments presented is that interspecific aggression is a transitory phase in the divergence of similar (often sibling) species, or that it is a case of "mistaken identity", in which the species chased somehow resembles a conspecific intruder sufficiently enough to elicit a misdirected territorial response (Murray 1971). However, against Murray's hypothesis, there is a lot of evidence which suggests that interspecific aggression can be a normal and vital part of the territorial behaviour in birds (Orians & Willson 1964; Cody 1969), coral reef fish (Clarke 1970, 1971; Low 1971; Colin 1971; Myrberg 1972, 1973; Myrberg & Thresher 1974; Sale 1975) and, in the fish of the African Great Lakes, *e.g.* Mbuna of Lake Malawi (Fryer 1959; Fryer & Iles 1972; Holzberg 1978; Marsh 1981; Sharp 1981; Ribbink *et al.* 1983a; Hert 1990; Robinson 1995), and fish of Lake Tanganyika (Kohda 1991).

The counter-argument to Murray's hypothesis has been (i) that there are often significant differences in size, behaviour and coloration of intruders attacked, *e.g.*, in the coral reef fish (Low 1971; Myrberg & Thresher 1974; Itzkowitz 1974; Ebersole 1977; Mahoney 1981), hence making it unlikely that interspecific aggression results from mistaken identity. (ii) That the great phenotypic

differences among the intruding species may reflect differences in the resources they attempt to utilize from the defended territories (Itzkowtz 1990). The resources most sought after and defended against heterospecific intruders include:

(a) Food, particularly when the territory occupant and intruders have overlapping dietary requirements, *e.g.*, in birds (Orians & Willson 1964), amphipods (Connell 1961; Stimpson 1970, 1973; Branch 1985), coral reef fish (Low 1971; Myrberg & Thresher 1974; Thresher 1976; Ebersole 1977), and in the Lake Malawi's herbivorous Mbuna (Sharp 1981).

(b) Eggs, or fry, *e.g.*, in coral reef fish (Albrecht 1969; Clarke 1970; Keenleyside 1972; Thresher 1976; Ebersole 1977; Itzkowitz & Mahie 1986), and in Lake Malawi cichlids (Mckaye 1984, 1990; Robinson 1995 - *e.g.*, guarding of fry by *Protomelas taeniolatus* females).

(c) Shelter holes, *e.g.*, in coral reef fish (Mckaye 1977; Greenfield & Greenfield 1982; Shulman 1985; Hixon & Beests 1989; Clarke 1989; Hixon 1991; Buchhein & Hixon 1992).

(d) Spawning sites that are attractive to conspecific females (*e.g.*, Alcock 1987) and in Lake Malawi cichlids (Fryer & Iles 1972; Mckaye 1984, Mckaye *et al.* 1990; Robinson 1995).

However, as a single territory may harbour more than one of these resources, the adaptive significance of interspecific territorial aggression is likely to be multifunctional. Some studies give convincing evidence, or suggest that this may be the case *e.g.*, in coral reef fish (Myrberg & Thresher 1974; Thresher 1976, 1977; Ebersole 1977), and in Lake Malawi cichlids (Ribbink *et al.* 1983a; Robinson 1995).

Given a variety of intruding species, with each preferring a different resource within the territory, each intruder is expected to be attacked relative to the presence of its own preferred resource within the territory, and its ability to utilize that resource (Itzkowitz 1990). In the Mbuna of this study, the frequency

of interspecific attacks were positively correlated with the population density of the intruders (Fig. 3.15). Thus, as the population increases, the probability of encounters between intruders and territory occupants increases, hence the frequency of interspecific attacks also increases. However, some of the species that were attacked as a result of their abundance may not necessarily be the ones that pose serious threats to any territory resources. Similarly, the species that were chased with relatively low frequency (Fig. 3.16) may have been attacked, simply as incidences of random encounter between them and the territory tenants. Also, the possibility of mistaken identity (*e.g.*, Murray 1971) as the cause of the observed interspecific aggression in the Mbuna seems remote because a high diversity of fish species (Fig. 3.16) with different colours and morphology (see Ribbink *et al.* 1983a for these differences) were attacked. Nevertheless, among the Mbuna that prefer small rocks, the most numerous species were sometimes those that also overlap most with the territory occupants in microhabitat requirements (Table 3.1, 3.2; Fig. 3.15). Therefore, both population density and the degree of overlap in microhabitat requirements seem to stimulate interspecific aggression in the Mbuna of this study.

What is at stake in the Mbuna community is the requirement for the males to establish territories in which to breed, feed and seek shelter. However, of great importance among these, is the need for them to locate and defend optimal sites in which males are capable of attracting females of their species, in order to breed and contribute to the gene pools of the future generations. And, since only males that have territories are capable of breeding (Fryer & Iles 1972; Ribbink *et al.* 1983a; Hert 1992), there is a high premium on optimal territory sites among the Mbuna with identical microhabitat requirements. This is clearly reflected in the high attack frequencies between species with similar microhabitat requirements, *e.g.*, between the introduced species, *C. afra* and the native species, *P. zebra*, between the introduced species, *P. callainos* and its congeneric native species, *P. zebra* and also between the introduced species *P. tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest'

(Fig. 3.15a-e & Fig. 3.16a-e). However, among these species, *C. afra* and *P. zebra* were the most antagonistic towards each other, and were both capable of taking over the territory of the other (Table 3.14). Similarly, in the removal experiment, most territories vacated by *C. afra* were recolonised by *P. zebra* (Table 3.15). Besides *C. afra* and *P. zebra*, other species with identical microhabitat requirements, *e.g.*, *P. callainos* and *P. zebra*, and *P. tropheops* 'orange chest' and *P. tropheops* 'red cheek' (Table 3.1, 3.2) also naturally reoccupied each other's territories (Table 3.14). The actual mechanism through which such natural interspecific territory turn-over takes place was not ascertained in this study, but it can be suggested that it happens:

(i) By displacement through confrontation by a stronger conspecific or heterospecific intruder. Only one such displacement was observed during the study period when a *P. tropheops* 'red cheek' male was ousted by a conspecific male. It is likely that many similar displacements take place among conspecific and heterospecific with similar space requirements, particularly if the contender is larger than the territory occupant. Territory acquisition by winning contests has been reported in a number of studies (*e.g.*, Maynard Smith & Parker 1976; Krebs 1982; Maynard Smith 1982; Enguist & Leimer 1983; Grafen 1987; Stamps & Krishnan 1994), and size discrepancy between the intruder and the territory occupant may be important in determining the outcome. For instance, Turner (1994) in his laboratory study of resident-intruder contests of the cichlid fish species, *Oreochromis mossambicus* found that resident territorial males often defeated intruders. But intruders were more likely to win when size discrepancies between residents and intruders were large.

(ii) By taking over territories that are temporarily vacated by the tenants when they feed far from their terrirories. Temporary territory abandonment often happens during the upwelling season when many territorial Mbuna, particularly, *C. afra*, *P. callainos* and *P. zebra* feed on the phytoplankton in water column for extended periods, sometimes for

more than two hours (pers. obs.). During such out-of-sight forays, supernumerary competitors of conspecific and heterospecific have opportunity to occupy the temporarily vacated territories. It is probable that it is at this time of the year that much of the natural interspecific territory turn-over takes place. Hert (1992), in her homing experiment of the Mbuna species, *Pseudotropheus aurora* found that the chance of a removed territorial male regaining its territory decreased with time of absence because conspecific males reoccupied the vacated territories. In the Mbuna of this study, it is also likely that some of the territories temporarily vacated by the occupants during the upwelling season may have been recolonised by conspecific males, but they could not be distinguished because the original territorial males were not marked.

Also, the Mbuna that leave their territories and feed high in the water column are more vulnerable to predation and illegal fishing. Thumbi West Island harbours predatory birds, such as African Fish Eagle, *Haliacetus vocifer*, White Breasted Cormorant, *Phalacrocorax carbo* and Pied Kingfisher, *Ceryle rudis*. These birds often catch Mbuna when they feed high up in the water column (pers. obs.). Similarly, illegal fishermen sometimes haul in their nets along the rocky shore and catch Mbuna when they are feeding in the water column. This has been confirmed by Smith (1993) who reports of Mbuna species being found in fish landings in Chembe, one of the enclave villages in Lake Malawi National Park. It is therefore, probable that some of the territorial Mbuna are taken by either predators or illegal fishermen, hence creating vacancies for conspecific and heterospecific with requirements similar to the original occupants.

(iii) By intruder persistence. As the population density of contesting males seeking territorial space increases, repeated intrusion could invariably increase the cost of territorial defence. The cost could be in the form of injury to the territory occupant, which could consequently cede space to competitors. During the study period, some of the supernumerary males

had injured lips and broken teeth, particularly among *C. afra* males, suggesting that they were once territorial, but probably they relinquished their territoriality because of repeated intrusion and injury. It can, therefore, be suggested that in the Mbuna, subordinates probably win space by persistently intruding into the occupied territories, until the strength of some occupants to defend their territories wears out. Persistence is important in territory acquisition, and it has been implicated in many territorial contest studies (*e.g.*, Nolan 1978; Yasukawa 1979; Patterson 1980; LaPrade & Graves 1992; Walton & Nolan 1986; Arcese 1987; Beletsky & Orians 1987; Eckert & Weatherhead 1987; Stutchbury 1991; Stamps & Krishnan 1995).

(iv) Nutritional constraints may impose a threshold below which the costs of maintaining territoriality may out-weigh the benefits of mate acquisition and other associated merits of territoriality. Consequently, territorial males in poor condition may abandon their territories in order to regain their condition. In *C. afra* and *P. zebra*, (Munthali, in press *a*) has shown that territorial males are disadvantaged by feeding over smaller areas, spend less time feeding, and consequently are in worse condition than the conspecific non-territorial males. Similarly, in *Oreochromis mossambicus*, maintenance of reproductive territories in aquaria results in the reduction of growth and eventual displacement of territorial males (Turner 1986). In the Mbuna of this study, nutritional constraints may also force some territory occupants to abandon territoriality, particularly in areas where the population of intruders is numerous and the energetic cost of defence may also be high. Consequently, this would open up vacancies for the conspecific and heterospecific non-territorial males. Abandonment of territories due to nutritional constraints may be high in the Mbuna that prefer small rocks, because they are restricted within smaller territories (Table 3.11), and it is unlikely that food is always adequate within their territories. Among the Mbuna that prefer large rocks, there was a high rate of territory abandonment (Table 3.14), probably in favour of larger

rocks on which they could obtain an adequate food supply.

Seasonal fluctuations in the territory sizes

Territories in which the individual Mbuna species of this study had site-specific dominance fluctuated seasonally (Table 3.11), but these fluctuations were significant only for the territories held by *P. callainos* and *P. zebra*. In many vertebrates, territory size fluctuations have been attributed to changes in their own population density and/or fluctuations in resource availability, *e.g.*, in fish (van den Assem 1967), birds (Ickes & Ficken 1970; Krebs 1971; Carpenter & MacMillan 1976) and amphibians (Simon 1975). Huxley (1934) assigned the term "rubber disc" to this type of territoriality, which permits the compression of territory size within limits to accommodate additional territory holders.

Koenig (1990), on the other hand, noted that the proximate determinants of territory size and duration of occupancy include territory quality, competition from intruders and neighbouring individuals and individual variation in competitive ability.

At Thumbi West Island, the population density of non-territorial intruders fluctuates seasonally (Fig. 4.3, chapter 4), and this seems to have an effect on the size of territories which Mbuna of this study could seasonally defend. Two important events may contribute to the seasonal fluctuation in population density of non-territorial fish in the 3 - 7m depth of the rocky habitat at Thumbi West Island: (a) Lake Malawi drops to its seasonally lowest water level during the stratified season, particularly, in November, by about 1 - 2 meters (Eccles 1984). Consequently, the fish that naturally live in the shallow water are compressed in lower depth zones, thereby increasing the number of fish foraging in the 3 - 7 meter depth zone. (b) Also, during the stratified season, primary production and food availability may be limited in Lake Malawi (Eccles 1974; Twombly 1981; Haberyan & Mhone 1991; Bootsma 1993a, 1993b). Therefore, there is a high probability that pressure on food resources might be high. Consequently,

most non-territorial fish forage over large areas in order to meet their requirements (pers. observ.). But by doing so, the rate of encroachment into defended territories and the frequency of attacks by territory tenants also increases (Fig. 3.16a-e).

However, since territorial defence is expensive in terms of energy, time engaged in chasing intruders and associated risks of injury (Brown 1964; Stamps 1977; Kodric-Brown & Brown 1978; Alock 1979; Wyman & Hotaling 1988), the size of a territory can be adjusted to minimize the cost/benefit ratio of territoriality (Koenig 1990). Therefore, it is not surprising that some of the Mbuna that were studied defended smaller territories during the stratified season (Table 3.11), when the density of intruders was highest. However, some of the Mbuna maintained inflexible territories (Table 3.11), suggesting that they were more vigilant in defending their territories. Also, it may imply that the territory sizes they maintain are optimal for their reproductive success and survival.

Also notable was the fact that the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' at Thumbi West Island defend smaller territories than conspecific in the northern Lake Malawi, where they originated. Two factors may be attributed to this disparity. (i) The population density of Mbuna in the northern Lake Malawi is generally lower than at Thumbi West Island (Ribbink *et al.* 1983a; also see chapter 2), hence territorial males in the northern Lake Malawi may be less constrained by density-dependent factors in establishing and defending territories. (ii) Since food may be more limited in the northern than southern Lake Malawi (Eccles 1974; Beadle 1981), territorial males probably defend larger territories in order to sustain their food requirements.

