A CONTRIBUTION TO THE ECOLOGY AND SYSTEMATICS OF THE GENUS PETROTILAPIA (PISCES : CICHLIDAE) IN LAKE MALAWI

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ABSTRACT

The nominal species Petrotilapia tridentiger Trewavas, a rock-frequenting fish from Lake Malawi, occurs in three distinct male and female colour forms at Monkey Bay. Field observations on courtship and aggression indicate that the three colour forms are distinct species. The taxonomy of the three species of Petrotilapia that occur at Monkey Bay is revised. P. tridentiger is redescribed and two new species, P. genalutea and P. nigra, are described. The three species are very similar morphologically and are considered to be sibling species. The only morphological character which reliably separates the three sibling species is live coloration. Live coloration is considered to be an important component of the specific mate recognition systems in Petrotilapia species. The coloration of a further fourteen forms of Petrotilapia is described and it is suggested that these forms are valid species.

Space resource partitioning plays an important role in facilitating the coexistence of Petrotilapia sibling species. Space is partially partitioned in terms of depth range. In shallow water, where all three species are sympatric, there are differences in the feeding sites used by the various Petrotilapia forms. Changes in niche breadth and overlap, which are associated with changes in the abundance of epilithic algae, indicate that competition for feeding space occurs between the three Petrotilapia species. The Petrotilapia species partition their resources according to a social dominance hierarchy. Dominant forms, such as territorial males, P. tridentiger females and schooling P. genalutea females, have access to rich food supplies which occur within the territories of certain highly aggressive Pseudotropheus species. Petrotilapia species are facultative and opportunistic feeders.

Speciation in allopatry is considered to be the mechanism which adequately explains the current diversity of the genus *Petrotilapia*. The importance of an integrative approach to future systematic and ecological research on Lake Malawi cichlids is stressed.

CHAPTER I

INTRODUCTION

The tropics are well known for their high diversity of plant and animal species, and for the frequent occurrence together of large numbers of closely related species (Cain, 1969). The Great Lakes of tropical Africa - Victoria, Tanganyika and Malawi, are particularly interesting in that they all have very speciose fish faunas which have evolved in a short time span (Fryer & Iles, 1972; Greenwood, 1974). The family Cichlidae is dominant in these fish faunas. Lake Malawi, which is estimated to be only two to three million years old (Beadle, 1974), has almost 300 described endemic species of cichlid and taxonomists and field biologists have recently suggested that there are probably as many as 500 cichlid species in the lake (D.S.C. Lewis, pers.comm.; K.R. McKaye, pers.comm.)

The cichlid faunas of Lake Tanganyika and Malawi are of further interest in that speciation is believed to have been intralacustrine (Fryer & Iles, 1972). The situation in Lake Victoria is different in that this lake was almost definitely fragmented into numerous isolated bodies of water during its formation (Greenwood, 1974).

A knowledge of species formation and persistence is a prerequisite for understanding the high species diversity encountered in the Great Lakes of Africa (Lowe-McConnell, 1969). Species persistence is primarily an ecological problem, one of its essential components being the coexistence of sympatric species, whereas species formation is primarily an evolutionary problem.

This thesis addresses the problem of species diversity in the genus Petrotilapia (family: Cichlidae) which is endemic to Lake Malawi. Prior to this work very little research had been conducted on this genus, consequently a certain amount of descriptive information must be presented before more conceptually complex aspects, such as species coexistence and evolution, can be considered.

One of the very basic problems with which this thesis deals is that of species definition. In Lake Malawi there are a large number of species which are very similar to one another morphologically and consequently present taxonomic difficulties (Lewis, in prep.a). In this thesis the various species of Petrotilapia are defined on the basis of morphology, behaviour and coloration and the new species which occur at Monkey Bay, the major study site, are described. An informal, brief description only of the other forms is presented as it is beyond the scope of this thesis to describe these fourteen forms formally. After a section on the biology of the genus, the problem of coexistence of the three species at Monkey Bay is considered. The thesis ends with a discussion on the mode of speciation in Petrotilapia.

The rock-frequenting cichlids of Lake Malawi, including Petrotilapia species, form the basis of the ornamental fish trade in Malawi. In order for Malawi to derive maximum benefit from this industry it is essential to strike a balance between exploitation and conservation. Before this can be achieved, it is necessary to have a sound knowledge of the biology of these fishes and this thesis also contributes towards that end.

INTRODUCTION TO LAKE MALAWI

Lake Malawi lies between latitudes 9°30' S and 14°30' S (Figure 1). It is situated in the Great Rift Valley of East Africa, which extends from the Red Sea through to the Zambezi River. The western shore and the southerly part of the eastern shore of the lake lies in Malawi and the remainder of the eastern shore lies in Mocambique and Tanzania. All the research presented in this thesis was conducted in Malawian territorial waters.