The impact of introduced Mbuna species on the native rock-dwelling cichlid species

The most obvious impact discerned in this study is that of interference

competition for optimal sites between the introduced and native species having similar microhabitat requirements. Among these species, the introduced species, *C. afra* and native species, *P. zebra* compete more intensively. This is supported by the following:

(i) *C. afra* and *P. zebra* strongly overlap in their requirements for rocks (Table 3.1) and holes (Table 3.2) they occupy;

(ii) they are staunchly aggressive towards each other (Fig. 3.16a & c);

(iii) they also naturally reoccupy each other's territories, and it appears *C. afra* dominates in taking over territories from *P. zebra* (Table 3.14); and (iv) the population of *P. zebra* increased significantly (Fig. 3.21) after some introduced species were removed from the experimental quadrat.

Similarly, an introduced species, *P. tropheops* 'red cheek' and its congeneric native species, *P. tropheops* 'orange chest' compete for rocks (Table 3.1) and crevices of similar size, and they are also antagonistic towards each other (Fig. 3.16d & e). However, *P. tropheops* 'orange chest' executed more attacks at *P. tropheops* 'red cheek' than vice-versa (Fig. 3.16d & e). *P. tropheops* 'orange chest' also naturally took over more territories that were originally occupied by *P. tropheops* 'red cheek' (Table 3.14) and where some introduced species were experimentally removed, it occupied 60% of the territories vacated by *P. tropheops* 'red cheek' (Table 3.15).

Another introduced species, *P. callainos*, on the other hand, seems to be fairly well integrated within the native Mbuna community at Thumbi West Island. It is the least aggressive towards heterospecific native species (Fig. 3.16b), and its ability to overlap its territories with a native species, *P. zebra*, may reduce the energetic costs, time and other risks associated with the defence of exclusive territories. However, since it also overlaps with *P. tropheops* 'orange chest' in its preferred holes, or crevices (Table 3.2), and also with *C. afra* in the rocks it occupies, it does experience some competition from these species. This is

bolstered by the facts that:

(i) it was the second most attacked species by both *C. afra* and *P. tropheops* 'orange chest' (Fig. 3.16a & e);

(ii) about 40% and 10% of the territories originally occupied by *P. callainos* at site # 5 were taken over by *C. afra* and *P. tropheops* 'orange chest', respectively (Table 3.14), whereas,

(iii) in the quadrat where some introduced species were removed, 37.5% of *P. callainos*'s territories were taken over by *P. tropheops* 'orange chest' (Table 3.15).

Competition is likely to play different roles depending on whether the limiting resource is food, or space (Branch 1984, 1985). Food is self-renewing, it may regenerate relatively quickly, and it is a relative requirement, as most organisms can share food without necessarily leading to exclusion (Branch 1984, 1985). This seems to be the case among the Mbuna of this study, in which the impact of introduced species on native taxa, or vice-versa, in terms of trophic ecology was not apparent. Probably direct competition between them does not take place because they feed in different sites with different intensity and they feed at different heights in the water column (Fig. 3.7a-d). When feeding on phytoplankton in the water column, introduced and native species overlap interspecifically without any noticeable antagonism between them (pers. obs.). This is probably because phytoplankton availability in Lake Malawi is unpredictable, and subjected to fluctuations in its abundance (Twombly 1983), therefore, it may not be economically defensible (Robinson 1995). The introduced species, *P. tropheops* 'red cheek' does, however, monopolise food within its exclusive territories, and some of its vacated territories were used by non-territorial fish (Table 3.14, 3.15) for feeding. But it is unlikely that the fish that are denied access to the food controlled by *P. tropheops* 'red cheek' may be nutritionally disadvantaged. On the contrary, in some Mbuna species non-territorial males, which normally forage over large areas, may be in better condition than territorial males, which often feed in restricted territories

(Munthali, in press *a*). Therefore, it is doubtful that any native species could be driven to extinction as a result of competition for food between the introduced and native Mbuna species at Thumbi West Island.

On the other hand, competition for breeding space, which is an absolute requirement for an organism to contribute to future gene pools, could have more profound effects because space does not multiply and it is not self-renewing (Underwood 1978, 1979; Branch 1984, 1985). Thus, space held by an organism remains unavailable to another, until the occupant dies, is ousted or relinquishes that space (Branch 1984, 1985).

In Mbuna, optimal sites within the rocky shore where individuals can successfully reproduce, are obviously limited. Evidence in support of this include:

(i) the persistent reoccupation of vacated territories by conspecific males where some introduced species were removed (Table 3.15);

(ii) an increase in number of territorial males of some native species after the removal of introduced species which have similar space requirements as the removed introduced species (Fig. 3.21); and

(iii) there are large numbers of adult supernumerary males of various species around Thumbi West Island (pers. obs.), presumably seeking optimal sites on which to establish territories. This shows that territoriality in Mbuna restricts breeding to territory owners. Similar behaviour has been observed in birds (*e.g.*, Southern 1970) and insects (*e.g.*, Whitham 1979).

It is also possible that some of the native Mbuna species excluded by the introduced species have been forced into sub-optimal habitats. A case in point is *P. zebra* at sites # 1 & 10 (Fig. 3.1), where some territorial males have occupied territories subjected to sand wash when the lake is rough. Consequently, territorial holes are sometimes filled with sand. This prompts males holding these territories to orally remove sand from their territories. If

optimal territory sites were readily available, these males could have opted to vacate their sand tormented territories in favour of better sites. Also, the occurrence of large numbers of *P. zebra* in areas dominated by large rocks (Table 3.3), suggests that many individuals of this species are forced to establish territories in marginal habitats, probably as a result of increases in the number of its own members, or an increase in the population density of an introduced species, *C. afra*, with which it competes for similar microhabitats.

Similarly, as already noted in this chapter, an introduced species *P. tropheops* 'red cheek', which prefers sediment-free large rocks (> 65 cm diameter) (also see Ribbink *et al.* 1983a), was seen at site # 1 (Fig. 3.1) defending smaller rocks interspaced by sand, suggesting that introduced species also face tougher competition from the native species, and in this particular case, from *P. tropheops* 'orange chest'.

Overall, therefore, results of this study suggest that where introduced species occur in large numbers, they may limit the population size of the territorial native species with which they overlap in microhabitat requirements, by occupying space which could otherwise be used by such native species. However, for any impact to deserve management intervention, it should be demonstrated that it would lead, in the long-term, to population limitation, or extinction of some of the native fish species at Thumbi West Island.

Introduced species have been at Thumbi West Island, probably for more than twenty years. The impacts they have had throughout these years on the native taxa is unknown. However, results of this study, suggest that the presence of the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' may not drive any of the native species with which they were compared into extinction. The facts in support of this view are as follows:

(i) There is considerable natural interspecific territory turn-over between the introduced and native species with similar microhabitat requirements

(Table 3.14). Thus, the population of males holding territories at any particular time fluctuates in response to these interspecific territory rotations. In terms of numbers of territorial males, none of the introduced species maintained constant dominance, because some of their territories were reoccupied by the native species. Therefore, some of the displaced native species manage to occupy and defend optimal sites, and have the opportunity to contribute to their population gene pools. Factors that may lead to the abandonment of territories have been discussed in this chapter.

(ii) Even in situations where a native species was observed in an area that was generally sub-optimal, it managed to occupy patches of suitable sites, and was capable of breeding. A good example is *P. zebra* which although it prefers areas predominated by small rocks ($\leq$ 65 cm), it also bred fairly well in areas predominated by large rocks (Table 3.6). Therefore, it is unlikely that its competition with *C. afra* would significantly reduce its reproductive success, or drive it into extinction.

(iii) The Mbuna breed throughout the year (Fryer & Iles 1972; Ribbink *et al.* 1983a; Marsh *et al.* 1986; also see chapter 2 of this thesis), and since males of these fishes are polygamous, and have intraspecific shared paternity (Fryer & Iles 1972; Ribbink *et al.* 1983a), males are capable of fertilizing many gravid females of their own species in a year. Therefore, the presence of introduced species may not detrimentally limit the population of native species at Thumbi West Island.

(iv) The native species, *P. zebra* and *P. tropheops* 'orange chest' which significantly increased in numbers after the removal of some introduced species (Fig. 3.21) are abundant and widely distributed at Thumbi West Island and in the Lake Malawi National Park as a whole (Ribbink *et al.* 1983). *Pseudotropheus zebra* also occurs in large numbers outside the park, and has a wide distribution in Lake Malawi as a whole, although there are some geographic variations (Ribbink *et al.* 1983a). Therefore, *C. afra* which competes with it for the same microhabitats is not a serious

threat to its continued existence.

(v) Even the ecological release (*sensu* Fausch & White 1981) exhibited by some native species, notably the non-territorial fishes that fed in the vacated territories after the removal of introduced species (Table 3.15), did not provide enough evidence that they might be deprived nutritionally as a result of the presence of introduced species. Non-territorial Mbuna are not as sedentary as territorial Mbuna, therefore, they are capable of searching for vacant spaces in which to feed.

(vi) Not all the interactions between the introduced and native species were negative. Certainly, the mutual defence of territories by an introduced species *P. tropheops* 'red cheek' and females of a native species, *Protomelas taeniolatus* that were guarding fry, is of greater benefit to the latter. *Pseudotropheus tropheops* 'red cheek' is a staunch territory defender. Therefore, by guarding fry in its territory, *P. taeniolatus* may have a high probability of protecting its fry from predators. This may also reduce the fry defense costs, consequently, *P. taeniolatus*'s feeding opportunities may increase. Even females that did not have fry often fed in territories defended by *P. tropheops* 'red cheek' males. It is not known why *P. taeniolatus* females are tolerated by *P. tropheops* 'red cheek' which is very aggressive. But I suspect that such behaviour could have developed as a result of *P. taeniolatus*'s persistent encroachment into *P. tropheops* 'red cheek's' territories, probably because these two species coincidentally have similar rock preferences. This is likely to be the case because there were also incidences when *P. taeniolatus* females were attacked by *P. tropheops* 'red cheek' (Fig. 3.16d), but they persistently returned and fed in territories defended by *P. tropheops* 'red cheek'. Low dietary overlap between them (Table 3.4) may also facilitate their coexistence in the same territories.

Culling as a possible management option

In terrestrial parks, culling is effective in the management of populations of large mammals that over-shoot their habitat thresholds. Examples of culling in terrestrial parks, include: Hippopotamus, *Hippopotamus amphibius* in Uganda (Blower & Brooks 1963) and Zambia (Steel 1967), Kob, *Adonota kob* in Uganda (Blower & Brooks 1963), Elephant, *Loxodonta africana* in Kenya (Simon 1963) and Zambia (Hanks 1979), Nyala, *Tragelaphus angasi* and Warthog, *Phacochoerus aethiopicus* in Malawi (Munthali & Banda 1985) and other ranching projects in Zimbabwe and South Africa (Riney 1963; Pollock 1969). However, in aquatic parks culling has not been used to regulate fish populations.

The most important merit that culling would have in the Lake Malawi National Park is the reduction in population size of members of introduced species whose loss could result in the increase of those native species which have similar microhabitat requirements as the culled introduced species. At least, the native Mbuna populations could increase to some degree (Fig. 3.21). Also, non-territorial native fish would have the opportunity to feed in the vacated territories previously occupied by the alien taxa (Table 3.15). However, where introduced species are involved, culling should be adopted as a management option only once it is apparent that without culling one or more of the fishes endemic to the Lake Malawi National Park would be driven to extinction.

This study has shed light on competition between the introduced and native species for territorial space and changes that take place after removal of introduced species in the rocky zone at three to seven meters depth. In this zone, the native species that are affected by introduced species are common and some have a wide distribution in the park, and Lake Malawi as a whole, so they are not in any immediate danger. However, the natural structure of the community may have changed as a result of the presence of alien species from elsewhere in the lake, and it may be probable that their presence may have subtle long-term

effects. Also, the use of space by the young of introduced and native species has not been assessed. But there is a high probability that competition for space among the young of these Mbuna takes place. In chapter 2 of this thesis, it has been shown that some of the introduced species have their breeding peaks preceding the breeding peaks of the native species. Thus, the introduced species may have an advantage of first recruiting their young in optimal habitats where their offspring may have priority in the use of optimal refuge space and food over the offspring of the native species, which are recruited later in the year. Therefore, there is a need for further studies to focus on the young of the introduced and native Mbuna in the Lake Malawi National Park.

Introduced species also occur in the shallow and intermediate zones. It is imperative, therefore, that work on the entire rocky shore communities at Thumbi West Island should be carried out to the point where the impact of the introduced species on the entire native Mbuna community in the park is fully understood before culling can be adopted as a management tool. Park management programmes should, however, aim at restricting further translocation of the introduced Mbuna to other islands which are currently free of such species.

Chapter 4

Abundance and Distribution of the Introduced Rock-dwelling Cichlid Species Around Thumbi West Island, Lake Malawi National Park, Malawi

Introduction

The extent to which introduced Mbuna species occur in Lake Malawi National Park has been reported by Ribbink *et al.* (1983a) and around Thumbi West Island by Trendall (1988a). The aim of the study reported in this chapter was to compare the population density of introduced and native species. The primary objectives were: (i) to find out the distribution pattern of the introduced species around Thumbi West Island, and (ii) to find out if an increase in population density of the territorial males of introduced species corresponded with a decrease in the number of territorial males of native species, and if so which species. It was assumed that for the introduced species to have a negative impact on the native taxa, the increase in number of their territorial males should correlate with a decline in number of territorial males of some native Mbuna species, particularly those that have similar microhabitat requirements as the introduced species. The introduced and native species that have similar microhabitat requirements have been identified in chapter 3 of this thesis.
(iii) The secondary objective was to monitor the population of non-territorial fishes during the upwelling (May - August), transition (September - October) and stratified seasons to find out if there were changes in their numbers. This information was particularly important in deducing the reasons some of the Mbuna species defended seasonally fluctuating territories (see chapter 3).

Methods

The population of introduced and native species was monitored at ten sites, in the 3 - 7m depth zone (see Figure 4.1). At sites, #: 1, 2, 4, 5, 7, 8, 9 and 10, 7m x 7m quadrates were established, while at sites, T1 and T2, permanent transects, 2m x 25m were established. These sites have been classified into two categories, *i.e.*, small and large rocks in chapter 3 of this thesis.

Monitoring of the populations of the introduced and native species was done

quarterly by means of SCUBA. Counts in established quadrates were done by laying line transects over the 7m x 7m quadrats. Two 6mm diameter nylon cords, 10m in length, held two meters apart by a galvanized pipe at each end were used. Thus, each quadrat was subdivided into three roughly equal compartments (*sensu*, Ribbink *et al.* 1983a). Counts in permanent transects were also done by laying two 6mm diameter nylon cords, 25m in length, held two meters apart by a galvanised pipe (as shown in Fig. 4.2). Fishes within the demarcated areas of the quadrat were counted after they had recovered from the diver's disturbance while laying the transects. These fishes were counted nine times and their mean numbers were divided by the quadrat size to give the population density of territorial males of each species. In the transects, individual species were counted three times, and their mean numbers were diveded by the transect size to give the population density of territorial males of each species.

The sampling period was correlated with the population size of the territorial Mbuna occurring at each study site to find out if there was a significant change in the population size of the introduced and native species.

Fig. 4.1. Map of Thumbi West Island, showing sites at which the population of introduced and native rock-dwelling cichlid species were monitored. Site *F* is the point at which the species translocated from the northern part of Lake Malawi were introduced. The quadrat at site number 6 was stolen, consequently, it was abandoned. Site number 3 has also been excluded on this map because the populations of Mbuna species at this site were manipulated by the removal experiment, see chapter 3 of this thesis.

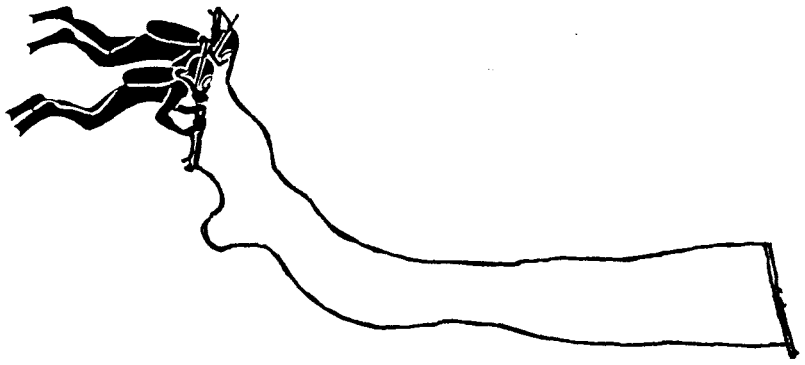


Fig. 4.2. An illustration of how a 25 x 2m transect was laid when counting fish at some permanently marked sites around Thumbi West Island, where the population of the introduced and native rock-dwelling cichlids were monitored.

Results

The population density of introduced Mbuna species is skewed, *i.e.*, it is much higher at sites, #: 3, 4 & 5, which are closer to where they were introduced (site *F*, Fig. 4.1), and lowest at sites farthermost from it, *e.g.*, sites, #: T1 and T2 (Fig. 4.1; Table 4.1). Also, there are interspecific differences in the rate of dispersal among these Mbuna. At the beginning of this study in August, 1992, there was no *C. afra* at some of the farthermost sites away from the site of introduction, such as at sites, #: T1 and T2. Similarly, *P. tropheops* 'red cheek' did not occur at sites, #: 7, 8, 9, 10, T1 and T2, but after twenty-four months, these species had colonised the new sites, and for *P. tropheops* 'red cheek', it significantly increased in population size at virtually all sites (Table 4.3). *Pseudotropheus callainos*, however, occurred at all sites at the beginning of the study, and at many sites its numbers either slightly increased, or dropped *e.g.*, at sites, #: 5 and T1. The only exception was at sites, #: 9 and 10, where its population size increased significantly (Table 4.3).

The other introduced species that significantly increased in numbers during the study period, within the 3 -7m depth zone were: *Labidochromis gigas* at sites, #: 1, 7 and 8; *Melanochromis* 'black-white' *johanni* at sites, #: 1 and 8, and *Pseudotropheus aurora* at sites, #: 5, 9 and 10. Otherwise, the population size of other introduced species either fluctuated, or slightly declined over the period of this study (Table 4.3).

The population size of a few native species also significantly increased during the period of this study (Table 4.3). These included *P. zebra* at sites, #: 1 and T2; *P. tropheops* 'orange chest' at site, #: 5; *P. tropheops* 'intermediate' at site, #: 1; *Petrotilapia nigra* at sites, #: 1 and 2; *Petrotilapia genalutea* at site, #: 2; *Pseudotropheus* 'aggressive brown' at sites, #: 2, 5 and T2; *Protomelas taeniolatus* at sites, #: 5 and 7; *Labidochromis pallidus* at sites, #: 2 and 5;

Melanochromis auratus at site, #: 9 and *M. vermivorus* at site, #: 9.

The native species whose population size declined significantly were: *Melanochromis chipokae* at site, #: 1; *Pseudotropheus tropheops* 'orange chest' at sites,#: 7 and *Petrotilapia nigra* at site, #: 9.

Other native species also decreased in numbers, but not significantly (Table 4.3). All of them are the species that are either weakly territorial, or may only be territorial during part of day *e.g.*, the *Melanochromis* species (Ribbink *et al.* 1983a), or have large home ranges, and hence difficult to accurately enumerate, *e.g.*, the *Melanochromis* and *Petrotilapia* species (pers. obs.), or are cryptic and difficult to count, *e.g.* the *Labidochromis* species (pers. obs.).

Overall, the population density of territorial males of the introduced and native Mbuna species at sites, #: 4 and 5 did not change significantly during the thirty months field observation (Table 4.3). It appears an equilibrium in numbers between territorial males of the introduced and native species has been reached at these sites.

Population of non-territorial fishes

The population of non-territorial fishes fluctuated seasonally (Fig. 4.3). However, this fluctuation was significant only in areas predominated by small rocks, where the highest number of non-territorial fishes was highest during the stratified (November - April) and upwelling (May - August) seasons. The drop in the lake level during the stratified season, *e.g.*, in November (Eccles 1974), which leads to the compression of fishes from shollow water to the 3 - 7m depth zone where this study was conducted, and increased foraging activities by many fishes during the upwelling season when food may be most abundant (Eccles 1974; Twombly 1981; Haberyan & Mhone 1991) may have contributed to the observed fluctuations in the population of non-territorial fishes.

Table 4.1. Comparison of the population density of territorial males of introduced and native species around Thumbi West Island at end of the study. The values in brackets are the percentage of the total population density at each sampling site. Monitoring of the fish populations was done every 3 months for 30 months.

Sampling site	Introduced species(No.m^{-2})	Native species(No.m^{-2})
1	1.12 (32.74)	2.31 (67.26)
2	1.33 (36.11)	2.35 (63.89)
3	1.67 (34.02)	3.24 (65.98)
4	2.33 (51.58)	2.18 (48.42)
5	2.47 (53.07)	2.18 (46.93)
7	1.12 (38.19)	1.82 (61.81)
8	1.20 (42.14)	1.65 (57.86)
9	1.24 (35.47)	2.27 (64.53)
10	0.65 (19.51)	2.69 (80.49)
T1	1.20 (29.80)	2.84 (70.20)
T2	0.71 (22.58)	2.45 (77.42)

Table 4.2. Comparison of the population density (number m^{-2}) of territorial males of introduced Mbuna species at each sampling site around Thumbi West Island at end of the study. rc = red cheek, bwj = black and white johanni and jj = joanjohnsonae. For full species names see appendix 1. Monitoring of the fish populations was done every 3 months for 30 months.

	Sampling sites										
	1	2	3	4	5	7	8	9	10	T1	T2
Introduced species											
C. afra	0.31	0.06	0.49	1.22	0.90	0.65	0.71	0.63	0.35	0.20	0.04
P. callainos	0.35	0.51	0.61	0.31	0.80	0.18	0.10	0.18	0.20	0.41	1.00
P. troph.'rc'	0.12	0.28	0.18	0.27	0.31	0.06	0.06	0.08	0.02	0.04	0.04
L. gigas	0.08	0.00	0.08	0.10	0.06	0.12	0.20	0.00	0.00	0.00	0.00
M. 'bwj'	0.08	0.00	0.18	0.18	0.16	0.02	0.00	0.00	0.04	0.00	0.00
M. 'jj'	0.00	0.06	0.00	0.04	0.02	0.00	0.00	0.00	0.02	0.04	0.06
A. 'blue'	0.10	0.00	0.02	0.04	0.02	0.16	0.08	0.02	0.02	0.00	0.00
P. aurora	0.06	0.00	0.00	0.02	0.04	0.02	0.00	0.10	0.31	0.00	0.00
L. strigatus	0.02	0.04	0.14	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
M. parallelus	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.12

Table 4.3. The change in population size of the introduced and native species after thirty months of field observation. The values presented are correlation coefficients (*r*) of the relationship between sampling period and population size. Note * = significant at 95% level, negative values show a decline in population size, and positive values show an increase in population size. rc = red cheek, bw = black and white johanni, oc = orange chest, i =intermediate, l = lilac and ab = aggressive brown. Sampling site number 3 has been excluded because some of the territorial males of the introduced Mbuna species were being experimentally removed. Monitoring of the fish populations was done every 3 months for 30 months.

	1	2	4	5	7	8	9	10	T1	T2
Introduced species										
Cynotilapia afra	0.59	0.83*	0.88*	0.33	0.58	0.87*	0.80*	0.70*	0.82*	0.85*
Pseudotropheus callainos	0.51	0.66	0.22	-0.60	0.59	0.05	0.80*	0.72*	-0.34	0.53
P. tropheops 'rc'	0.81*	0.95*	0.75*	0.77*	0.85*	0.86*	0.86*	0.86*	0.78*	0.78*
P. aurora	0.00	0.00	0.41	0.75*	0.03	0.00	0.70*	0.88*	0.00	0.00
Labidochromis gigas	0.78*	0.00	0.66	0.66	0.73*	0.76*	0.50	0.00	0.00	0.00
L. strigatus	0.00	-0.51	0.04	0.43	0.00	0.00	0.00	0.00	0.00	0.00
Melanochromis 'red'	0.00	0.00	0.31	-0.34	0.00	0.00	0.00	0.00	0.00	0.00
M. parallelus	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.78	0.78	-0.92*
M. joanjohnsonae	0.00	0.08	0.12	0.44	0.00	0.38	0.35	0.38	0.59	0.45
M. 'bw' johanni	0.73*	0.00	0.52	0.65	0.00	0.89*	0.00	0.42	0.00	0.00
Aulonacara 'blue'	0.09	0.00	0.06	0.59	0.33	0.36	0.58	-0.72*	0.00	0.00
Native species										
Pseudotropheus zebra	0.72*	-0.19	0.57	0.64	0.06	0.45	0.40	0.31	0.58	0.99*
P. troph.'oc'	0.19	0.49	0.22	0.89*	-0.69*	0.62	0.51	0.59	0.00	0.56
P. troph.'i'	0.88*	0.00	-0.35	-0.33	-0.61	0.52	0.46	-0.62	0.00	0.00
P. troph.'l'	0.00	0.00	0.16	0.60	0.61	0.00	0.00	0.00	0.00	0.00
P. 'ab'	0.00	0.94*	0.58	0.93*	0.00	0.00	0.00	0.00	0.00	0.98*
P. 'tiny'	0.09	0.08	-0.59	-0.25	-0.55*	0.66	-0.21	-0.69	0.00	0.00
Petrotilapia nigra	0.71*	0.74*	0.64	0.29	-0.12	0.33	-0.72*	-0.38	-0.13	-0.58
P. tridentiger	0.00	0.48	0.00	0.48	0.00	0.00	0.00	0.00	0.99*	0.99*
P. genalutea	0.00	0.70*	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Protomelas taeniolatus	0.00	0.00	-0.01	0.85*	0.75*	0.00	0.32	0.00	0.00	0.00
Labeotropheus fuelleborni	0.35	0.66	0.29	-0.05	0.29	0.36	0.62	0.22	0.64	0.83*
L. trawavasae	0.29	0.59	0.00	0.00	0.00	0.00	0.03	-0.22	0.22	-0.13
Labidochromis pallidus	0.00	0.97*	0.53	0.70*	0.00	0.00	0.00	0.00	0.00	0.00
Melanochromis auratus	0.07	0.67	-0.06	0.38	0.15	0.61	0.77*	0.45	-0.08	0.58
M. vermivorus	0.04	0.64	0.64	0.54	0.23	0.05	0.70*	0.69	0.85*	-0.12
M. chipokae	-0.76*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