Lake Malawi is approximately 600 km long, 16 to 80 km wide and covers an area of 29 604 km^2. The lake consists of a single basin with a maximum depth of about 700 m near the western shore north of Nkhata Bay (Figure 2). The water surface is approximately 500 m above sea level. The water in Lake Malawi is exceptionally clear (Muntz, 1976). Fryer (1959) records that a 200 mm diameter Secchi disc was normally visible at 16 m just offshore at Nkhata Bay. Near Monkey Bay, eighteen Secchi disc readings taken between 1960 and 1962 varied between 10 m and 22 m, with a mean of 15.25 m (Muntz, 1976). Malawi has a tropical climate but marked seasonal variations in wind, temperature and precipitation do occur (Eccles, 1974). There are two major seasons:

(a) The cooler, dry season from April to September which is characterized by steady south-east trade winds which blow along the axis of the lake.

(b) The hot season from October to March with rainfall occurring predominantly in the latter part of this season. Winds during this season are irregular and of short duration (Beauchamp, 1953). Water

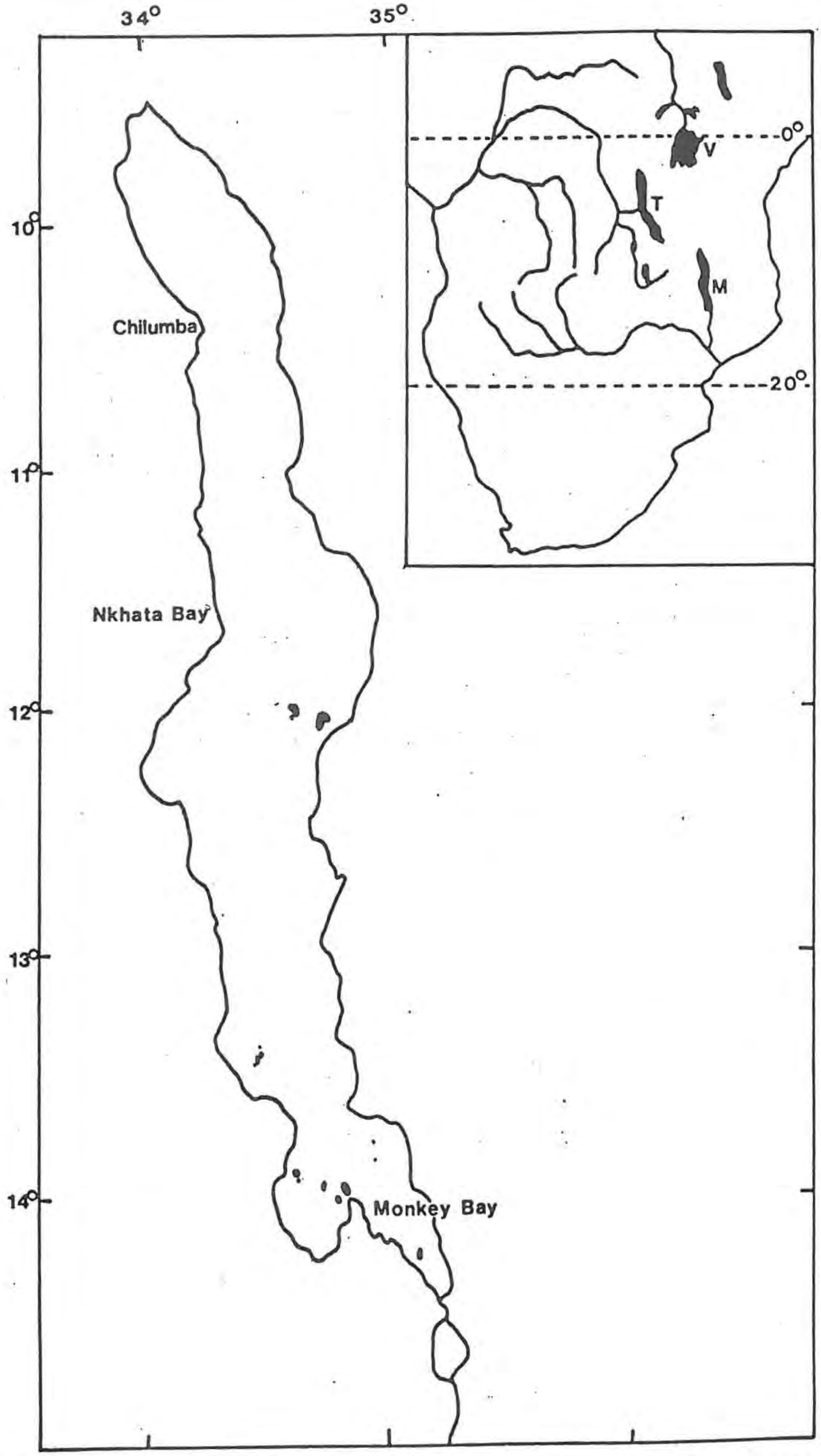

Figure 1. Map of Lake Malawi with an inset of central and southern Africa showing Lake Victoria (V), Lake Malawi (M) and Lake Tanganyika (T).