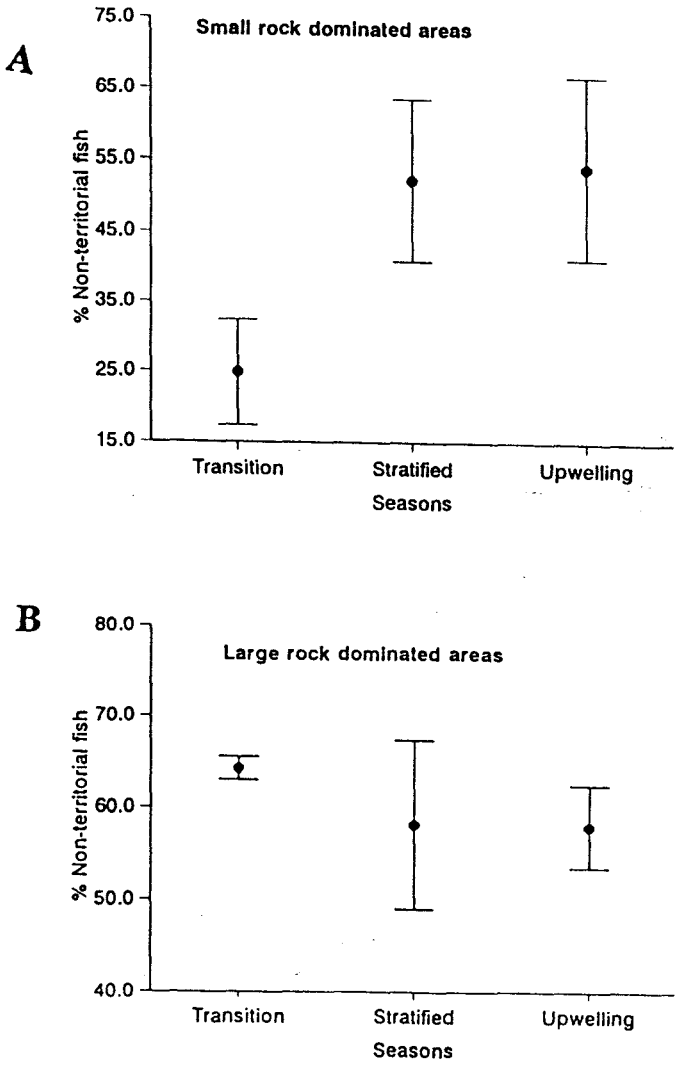


Fig. 4.3. Fluctuations in the population density of non-territorial fishes in the 3 - 7m depth zone of the rocky habitat at Thumbi West Island. A = small rock predominated areas, and B = large rock predominated areas. The seasons are transition (September - October), stratified (November - April) and upwelling (May - August).

Discussion

The Mbuna species translocated from the northern part of Lake Malawi may have been introduced at Mitande point (site *F*, Fig. 4.1), Thumbi West Island, probably over twenty years ago (Ribbink *et al.* 1983a). During this period, only *Pseudotropheus callainos*, *Cynotilapia afra* and *P. tropheops* 'red cheek' have managed to substantially increase in numbers and cover the whole island, within the 3 - 7m depth belt of the rocky habitat (Table 4.3). Besides, *P. callainos*, *C. afra* and *P. tropheops* 'red cheek', the majority of other introduced species within the 3 -7m depth zone, only occur in small numbers, and they have not been able to cover the whole island (Table 4.2). This distribution pattern confirms the observations made by Ribbink *et al.* (1983a) that the majority of Mbuna are highly stenotopic.

In terms of numbers the highest population densities of the majority of the introduced species are found at sites # 3, 4 & 5 (Table 4.2), which are nearest to the point where introductions were made (site *F*, Fig. 4.1). Although many factors can influence population growth of fish, or other animals (Rothschild 1986; Wootton 1990), the following factors may have contributed to the observed population densities and distribution of introduced species around Thumbi West Island:

Size of founder population

Although there is no record of how many species were introduced, nor how many individuals of each species were released (Ribbink *et al.* 1983a), it is likely that the introduced species which are established at Thumbi West Island were introduced in sufficient numbers to establish reproducing populations. It is also probable that the species that are most abundant, and widely distributed were introduced in much larger numbers than others which have not been as successful. Small and fragmented populations may tend to be vulnerable to inbreeding depression.

Ability to secure a breeding territory

As only male Mbuna with territories are capable of breeding (Ribbink *et al.* 1983a; chapter 3), the success of each species to multiply in numbers may be constrained by the ability of its males to secure territorial sites in which to breed. In this respect, there are differences among the introduced species at Thumbi West Island. For instance, the introduced species that are most abundant at many sites (Table 4.2), *e.g.*, *C. afra*, is highly aggressive and competitive in securing breeding territories, while *P. callainos* though not as aggressive, is capable of overlapping its territories with some of the native species, albeit its microhabitat requirements being similar to such native species (chapter 3). Another introduced species, *P. tropheops* 'red cheek' which has also succeeded in building up its population around Thumbi West Island, is aggressive and strongly territorial. The rest of the introduced Mbuna species in the 3 - 7m depth zone which have not increased significantly in numbers (Table 4.2) are weakly territorial, *e.g.*, *Labidochromis strigatus* and the *Melanochromis* species (Ribbink *et al.* 1983a; pers. obs.). These species do not have fixed territories. Consequently, when they attempt to mate in their neighbours' territories, they are often attacked by sympatric heterospecific territorial males. Therefore, their reproductive success, and population growth seems to be hampered by their inability to secure and defend fixed breeding territories. Also, the probability of egg predation in the weakly territorial Mbuna may be high because many specialized and opportunistic fishes are attracted during spawning and, unless such predators are adequately restrained through staunch territoriality, the spawned eggs may easily be devoured before the female takes them into her mouth for brooding. Consequently, this may further reduce the opportunities for the weakly territorial introduced Mbuna to increase in numbers.

Density-dependent intra-specific aggression

It has been suggested that intra-specific aggression may facilitate dispersion of surplus individuals of a species (Immelmann 1980; Branch 1984; chapter 3).

This is likely to occur when a population in a particular habitat has increased to the point where pressure is placed on its carrying capacity. In Mbuna, the demand for optimal territory sites is very high, and there are many adult supernumerary males that are unable to defend territories. Besides this, territorial males are highly aggressive towards conspecific supernumerary males (see chapter 3). Consequently, males without territories may be forced to move into new sites where they may establish themselves. This seems probable because it is the introduced species that are most aggressive intra-specifically, *e.g.*, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' (chapter 3) that are also most abundant and widely distributed around Thumbi West Island.

Microhabitat suitability

It has been shown in chapter 3 that the Mbuna have specific microhabitat preferences, and presumably, the carrying capacity of each species at any particular site is dictated by the availability of each species' preferred microhabitat. In this context, upon initial colonization the population may grow exponentially, up to the capacity of the available territorial space. Then the excess males would exist as supernumeraries. It is, therefore, possible that at sites where the population of some Mbuna species did not change during the entire study period, such sites may have attained their carrying capacity. The patch distribution of some of the introduced species, such as *Labidochromis strigatus*, *L. gigas*, *Melanochromis joanjohnsonae*, *Pseudotropheus aurora* and others (Table 4.3) may also be dictated by the availability of their preferred microhabitats. Even some of the introduced species that have covered the whole Island, *e.g.*, *P. callainos*, *C. afra* and *P. tropheops* 'red cheek', are not uniformly distributed. There are many patches around Thumbi West Island, where none of these species occur, due to lack of suitable habitat. Similarly, it is improbable that at any site around Thumbi West Island these species would significantly increase beyond the limits of the vacant patches of their preferred microhabitats.

On the question of whether increases in the number of territorial males of introduced species would correspond with declines in the population size of territorial males of some native species, it has been difficult to make direct correlations because a number of factors may influence the decline in the population size of territorial males of native species. Some of these factors have been discussed in chapter 3 of this thesis. Nonetheless, where the introduced species, *C. afra* has significantly increased in numbers, around Thumbi West Island, the population size of the native species, *P. zebra* which overlaps with it in microhabitat requirements did not decline significantly during the period of this study (Table 4.3). This may suggest that *C. afra* colonises vacant spaces, and even where it may displace *P. zebra*, only a few individuals may be affected (chapter 3). However, at site # 7 (Table 4.3), where *P. tropheops 'red cheek'* has significantly increased in population density, the population size of its sibling native species, *P. tropheops* 'orange chest' has significantly declined. At this site, the number of *P. tropheops* 'orange chest', declined from 21 in April 1993 to 14 in November, 1994, *i.e*, representing a net loss of seven territorial males. During the same period, *P. tropheops* 'red cheek' increased from one territorial individual to three territorial males, representing an net increase of only two territorial males. It is unlikely that the two males of *P. tropheops* 'red cheek' that established territories at site # 7 may have displaced seven territorial males of *P. tropheops* 'orange chest'. In the *P. tropheops* species, abandonment of territories is common (chapter 3). The possible reasons that could lead to territorial abandonment by Mbuna have been discussed in chapter 3 of this thesis. It is possible, therefore that the two *P. tropheops* 'red cheek' males that established themselves at site # 7 may have reoccupied spaces that had been vacated by the native species, *P. tropheops* 'orange chest', without necessarily displacing it.

Similarly, at many sites, particularly farther from the point of introduction, most introduced species occur in low population densities (Table 4.2).

Consequently, it is unlikely that they would exert any significant density-dependent aggression that would lead to exclusion of native species that overlap with them in the microhabitat requirements. Also, at many places, the population size of introduced species seems to be limited by the small patches of suitable microhabitats. A case in point, is the presence of *C. afra* at sites predominated by large rocks, or the presence of *P. tropheops* 'red cheek' at sites predominated by small rocks.

Since residents have a higher probability of repelling intruders than non-residents (Braddock 1949; De Boer & Heuts 1973; Brown & Green 1976; Figler & Einhorn 1983; Figler *et al.* 1986; Buchheim & Hixon 1992; Turner 1994), it is also unlikely that introduced species may always have an edge in taking over territories from native species to the extent that some of the native taxa would be driven into extinction. Displacement of resident native species by attrition may not be accomplished without costs of injury. However, it may also be argued that introduced species are occupying space which could otherwise be used by the native species. But as discussed in chapter 3, there are many constraints that negate the possibility of all territorial males to maintain territoriality for life. Also as shown in chapter 3, introduced and native species with similar space requirements naturally exchange their territories, hence massive exclusion of native species by the alien Mbuna may probably never take place. What is probably happening is that the population of territorial males of the introduced and native Mbuna species may reach an equilibrium at which a few individuals may displace each other, but not significantly as to drive any native species into extinction. Both introduced and native species are also likely to be subjected to the stochastic forces that would probably operate in a manner that no detrimental exclusions between species with identical microhabitat requirements may occur.

Overall, results of the study reported in this chapter:

1. **Confirm the stenotopy of Mbuna (see Ribbink *et al.* 1983a; Ribbink 1991, 1992).**
2. **Show that the patchy distribution of introduced Mbuna, is probably because of interspecific differences in their microhabitat preferences.**
3. **Suggest that size of founder population, ability to secure breeding territories, and density-dependent intra-specific aggression may influence population growth and facilitate the distribution of introduced Mbuna species around Thumbi West Island.**
4. **Show that although at some sites around Thumbi West Island, some introduced species had increased significantly, while some native species declined significantly, such declines could not directly be attributed to displacements by the introduced species. Natural abandonment of territories by the territorial Mbuna may occur due to other factors, such as nutritional constraints (Munthali, in press *a*; also see chapter 3 for other factors). Introduced and native species may, therefore, coexist at some equilibrium where some minor displacement may take place, but not so serious as to drive any native species into extinction.**
5. **Show four categories of introduced species were discerned:**

   (a) those that are strongly territorial and are most abundant and widely distributed, around Thumbi West Island within the 3 - 7m depth zone, *e.g.*, *Pseudotropheus callainos*, *Cynotilapia afra* and *Pseudotropheus tropheops* 'red cheek'.

   (b) Those that are weakly territorial, are fewer in number and have limited distribution around Thumbi West Island, *e.g.*, *Labidochromis strigatus* and *Melanochromis parallelus*.

   (c) Those that either have large home ranges, or are cryptic and hence difficult to count, *e.g.*, *Melanochromis joanjohnsonae* and *Labidochromis strigatus*.

   (d) Those that normally occur in the intermediate zone, but incidentally occur in the 3 - 7m depth zone in low numbers and are patchily

distributed, *e.g.*, *Pseudotropheus aurora*, *Melanochromis* 'black-white *johanni* and *Labidochromis gigas*.

6. Show that the population of non-territorial fishes fluctuate in areas predominated by small rocks, probably in response to changes in the lake level and increased foraging during the stratified season when food may be most scarce (Eccles 1974; Twombly 1983; Haberyan & Mhone 1991), or during the upwelling when most fish species may be attracted into the rocky shore due to food abunadance.
7. I recommend that monitoring of the populations of introduced Mbuna should continue, comparing communities which have high numbers of introduced species and those that have the least numbers. As the population of introduced species build up in the latter communities a lot more knowledge about their interaction with the native taxa may be gained.

Chapter 5

Conservation of Mbuna (Cichlidae) of Lake Malawi

Introduction

While acknowledging the potential risks that introduced Mbuna species may impose on the native taxa of Lake Malawi National Park, to sustain Lake Malawi's biodiversity, the aim should be to prevent extinction of any species, regardless of where it occurs in the lake. Lake Malawi is vast (28,800 km^2) (Patterson & Kachinjika 1994), and as noted in chapter one of this thesis, every region of this lake has species that are endemic to it (Ribbink *et al.* 1983a), and not all of them are represented in the Lake Malawi National Park. The question then arises, what is the Mbuna's status in the whole of Lake Malawi? To address this question, in this chapter, I review the factors that potentially threaten Lake Malawi's ecosystem integrity, focusing particularly on the Mbuna. Measures that could promote conservation of Mbuna, and safeguard Lake Malawi's ecosystem integrity have also been suggested.

Conservation as used in this chapter denotes management of human use of the Malawi's fish resources so that they yield the greatest sustainable benefit to present generations, while maintaining their potential to meet the needs and aspirations of the future generations.

Reasons for conserving the Mbuna of Lake Malawi

Although the Mbuna of Lake Malawi have received comparatively less attention in terms of conservation than the other fishes, they are unique and are of multiple values to the Malawian people. These values include:

National heritage

As all the Mbuna species occurring in Lake Malawi are endemic to it, all Malawians have a virtuous obligation to ensure that none of the species is exterminated due to over-exploitation, and/or poor land use practices. However, for this to be achieved, the general public and politicians, in particular need to

be informed about the Malawi's privilege for having such a resource as the Mbuna, which besides their aesthetic appeal, belong to one of the most speciose fish families in the world. Lake Malawi is recognised throughout the world because of its rich biodiversity, and it is for this reason that Lake Malawi National Park was declared a World Heritage Site by UNESCO in 1984. Therefore, Malawians have an obligation to conserve Lake Malawi's biodiversity in conformity with the international expectation. The current out-reach education programmes, undertaken by the Department of National Parks and Wildlife and the Wildlife Society of Malawi need to be expanded, involving Fisheries Department, Agriculture Extension Services, Ministry of Education and Non-governmental Organisations, involved with the protection of the environment. Even church denominations should be incorporated in the campaign to safeguard Lake Malawi and its rich ichthyofauna from over-exploitation and impairment due to land degradation.

Export trade

Although little is known about the ornamental fish trade by the general public in Malawi, it is very vital to Malawi's economy. It primarily serves two functions; firstly, it brings valuable foreign revenue to Malawi and provides employment and secondly, it stimulates interest and advertises the lake and its fauna in a number of countries (Ribbink *et al.* 1983b). Whereas food fishes are also being exported, the increasing local demand may curtail their export outlet because of the dwindling catches (Turner *et al.* 1992; CODA & Partners 1993; Tweddle & Makwinja 1994). In terms of marketability, the Mbuna adjure higher prices than all the food fish species combined. For instance, a pair of a rare species, such as *Protomelas moori* fetched US$ 600 (Mk 9,000) the first time it hit the American market (Ribbink *et al.* 1983b), while a tonne of assorted food fish species cost on average between US$ 36.90 (Mk 553.51) and US$ 66.69 (Mk 963.13) (Department of Fisheries 1993). Therefore, the ornamental fish trade should be viewed as an extremely important additional industry of great value, providing foreign exchange to Malawi.

However, the largest threat to the ornamental fish trade, besides the fears that it may be operating unsustainably because of lack of surveillance on its harvesting strategy, is that many of the fish currently popular on the markets of the world are being bred and sold at low prices overseas (Ribbink *et al.* 1983b; Woeltjes 1995). Nonetheless, for Malawi, due to large variety of species that can be exported, and also since many enthusiasts may prefer wild-caught fish and even breeders may prefer to re-vitalize their stock (Ribbink *et al.* 1983b), the ornamental fish trade may continue to thrive in Malawi.

Tourism

Malawi has a wide range of landscape types, offering a variety of attractions for tourists. These landscape types, and the National Parks and Wildlife Reserves occurring within them fall into five main categories: Lake Malawi, Shire River, African Rift Valley Escarpment, Central African Plateau and High Plateau (Carter, 1985). However, of these landscapes, Lake Malawi is one of the most popular tourist destination (Anon. 1989). Its attraction can mainly be attributed to its geology, freshwater and diverse ichthyofauna. Among the latter, the Mbuna are aesthetically the most appealing, and behaviourally the most fascinating. Consequently, most tourists visit Lake Malawi to have an *in situ* view of the Mbuna in their natural environment. One of the most popular destinations on the lakeshore is the Lake Malawi National Park. This park because of the high diversity of fish it protects (chapter one), receives more visitors and earns more revenue annually than any other park in Malawi (Munthali 1990; Jalale 1993). Therefore, the Mbuna earns foreign revenue through extractive exploitation, *e.g.*, ornamental fish trade and through non-extractive means, *e.g.*, tourism. This diversification allows for quantum improvements in the profitability, since the two enterprises can be added to each other.

The presence of species endemic to the northern Malawi (chapter one) has substantially contributed to the species richness in the Lake Malawi National Park, and as long as their presence does not constitute any danger to the continued survival of native species, they would remain as an asset to the park's tourist attraction and as subjects of research.

In terms of wildlife-based tourism, Malawi may not compete effectively with other countries for tourist attraction because the carrying capacity for large mammals is not as high as in many sister states within the Southern African Development Community (SADC), and also Malawi has relatively few endemic terrestrial species. However, the Mbuna of Lake Malawi of which 100% are endemic to Malawi offers the most competitive advantage for Malawi's tourist attraction.

Science

Many scientists are interested in the Lake Malawi and its fishes. What lures them is the astounding evolution and radiation of the cichlid fauna of Lake Malawi. Since the Mbuna are also good candidates for laboratory studies, they are among the most popular subjects of behavioural studies all over the world.

Food

The extent of Mbuna exploitation for food has received little attention, because it has always been assumed that they only constitute a small proportion of the overall fish species caught for food. Usually, the Mbuna only occur as incidental catches (Ribbink *et al.* 1983b; Tweddle 1992). However, many fishers are willing to switch into large scale exploitation of Mbuna for food if the preferred food species continue to decline (Munthali, in press *b*). However, due the sedentary nature of the Mbuna, and the fact that most Mbuna species only occur in small populations, they can not sustain the burgeoning human population dependent on fish for food and cash income. The Mbuna's vital contribution to Malawi's economy is its quantum earning of foreign revenue through ornamental fish

trade and tourism, which would greatly exceed its value as a food resource.

Potential threats to the Mbuna of Lake Malawi

Factors that may negatively affect the sustainability of Lake Malawi's biodiversity are many, but the most important ones that could have direct, or indirect implications on the integrity of the Mbuna community structure include the following:

Overfishing

The Malawi's fisheries sector is important to the economy in two respects. First, as a food, by providing nearly 75% of the animal protein consumed by people in Malawi (Bland 1992; Bland & Donda 1994). Second, it is a significant source of off-farm employment to the lakeshore people, by directly providing jobs for some 32,000 fishers, and another 200,000 people in fish processing and trading activities (Bland 1992). Overall, the fisheries sector contributes about 4% to Malawi's Gross Domestic Product (GDP). However, despite the apparent importance of the fisheries to the people, current trends in the fish landings are in the decline, more particularly so for the most popular food fish species, such as *Oreochromis* species (Turner *et al.* 1992; Tweddle & Makwinja 1994) and many anadromous and riverine fishes (CODA & Partners 1993; Tweddle 1992). Turner (1977a & 1977b) has reported that with the advent of trawl commercial fishery, the number of species caught in the heavily fished areas in southern Lake Malawi from 1971 - 1974 declined, and that over 20% of the species disappeared from the catches. Currently, CODA & Partners (1993) have also reported that catches by the Maldeco Company, the most capital intensive fishing industry in Malawi, have declined by 60% from previous years' catches. In Lake Malombe (Fig. 5.1), increased fishing pressure with small-meshed nets has severely depleted fish stocks and, it is suspected that some species may have been exterminated (CODA & Partners 1993).

Two main factors may have contributed to the overfishing problems:

(i) *Limited economic incentives*

In Malawi, economic growth is largely dependent on increasing agricultural production. The argument in favour of this approach is that agriculture employs most rural people, and therefore, is considered the key means of meeting demands for food and cash that provide increases in the wealth needed to improve the people's living standards. However, dependence on agriculture for improving the rural communities' welfare has been frustrated by many constraints, among them are increases in human population and dwindling arable land, drought, high costs of agricultural inputs, poorly defined incentives (*e.g.*, inflexible credit policies and terms, poor marketing systems and supportive infrastructure), and low prices for export crops (Anon 1991a). Consequently, agriculture has failed to sustain the increasing demand for food, and wealth required for improving rural people's living standards. Malawi, also has limited off-farm employment opportunities to offer to its people, most particularly those in the rural areas. For the people along much of the lake shore, where drought is a permanent natural occurrence, economic opportunities are even more limited, therefore, most people on the shores of Lake Malawi have to fish for a living. The majority enter their fishing career at a fairly young age (*e.g.*, 17 years) and remain in it almost throughout their lives (Munthali, in press *b*). Consequently, this creates heavy pressure on the fish resources.

(ii) *Malawi's fish are an open-access resource*

The fishes of Malawi's lakes and rivers are open-access resources in which the Fisheries Legislation does not prohibit the free movement of people from one stock impoverished area to another where fish may be more abundant. Consequently, areas which have rich fish stocks also get overfished. The traditional controls, through chiefs and village headmen who regulated access to all fishing pitches within their territorial units (Bland 1992), and the ritual prohibition of fishing certain areas, and the role of magic and taboos that

regulated number of fishers at each fishing ground (Berry & Petty 1992) have all been marginalised by the Fisheries Legislation and have disintegrated. Mechanisms, such as closed fishing seasons and regulation of net mesh size have not been adequately enforced because of poor financial resources and inadequate law enforcement personnel (Tweddle 1992). Consequently, overfishing continues to be a problem.

Tweddle (1992) hypothesised that the decline in per capita consumption of fish in Malawi as the fish catches dwindle and human population dependent on fish increases, would shift the fishing activities to the less important species, such as Mbuna. Munthali (in press *b*) has confirmed that this is already the case in the northern part of Lake Malawi. Similarly, a high proportion of fishers in the enclave villages of Lake Malawi National Park are willing to exploit Mbuna as a commercial food fish species, if the preferred species continue to dwindle (Munthali, in press *b*). Smith (1993) also confirmed the presence of Mbuna in the fish landings in Chembe, one of the enclave villages in the park. However, the impact of large scale exploitation of Mbuna for food may be enormous because many of them are localised, some only occur in small isolated populations (Ribbink *et al.* 1983a) and population growth of some of the Mbuna species is very slow as evidenced in chapter 4.

Ornamental fish trade

The Mbuna are the mainstay of ornamental fish trade in Malawi. As noted in chapter one, this trade started in 1962, and peaked in the 1970s when over 400 000 fishes were being exported annually by three companies to Europe, Asia and America (Ribbink *et al.* 1983a). Since the early eighties, only one ornamental fish exporting company has operated from Lake Malawi, but the volume of export is probably greater now than at anytime in the past (CODA & Partners 1993). Ribbink *et al.* (1983b) reported that a number of Mbuna were threatened and in need of protection, and recommendations regarding their protection were

made to the Malawi's Fisheries Department. However, the Mbuna export trade is operating in a manner in which its sustainability can not be guaranteed. The following factors hoist doubts about the sustainability of this trade:

(i) ***Harvesting of Mbuna is done in a laisser-fair manner.***

The vital statistics, *e.g.*, population size and sex ratios of the exploited Mbuna, upon which sound harvesting quotas are supposed to be based are not monitored. Consequently, some of the Mbuna species that are restricted to small areas, and present in low numbers may be over-exploited. However, reducing such populations further, may exacerbate homozygosity and eventual extinction. Similarly, ornamental fishermen capture selectively, taking not only the most attractive species, but also the most attractive and largest individuals of a species (Ribbink *et al.* 1983b). Consequently, they impose an artificial selection, that leave the less attractive individuals in a population, and this would be more pronounced in small isolated populations. In chapter 3 of this thesis, it has been shown that after repeated removal of territorial males, the size of males in some species, *e.g.*, *Pseudotropheus callainos* and *Pseudotropheus tropheops* 'red cheek' decline significantly. Smaller and immature males are incapable of successfully breeding (pers. oberv.), therefore, repeated removal of restricted small populations of Mbuna, could in the long-term exterminate such populations.

Signs of over-exploitation of some Mbuna populations were evident in the early 1980s, when Ribbink *et al.* (1983b) reported significant declines in the population of *Melanochromis* 'red' at Chizumulo Island and *Pseudotropheus callainos* at Nkhata Bay. Munthali (in press *b*) has also reported the decline of *P. callainos* at Nkhata Bay, and has attributed ornamental fish trade as the primary factor for its reduction in population size.

The ornamental fish trade having operated for many years without any monitoring of the populations being harvested, and also since demand for some species may stimulate over-exploitation, it is probable that other Mbuna

populations have also been negatively affected by this trade.

(ii) *Accidental contamination of endemic communities with species from elsewhere in the lake*

The ornamental fish trade has also been responsible for the intra-lacustrine translocation of endemic Mbuna species from areas of their origin to other parts of the lake (chapter one). This happens because of negligence by the ornamental fishers. Since the discovery of Mbuna species at sites where they do not naturally occur by Ribbink *et al.* (1983a), there has been no follow-up monitoring to find out if further intra-lacustrine translocation have taken place. However, as earlier noted that the harvesting of Mbuna for ornamental fish trade is carried out in a laisser-faire manner, the extent of contamination of endemic communities with Mbuna species from elsewhere in the lake is probably worse now than before. Consequently, there is an urgent need to assess the impact of ornamental fish trade on the endemic communities on a much larger scale than only focusing on Lake Malawi National Park.

Land degradation

In demographic terms, Malawi, with an annual growth rate of 3.7%, has a rapidly growing human population. The population is approximately 8.5 million of which 89% are full time engaged in agriculture (Anon. 1991a; Anon. 1992). Arable land is limited, and with this large population size, land holdings are generally small, averaging about 1.1 hectares per family of four people (Anon. 1991a). With such small holdings, the landless cultivate marginal lands with steep slopes, causing soil erosion. The estate agricultural sector which is dominated by tobacco growing whose processing requires wood fuel also contributes to the deforestation (22,400 ha.annum^{-1}) (CODA & Partners, 1993). This coupled with the high fuelwood energy dependence by both the rural and urban residents aggravates deforestation in Malawi. It is estimated that by the year 2000, fuelwood demand (10.5 million m^3) will be unmatched by a potential

supply of only 6.4 million m^3 (CODA & Partners 1993). This implies that deforestation of the relic forests even in the rugged steep unprotected areas will intensify, hence exacerbating soil erosion and land degradation.

For the whole of Malawi, it is estimated that the rate of soil erosion on flat arable land is 20 tonnes ha^{-1}/year and 40 tonnes ha^{-1}/year in the most densely populated and hilly areas (Anon. 1991b). The effects of soil erosion on the Mbuna, or aquatic ecosystems have never been comprehensively assessed in Malawi, but they may include:

(i) ***Sedimentation***

The sediment load deposited in Lake Malawi, and its associated riverine drainage may be in the order of 50 million tonnes $annum^{-1}$ (CODA & Partners 1993). The most obvious impact of sedimentation discerned so far, is the decline in the riverine and anadromous fisheries *e.g Opsaridium microlepis, O. microphalus, Barbus johnstoni, B. eurystomus, B. litamba and Labeo mesops* (CODA & Partners 1993). It is probable that large silt loads from the degraded steep marginal lands may cover the rock substrata, and consequently reduce epilithic algae production and alter, or seal holes in which the Mbuna breed. At Nkhata Bay (Fig. 5.1), where soil erosion is estimated at 43 tonnes/ha.$annum^{-1}$ (Anon. 1991b), the density of Mbuna seem to have declined over the past ten years due to siltation (Munthali, in press *b*).

(ii) ***Pollution***

Malawi does not face any widespread water pollution problem, given the limited industrial base and a relatively strong regulatory framework for industrial effluent disposal (Anon. 1991b). Consequently, the level of heavy metals, such as chromium, cadmium, mercury, selenium and lead, in the water system is low and well within the World Health Organization's (WHO) standards (Anon. 1991b). However, as it may be expected with the domination of agriculture in the Malawi's economy, the estate sector in particular depends on chemical

inputs, such as fertilizer and pesticides to raise agricultural productivity. But due to limited adoption of physical land conservation structures in the steep marginal lands, agro-chemical seem to have increased concentrations of nitrites and nitrates in the surface water supplies, resulting in increased algae growth in several reservoirs in some parts of the country (Anon. 1991b).

Increased nutrient input in Lake Malawi may lead to increased primary productivity and fish production. But this would depend on the species composition of the phytoplankton. If the phytoplankton can easily be utilized by zooplankton and fish, then nutrients and biomass will accumulate at higher trophic levels that are useful to human consumption (Bootsma 1993a). However, if algae, or phytoplankton biomass cannot be utilized by higher trophic levels, their decomposition would increase the demand for oxygen, increasing the anoxic zone, hence reducing the available fish habitat (Bootsma 1993a).

Agro-chemical and toxic chemicals, such as arsenic, used as a cattle acaracide, and dieldrin and aldrin, used in termite protection are also commonly used in many parts of Malawi (Anon. 1991b). It is likely that the use of these chemicals over the past many years, particularly, the organochlorinated chemicals may have entered various food chains, both in the terrestrial and aquatic ecosystems. Toxins in the surfacial sediments may accumulate and be introduced to the food web, either through deposit feeders, or sediment resuspension (Bootsma 1993a). In Lake Nakuru, Kenya, Lincer *et al.* (1981) found that where the riparian population were using DDT and dieldrin against crop pests and toxaphene as an acaricide, high levels of DDE, a derivative of these chemicals were detected in algae and bottom-feeding fishes. They also found high concentrations of DDE (5.75 mg. l^{-1}) in the African darter, *Anlinga rufa* that fed on these fishes. The level of chemical pollution in Lake Malawi has never been assessed, and it is not known if chemical pollution has had any significant effect on the Mbuna, or Lake Malawi's biota. Lake Malawi because of its large volume and relatively small outflow, has a long flushing time, such that even if the pollution rates may

be high, dilution may result in the pollutant going undetected for many years (Bootsma 1993a). But once hazardous concentrations of the pollutant are reached, elimination of pollution source will not have immediate benefits, unless mechanical other than flushing are efficient at removing such pollutants (Bootsma 1993a). It is imperative, therefore, that the level of pollution in Lake Malawi should be assessed, and a monitoring programme initiated in order to obviate critical pollution levels that would be almost impossible to eliminate from the lake and its associated drainage systems. The effect of chemical pollution on Mbuna has never been assessed, but since they most of them are sedentary, increases in concentration of toxic chemicals may be detrimental to their survival.

Measures that could promote conservation of Mbuna and Lake Malawi's ecosystem integrity

(i) Diversification of the economic base of the lakeshore people

To alleviate pressure on the Lake Malawi's fish resources, there is need to carry out feasibility studies on alternative economic activities for the lakeshore people, who are currently almost exclusively dependent on fish for a living. Potential areas of consideration include:

Irrigation farming

In many lakeshore areas, rainfall is one of the factors limiting agricultural production. Therefore, if the government can evaluate the feasibility of irrigation farming, and introduce subsidized loans for the local people to adopt irrigation agriculture, it may be possible for the lakeshore people to diversify their income base. This would consequently ease pressure on the fisheries resources. However, great caution would need to be effected, through prudent land husbandry in order not to increase the inflow of agro-chemicals into the lake which may jeopardise the lake's ecosystem integrity.

Aquaculture

Despite many years of effort in trying to develop aquaculture in Malawi, the success in this endeavour has been minimal, partly because up to now the local fish species that can profitably be farmed have not been identified. Consequently, research in this field need to be intensified so that appropriate local fish species are identified for aquaculture development along the shores of Lake Malawi. Back-up services, such as short-term loans and out-reach extension education would be necessary for such a programme to take off to its sustainable fruition. However, alien species should never be used for aquaculture along the lakeshore to prevent accidental contamination of the lake. Also disposal of effluent from aquaculture would need to be carefully planned, *e.g.*, used for fertilizing agricultural crops.

Game farming

In Malawi as the human population continues to grow, the demand for fish and animal protein may not be sustained. Consequently, there is need to integrate conventional fisheries with captive breeding and stall feeding of some wild game species. Of particularly interest are those that easily adapt to agricultural farming systems, *e.g.*, Common duiker, *Sylvicapra grimmia*, Cane rat, *Thryonomys swinderianus*, *etc.* In Ghana it has been demonstrated that the cane rat can be raised for quality meat in boxes in human dwellings (Asibey 1974; Asibey & Child 1990). Therefore, captive breeding and stall feeding of some game animals may provide opportunity to the lakeshore people to increase game meat production for subsistence and cash. This would also assist in easing pressure on the Lake Malawi's fisheries resources. The animals suggested for captive breeding are commonly available throughout Malawi. However, for such a programme to succeed, the government through the Department of Parks and Wildlife and the Department of Fisheries would need to raise funds that could initially cater for the capture of wild animals, distribution to eligible farmers, research and out-reach extension education. Since it may be difficult to implement a project of this nature on a large scale, pilot areas could be

identified, and depending on its success, it could be expanded to cover the whole lakeshore.

Cottage industry

Lake Malawi is one the most popular destination for tourists visiting Malawi (Anon. 1989). Therefore, local people along the lakeshore have the opportunity to develop the cottage industry, which could target tourists as its principal clientele. There is need to assess the economic feasibility of small scale business along the shores of Lake Malawi. Among the things that can be encouraged for exploitation are setting up bed-and-breakfast, or restaurant facilities which can cater for the needs of backpack tourists who frequent Lake Malawi throughout the year. Basket weaving from *Hyphaene* palm leaves, a craft that is prevalent along the lakeshore can also be encouraged. With proper education, *Hyphaene* palm leaves can be sustainably harvested from year to year without jeopardizing the life of palm trees. As regards catering for tourists, in Chembe, one of the enclave villages in Lake Malawi National Park, five local entrepreneurs make as much as US$ 92717, or at the current Malawi currency value, about MK 1,390,758 per annum by offering bed, restaurant and local transport to tourists (Grenfell 1993). These people also provide employment to fellow villagers, hence attenuate pressure on the fish resources. Therefore, such entrepreneurship needs to be encouraged throughout the lakeshore as a means of reducing dependence on fish for cash income. However, to get these people started the government should make loans easily accessible at affordable interest rates.

(ii) Monitoring of the ornamental fish trade

The key to sustainable Mbuna utilization is the determination of the status of all the exploited endemic species. Harvesting quotas need to be constantly reviewed, based on the exploited species' vital statistics. This is the only way isolated small populations can be safeguarded from over-exploitation. Evaluation of the impact the ornamental fish trade has had on endemic communities, and continuous

monitoring of the populations being exploited are also necessary. Consequently, there is an urgent need for the Fisheries Department to train personnel who can carry out underwater field surveys, and in depth ecological studies of the exploited fish, with a view of implementing wise conservation measures and, if necessary species in the most critical status could be submitted for appendix listing under the Convention on International Trade in Endangered Species of Flora and Fauna (CITES).

(iii) Procteted areas and sustainance of Lake Malawi's ecosystem integrity

Protected areas (National Parks, Wildlife and Forest Reserves), besides preserving representative examples of terrestrial biotic communities, play an important role in safeguarding the ecosystem integrity of Lake Malawi, and its associated drainage systems. This is achieved through the protection of the lake's catchment area from adverse land use practices, and in situ conservation of some endemic aquatic ichthyofauna of Lake Malawi (*e.g.*, Lake Malawi National Park, chapter 1) and its drainage system (Tweddle 1985).

Topographically, Malawi can be divided into three regions: (i) the rift valley floor which is occupied by the lake, and which for much of its length, is bounded by steep escarpments (Eccles 1984) (Fig. 5.1). (ii) The plateau region, between 760 and 1400 m.a.s.l. This land unit is characterised by gentle slopes and is interspaced by broad valleys, and it encompasses the main agricultural production areas. (iii) The plateaux, with rugged steep areas between 1400 and 2500 meter in elevation (Fig. 5.1). As much as 51% of the catchment of Lake Malawi and the major rivers draining into it lies within this land unit. Fortunately, a good proportion of this rugged land is protected by the Malawi Government's Act of Parliament, in the form of National Parks, Wildlife and Forest Reserves (Fig. 5.2), which account for about 22%, of the Malawi's total land area (94,276 km^{-2}).

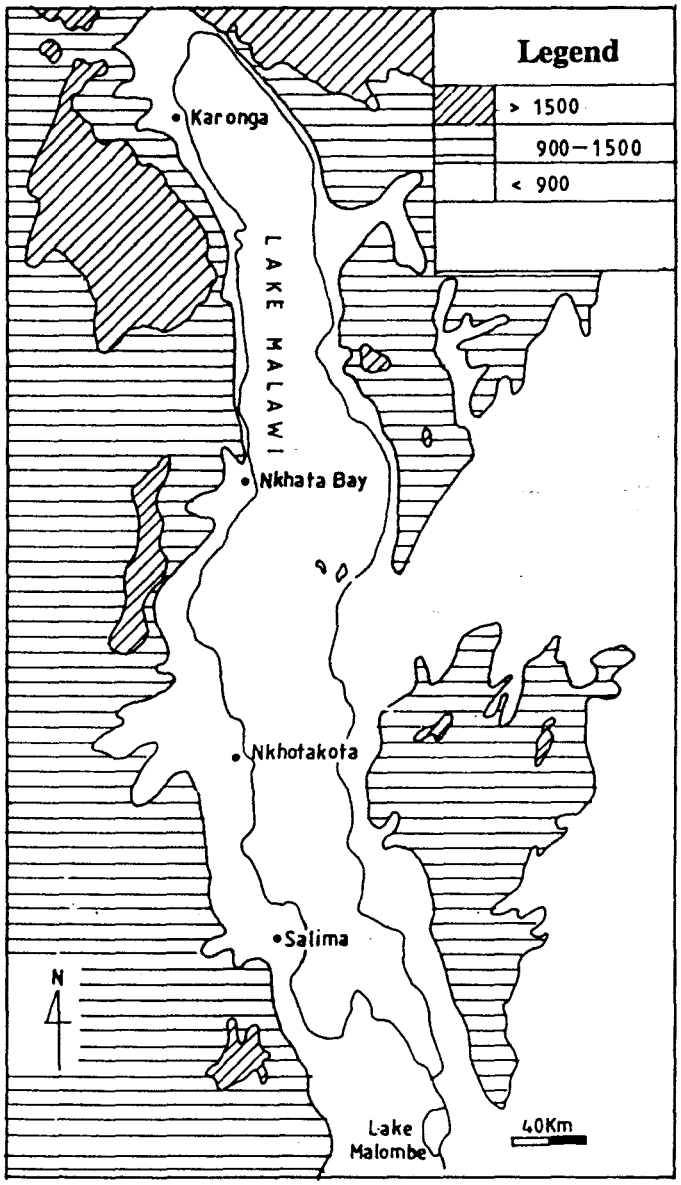


Fig. 5.1. Map of Lake Malawi and the landscape topography around it. The legend in the map shows the elevation in metres above sea level of each landscape unit around Lake Malawi.

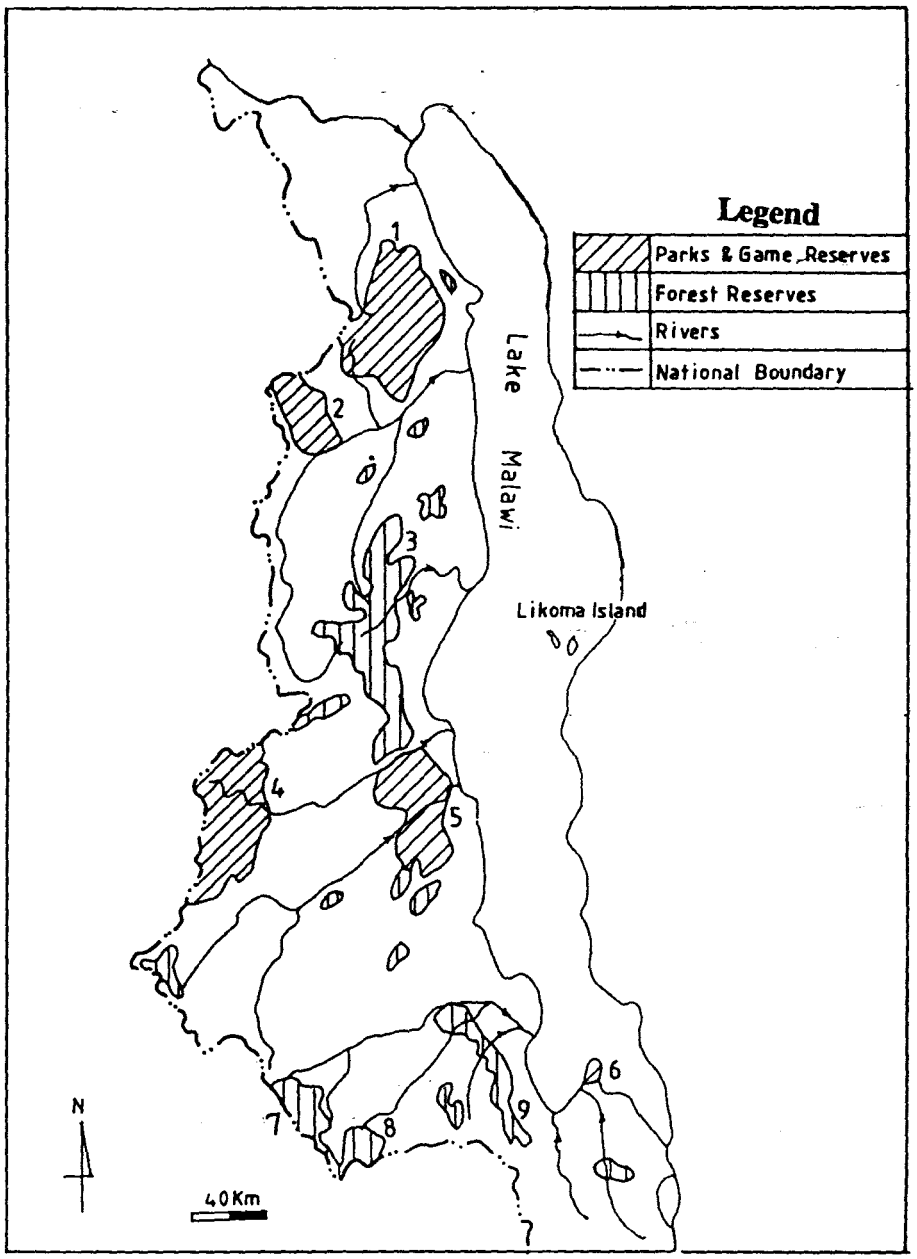


Fig. 5.2. Map of Malawi with insets of major protected areas that preserve Lake Malawi's catchment area: 1 = Nyika National Park, 2 = Vwaza Wildlife Reserve, 3 = Viphya Forest Reserve, 4 = Kasungu National Park, 5 = Nkhotakota Wildlife Reserve, 6 = Lake Malawi National Park, 7 = Dzalanyama Forest Reserve, 8 = Mchinji Forest Reserve and 9 = Thuma/Dedza Forest Reserve.

Arable land in Malawi is, however limited, and the demand for the abolishment of protected areas for purposes of cultivation and/or settlement is on the increase. To the majority of the people in rural areas, removing a small proportion of land from a wildlife park or reserve, or deproclaimation of protected areas seem to offer an immediate and effective solution to shortage of land. However, altering the boundary, or abolishing protected areas offers a very short-sighted and short-term solution to the problem for which more radical solutions are needed, such as reducing the human population growth through birth control measures and family planning. Complete abolishment of protected areas may certainly impoverish the country's rich terrestrial biodiversity and due to land degradation, lead to permanent impairment of the Lake Malawi's ecosystem integrity. The government should, therefore, endeavour to maintain all protected areas in their current status. However, the management strategy of these areas should aim at integrating biological conservation with economic development of the rural people, so that they can directly benefit and appreciate the importance of these protected areas. Munthali & Mughogho (1992), Munthali (1993), Bell *et al.* (1993) and Mkanda & Munthali (1994) have discussed ways in which local people can benefit from protected and marginal areas in Malawi. Cultivation of unprotected steep slopes of the Lake Malawi's catchment area should also be discouraged, but instead people should be encouraged to embark on wildlife-based enterprises such as beekeeping, harvesting mushrooms, saturniidae larvae and other edible insects which may earn local people more cash income than conventional agriculture in marginal areas (Munthali & Mughogho 1992).

Overall, the Mbuna of Lake Malawi are of multiple values to the Malawi's economy. Therefore, it is of utmost importance that all the potential threats are recognised, assessed and monitored, and where necessary mitigative measures should be implemented to prevent human-induced extinction of any of the Mbuna species, regardless of where it occurs in the Lake Malawi.

Chapter 6

General Discussion and Conclusion

This chapter provides a synthesis of previous discussions and extends the work to provide a better understanding of the interaction between the introduced and native species.

This thesis proceeded on the premise that the presence of introduced Mbuna species in the Lake Malawi National Park may pose a threat in the long-term to the diversity of native Mbuna species. The key hypotheses addressed were:

1. **that the introduced species having originated from a region of Lake Malawi which is generally poor in nutrients and introduced into an area which is richer in nutrients (Eccles 1974; Twombly 1983; Haberyan & Mhone 1991; Bootsma 1993a, 1993b), would cope better with periods of limited primary productivity and nutrient scarcity, which occur seasonally and frequently in an oligotrophic lake, such as Lake Malawi (Lowe-McConnell 1975). Consequently, they may improve in their condition and fecundity, and this would account for their increase in population density in the Lake Malawi National Park, where they have been introduced;**
2. **that introduced Mbuna species may have succeeded to establish themselves in the seemingly crowded community at Thumbi West Island, probably because: (a) there is no competition, consequently, introduced species are filling unused space; (b) the introduced and native species are ecological equivalents, so there is no threat, unless the introduced species are fitter, *e.g.*, by dominating in the use of essential resources, such as food and/or breeding space; (c) the introduced and native Mbuna species coexist through ecological separation, such as by utilizing different microhabitats within the rocky shore.**

Results on condition factor and fecundity (chapter 2) suggest that some of the introduced species, *e.g.*, *Pseudotropheus callainos* and *P. tropheops* 'red cheek' may have responded positively to enhanced nutrients in the southern Lake Malawi where they have been introduced. These species were found to have better condition factors, and higher relative fecundity in the park than at sites of their origin in the northern Lake Malawi. The introduced species, *Cynotilapia afra*, *P. callainos* and *P. tropheops* 'red cheek' at Thumbi West Island, also start to reproduce at relatively smaller size than the native species with which they overlap in microhabitat requirements (chapter 2). In so doing, they may probably be maximising their life-span fecundity. Furthermore, although the number of eggs produced by *P. tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest' did not differ significantly, the former had higher gonad indices than the latter. Consequently, it may also have a high probability of producing large offspring which may have high competitive abilities for essential resources (chapter 2). However, the disparity in the gonad indices between *P. tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest' may simply reflect their genetic differences, probably with no overt implications on the size of the offspring they produce.

Although the introduced species' fecundity indices in the park were superior over conspecifics in northern Lake Malawi, and the native species they were compared with, such disparities can not be attributed entirely to differences in nutrient regimes between the northern and the southern Lake Malawi. This is because no study has ever been undertaken to quantify dietary influences separately from other environmental variables that may influence fecundity. Consequently, there is need for field and laboratory studies to confirm the role of different nutrient regimes on the fecundity of Mbuna species.

The absolute fecundity of introduced species, or high relative fecundity exhibited by the introduced species also does not necessarily indicate success in their population growth in the Lake Malawi National Park. Factors such as survival

of offspring after recruitment to maturity, and their ability to secure breeding territories and contribute to the gene pools of the future (chapter 3 & 4) may be more important determinants of each introduced species' successful population growth in the park.

In Mbuna, just as in other cichlids, there is generally a high degree of parental care (Fryer & Iles 1972; Barlow 1977). Males of most Mbuna species defend breeding territories, and there are complex sets of courtship behaviours which lead to the female picking up the eggs in her mouth (chapter 2). The eggs are kept in the mouth until the embryos develop into the free-swimming young (chapter 2). Recruitment to the community first occurs when the female deposits free-swimming young among the rocks (Fryer 1959; Fryer & Iles 1972; Trendall 1988b). However, unlike the other rock-dwelling cichlids of Lake Malawi, such as *Protomelas taeniolatus* which guard brood of free-swimming young, and retrieve them when predators threaten (Trendall 1988b; Robinson 1995), guarding of young in the Mbuna has never been observed. Consequently mortality after recruitment is very high, and according to Trendall (1988b), only about 10% of the juvenile Mbuna may survive more than three weeks after being recruited to the rocky habitat.

Priority residence effects (*e.g.*, Braddock 1949; De Boer & Heuts 1973; Brown & Green 1976; Figler *et al.*1986) have been observed in the juvenile Mbuna (Trendall 1988b). Thus, the presence of juveniles of one species in a habitat can decrease, or prevent subsequent recruitment of the same or different species. At Thumbi West Island, Trendall (1988b) reported that the presence of a juvenile fish under a rock reduced both the number of recruits that became resident and the length of stay by juveniles that became resident. He further noted that the first recruits to occupy a space were more successful than subsequent recruits, and attributed such success to aggressive behaviour by residents, which he observed in very small Mbuna both in the field and aquaria. Therefore since some of the introduced species' breeding peaks precede the breeding peaks of

the native species with which they overlap in microhabitat requirements (chapter 2), it can be assumed that due to priority residence effects, the introduced species' offspring may have a competitive edge in the use of essential resources, *e.g.*, refuge over the native species whose peak recruitment occurs later in the year. If territoriality in the Mbuna develops at such an early stage, then in the long-term, introduced species that have their peak recruitment earlier than the native species with which they overlap in microhabitat requirement may dominate in occupying optimal breeding territories (chapter 3). This may have greater consequences on the population growth of native species. However, nothing is currently known about space utilization, and interaction between the juveniles of introduced and native Mbuna species in the park. Therefore, future studies should also focus on juveniles in order to gain more knowledge about the interaction of alien and native species in Lake Malawi National Park.

With regards to the question of whether introduced and native species exclude each other or if they coexist, results of the study reported in chapter 3 suggest that both competitive exclusion and coexistence occur.

Competitive exclusion

Competitive exclusion normally occurs when ecologically similar species utilize the same resources in a closed and stable environment (Gause 1934; MacArther 1972; Sale 1976; Pianka 1978). In the case of the Mbuna of this study, there are similarities in the microhabitat requirements by the introduced and native species (chapter 3). Consequently, interference competition is apparent between them (chapter 3). This competition is manifested because these Mbuna species need to establish territories in which they breed, feed and sometimes seek shelter. Of great importance among these, is the need for them to locate and defend optimal sites (defined in chapter 3) in which males are capable of attracting conspecific females, in order to breed and contribute to the gene pools of the future generations. The choice of optimal territory sites is however, constrained by the fact that females preferentially mate with males that defend

significantly smaller holes, or crevices among the rocks, probably because such holes minimise the risks of egg predation during spawning (chapter 3). Consequently, there is a high premium on territory sites with small holes, or crevices. However, optimal territory sites are limited around Thumbi West Island, so the presence of introduced Mbuna species may constitute a threat, in that they occupy space that could otherwise be occupied by the native species with similar space requirements. Evidence in support of this includes:

(i) natural interspecific territorial turn-over between the introduced and native species with similar microhabitat requirements;

(ii) the presence of large numbers of adult supernumerary males of both introduced and native species that are unable to establish breeding territories, and;

(iii) an increase in number of the native Mbuna species, *P. zebra* and *P. tropheops* 'orange chest' after experimentally removing the introduced species which have similar space requirements as them, suggesting that the latter may be displacing the native species (chapter 3).

The probability of the native species being displaced by introduced species may increase as the population density of introduced species increases, because the rate of encounters between them and native species increases. Consequently, the introduced species may gain access to some territory sites occupied by native species by attrition, or persistent encroachment into the territories occupied by the native species, particularly those that have similar space requirements as introduced species. This seems likely because over the past twenty years, the introduced species that have increased in number and expanded their distribution around Thumbi West Island are the most aggressive and strongly territorial, *e.g.*, *C. afra* and *P. tropheops* 'red cheek'. The only exception to this is *P. callainos*, which though not as aggressive interspecifically, is capable of overlapping its territories with some native species, albeit its microhabitat requirements being similar to such native species (chapter 3 & 4).

Even if the introduced species do not directly displace the native species, the native species' opportunities to utilize the available breeding sites may be limited because such sites are being occupied by the expanding populations of introduced Mbuna species. However, other introduced species within the 3 - 7m depth zone, which occur in small numbers and have restricted distribution (chapter 4), may be marginalised or displaced by the native species that may be more competitive at exploiting optimal microhabitats. Therefore, in terms of space utilization, the least abundant introduced Mbuna species may have the least impact on the native Mbuna species. Future studies should also focus on the introduced species that have been less successful, in order to gain more knowledge about the interaction between introduced and native species in the Lake Malawi National Park.

Overall, in terms of competitive exclusion, results reported in chapter 3 of this thesis suggest that where introduced species occur in large numbers, they may limit

the population size of territorial native species with which they overlap in microhabitat requirements, by occupying space which could otherwise be used by such native species. However, it is unlikely that the introduced species, *C. afra*, *P. callainos* and *P. tropheops* 'red cheek' would drive any of the native species with which they were compared to extinction. The principal arguments in support of this are (chapter 3):

(i) The population of males holding territories at any particular time fluctuates in response to the natural interspecific territory turn-over. In this respect, none of the introduced species maintained absolute dominance, because some of their territories were reoccupied by the native species. Therefore, some of the displaced native species, or their supernumerary males manage to occupy and defend optimal sites, and have the opportunity to contribute to their population gene pools. Even at sampling sites, #: 4 & 5 (Table 4.1, chapter 4), where the proportion of territorial males of native Mbuna species is below 50%, during the 30

months of field observation, both the population of introduced and native Mbuna holding territories did not change significantly (Fig. 4.3, chapter 4), suggesting that an equilibrium between them may have been reached. Further monitoring of these populations is recommended in order to detect trends that may shed more light on the potential or actual impacts of introduced Mbuna on the native taxa in Lake Malawi National Park.

(ii) Even in situations where a native species was observed in a microhabitat that was largely not of its preference, it managed to occupy patches of suitable sites, and was capable of breeding, *e.g.*, *Pseudotropheus zebra* at sites predominated by large rocks (chapter 3).

(iii) The Mbuna breed throughout the year (Fryer & Iles 1972; Ribbink *et al.* 1983a; Marsh *et al.* 1986; also see chapter 2 of this thesis), and since males of these fishes are polygamous, and have intraspecifically shared paternity (Fryer & Iles 1972; Ribbink *et al.* 1983a), territorial males are capable of fertilizing many gravid females of their own species in a year. Hence, the presence of introduced species may not detrimentally limit the population of native species at Thumbi West Island, particularly as none of the introduced species maintain total dominance over the native species.

(iv) The native species, *P. zebra* and *P. tropheops* 'orange chest' which significantly increased in numbers after the removal of some introduced species are abundant and widely distributed at Thumbi West Island and in the Lake Malawi National Park (Ribbink *et al.* 1983a). *Pseudotropheus zebra* also occurs in large numbers outside the park, and has a wide distribution in Lake Malawi as a whole, although there are some geographic variations (Ribbink *et al.* 1983a). Therefore, *C. afra* which competes with it for the same microhabitats is not a serious threat to its continued existence.

(v) The ecological release (*sensu* Fausch & White 1981) exhibited by some native species, notably the non-territorial fishes that fed in the vacated territories after the removal of introduced species (chapter 3), did not

provide enough evidence that they might be deprived nutritionally as a result of the presence of introduced species. Non-territorial Mbuna are not as sedentary as territorial Mbuna, therefore they are capable of searching for vacant spaces in which to feed.

(vi) Not all of the interactions between the introduced and native species may be negative. Though based on limited data, the mutual defence of territories by some males of an introduced species *P. tropheops* 'red cheek' and some females of a native species, *Protomelas taeniolatus* that guard fry, is of greater benefit to the latter, as it reduces the cost of defence for its fry, while at the same time it maximises its opportunities to feed. Further field studies are needed to substantiate this association.

What is probably happening is that upon initial colonization, the population of introduced species may grow exponentially, depending on the availability of suitable microhabitats, and an equilibrium between the number of territorial males of introduced and native species may be reached. This appears to be the case at sites, #: 4 & 5 (chapter 3). Competition for breeding space would only intensify once the carrying capacity in a particular area has been reached, and it is at this stage that some individuals of the introduced and native species seem to take each others territories (see Table 3.14, chapter 3), but not at an intensity which drives the other to extinction.

The displacements observed between the introduced and native species are minor in comparison with the intraspecific exclusions from breeding territories. Within each species, particularly those that occur in large numbers, only a small proportion of males are capable of establishing breeding territories (*e.g.*, see removal experiment, chapter 3). This suggests that competitive exclusion as a consequence of limited breeding space is an inherent phenomenon within the Mbuna community. However, as hypothesised in chapter 3, it is unlikely that all territorial males maintain their territoriality for life. Factors such as nutritional constraints (Munthali, in press *a*), predation, illegal fishing, intruder

persistent encroachment (chapter 3), senescence, or natural death may force some of the territory tenants at some stage to abandon their "residence". Consequently, this would open up vacancies for both conspecific and heterospecific supernumerary males. Therefore, there might be a considerable territory turn-over between territorial and non-territorial males. Further field studies are needed to confirm this hypothesis.

Coexistence

Ecologically similar species may coexist by (i) exploiting different habitats, or microhabitats, (ii) eating different food, or (iii) by being active at different times of day (Pianka 1978). With the exception of diet, in the study reported in chapter 3, both the microhabitat preference and diurnal activities of the introduced and native Mbuna species were assessed. In terms of microhabitat requirements, two guilds have been discerned (chapter 3): (i) the small rock guild, *i.e.* species that prefer rocks $\leq$ 65 cm and holes $\leq$ 10 cm in diameter, *e.g.*, the introduced species, *C. afra*, *P. callainos* and a native species, *P. zebra* and (ii) the large rock guild, *i.e.*, species that prefer rocks $>$ 65 cm and holes $>$ 10 cm in diameter, *e.g.*, the introduced species, *P. tropheops* 'red cheek' and its sibling native species, *P. tropheops* 'orange chest'. Consequently, in terms of space requirements for breeding, species within each guild are in great conflict, leading to the displacements discussed above, and in chapter 3 of this thesis. However, with regard to trophic ecology, the Mbuna that prefer small rocks fed at different sites with different intensity and they also fed at different heights in the water column. This segregation seems to facilitate their coexistence in the same microhabitats. However, this is not the case with the Mbuna of the large rock guild, whose territory choice depends on availability of large rocks. Territories held by these species were often far apart (chapter 3). However, it is not known whether this is incidental or if it is due to competition between them. Nonetheless, the occurrence of their territories distantly apart, seems to facilitate their coexistence in the same rocky habitat at Thumbi West Island.

Fryer and Iles (1972) also noted that many of the rock-dwelling cichlid species that exploit similar resources, both in diet and space coexist. Even sibling species (*i.e.*, members of the same species complex) can coexist in the same habitat, and their territories may overlap (Holzberg 1978; Marsh 1981). In chapter 3 of this thesis, it has also been shown that an introduced species, *P. callainos* and its sibling native species, *P. zebra* coexist and overlap their territories.

Conclusion

Introduced Mbuna species have been in the park for more than twenty years. The impacts they have had throughout these years on the native taxa are unknown. The 30 months studies reported in this thesis, are of short duration to adequately illuminate the impacts introduced species have had on the native fish species in the Lake Malawi National Park. However, despite this constraint, results reported in this thesis shed some light on:

(i) the possible factors that may contribute to the successful population growth and distribution of introduced Mbuna species around Thumbi West Island;

(ii) interference competition between them and the native rock-dwelling cichlid species, and;

(iii) the changes that take place after removal of some introduced species in the rocky zone at 3 - 7m depth. In this zone, results based on 30 months of field observations show that some introduced and native species have identical microhabitat requirements. Consequently, they compete and displace each other from territory sites. However, as none of the introduced species maintained constant territorial dominance, it seems unlikely that any of the native species that overlap in microhabitat requirements with the introduced species would be driven to extinction because of interference competition. Similarly, the native species that are affected by the introduced species are common and some have a wide distribution in Lake Malawi National Park, and Lake Malawi as a whole,

therefore, they are not in any immediate danger.

One of the management options considered for mitigating the impact of introduced Mbuna species on the native taxa, is culling. In terrestrial parks, culling is effective in regulating populations of large mammals that over-shoot their habitat thresholds. However, in aquatic parks, culling has not be used to regulate fish populations. The most important merit that it would have in the Lake Malawi National Park, is the reduction in population size of introduced species. At least, some of the native Mbuna populations could increase to some degree (Fig. 3.21, chapter 3). Also, non-territorial native fish species may have the opportunity to feed in the vacated territories, previously occupied by the alien taxa (Table 3.15, chapter 3). However, where introduced species are concerned, culling should only be adopted as a management option once it is apparent that without it, one or more of the native fish species endemic to the park would be driven to extinction. Since results reported in this thesis do not suggest that this might be the case, culling of the introduced species in Lake Malawi National Park is currently not recommended for the species studied in the 3 - 7m depth zone. Similarly, translocation of endemic species from one part of the lake to the other should be strictly prohibited, as different species may interact differently. Also, it should be noted that results reported in this thesis may have limited application to other species which may behave differently, and have different ecological requirements from the species on which studies reported in this thesis were focused.

Introduced species also occur in the shallow and intermediate zones. It is imperative, therefore, that studies be undertaken to the point where the impact of the introduced species on the entire native Mbuna community in the park is fully understood before culling can be re-evaluated as a management option for mitigating the problem of introduced species in the Lake Malawi National Park. Other areas that require further studies include:

(i) Space utilization and survivorship of juveniles of the introduced and native species.

(ii) Laboratory studies to confirm the role of different nutrient regimes on the condition and fecundity of the Mbuna.

(iii) Interactions between the native species and the introduced species whose populations have not substantially increased over the past twenty years.

(iv) Monitoring of populations of the introduced and native species in the established permanent quadrates at 3 - 7m depth zone around Thumbi West Island should continue, in order to shed more light on population trends, and the impacts introduced species may have on native species. This is particularly important because the natural structure of the native Mbuna community has changed as a result of the presence of species endemic to other parts of the lake. The introduced species probably have subtle long-term effects, which may only be detected by long-term monitoring of their populations in relation to the native species with equivalent ecological requirements.

(vi) Future studies should also look into the possibility of hybridization between the introduced and native species.

Since the studies reported in this thesis are the first to focus on the processes of population growth and competition between the introduced and native Mbuna, they have contributed to the understanding of the inter-relationships between the introduced and native species, and have laid the foundation for future studies that would supplement the knowledge so far gained. Also, the knowledge gained from the population growth and distribution of Mbuna, and in particular from the removal experiment (chapter 3), has direct implications on the ornamental fish trade, currently operating on a *laisser-faire* basis in Lake Malawi. In chapter 3, it has been shown that after repeated removal of territorial males, the size (SL) of some Mbuna species declines significantly. However, smaller and immature males are incapable of breeding successfully. Consequently, repeated removal of restricted small populations for the ornamental fish trade may in the

long-term exterminate such populations. Similarly, in chapter 4 of this thesis, it has been shown that the populations of some Mbuna species grow very slowly, and have restricted distributions. Repeated harvesting of such species would exacerbate homozygosity with the danger of eventual extinction. This knowledge is important in that it could be used in the formulation of harvesting quotas for the localised Mbuna species that are exported from Lake Malawi.

The Mbuna of Lake Malawi are unique, and have multiple values to the country (chapter 5). Therefore, conservation efforts to save them from extinction should not only focus on Lake Malawi National Park, but on Lake Malawi as a whole (see chapter 5 for recommendations), because not all the Mbuna species occurring in Lake Malawi have representatives in the Lake Malawi National Park.

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Appendix 1. List of the common rock-dwelling cichlid species found at Thumbi West Island, Lake Malawi National Park (see Ribbink et al. 1983 for a comprehensive list)

Introduced species

Aulonacara 'blue'

Cynotilapia afra

Labidochromis strigatus

L. gigas

L. freibergi

Labeotropheus fuelleborni 'yellow-flank'

Melanochromis parallelus

M. 'red'

M. 'black-white' *johanni*

M. joanjohnsonae

Pseudotropheus callainos

P. aurora

P. livingstonii 'likoma'

P. jacksonae

P. tropheops 'red check'

P. tropheops 'membe'

P. zebra 'fusco'

(b) native species

Cyathochromis obliquidens

Dimidiochromis compressiceps

D. kiwinge

Genyochromis mento

Labidiochromis vellicans

L. pallidus

L. 'blue bar'

Labeotropheus fuellebornii

L. trewavasae

Melanochromis melanopterus

M. cf. *chipokae*

M. auratus

M. vermivorus

Nimbochromis linni

N. livinhstoni

N. polystigma

Peudotropheus zebra

P. cf. *heteropictus*

P. livingstonii

P. tropheops 'lilac'

P. tropheops 'orange chest'

P. cf. *gracilior*

P. tropheops 'intermediate'

P. tropheops 'broad mouth'

P. cf. *microstoma*

P. tropheops 'gold otter'

P. elongatus 'slab'

P. elongatus 'yellow tail'

P. elongatus 'aggressive'

P. 'aggresive brown'

P. 'aggressive blue'

P. 'tiny'

P. socolofi

Petrotilapia tridentiger

P. genalutea

P. nigra