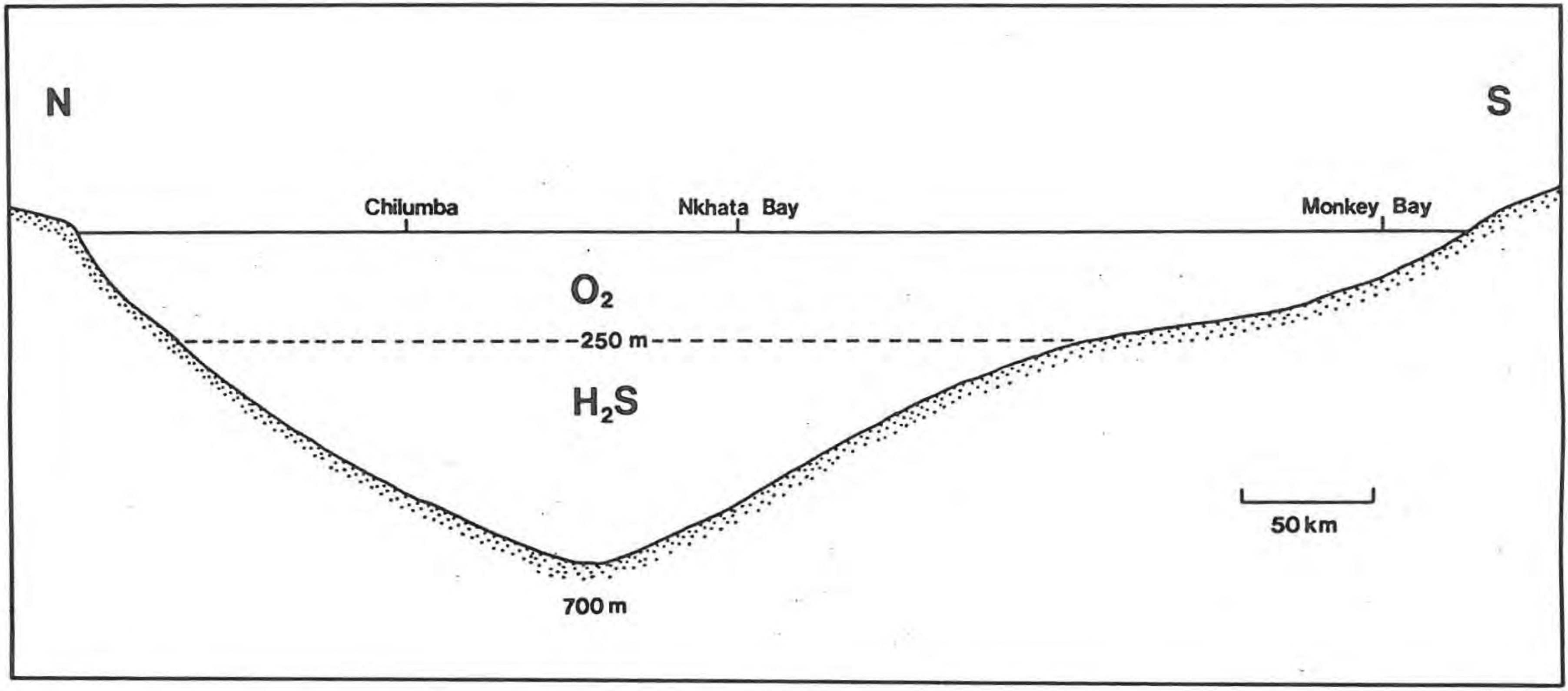

Figure 2. A diagrammatic longitudinal section through Lake Malawi (after Beauchamp, 1953).

surface temperatures between May 1979 and November 1980 ranged from 23.0°C in July and August to 30.5°C in January (personal observation). During the hot season there is a marked thermocline but Beauchamp (1953) has suggested that the lake may occasionally become homothermal in the cooler, windy season. Even when an obvious thermocline is present, some mixing does take place between the epilimnion and hypolimnion and dissolved oxygen occurs down to about 250 m. Beyond this depth the water is anoxic and contains hydrogen sulphide. According to Beauchamp (1953) sudden changes in oxygen content can take place at 150 m which present physiological problems to any animal life at this depth. The strong south-easterly trade winds can cause upwelling of nutrient rich water, especially in the south of the lake (Eccles, 1974). Furthermore the annual runoff from the land (which is equivalent to a rise in the level of the lake from 1.73 m to 2.5 m (Eccles, 1974)) should be a source of nutrient salts. In addition to the documented seasonal fluctuations in temperature, there should be a seasonal fluctuation in nutrients and in primary productivity.

Many of the cichlid fishes are confined to the littoral zone (0-40 m deep). This region mainly comprises rocky areas interspersed with sandy stretches, although aquatic plant beds intermingled with patches of sand and scattered rock also occur. Many of the islands are entirely rock, but some of the larger ones contain sandy beaches as well as rocky shores. A particular community of fishes is usually associated with each of the habitats (sand, rock or plant beds) of the littoral zone (Fryer, 1959).

PREVIOUS STATUS AND KNOWLEDGE OF PETROTILAPIA

In 1925-6 Dr C. Christy was responsible for making a large collection of Lake Malawi fishes including over 3 500 cichlids (Jackson, 1961). Trewavas (1935), after examining the Christy collection at the British Museum (Natural History), published a synopsis of the cichlids in which the species are listed and a key presented. Jackson (1961) reports that full descriptions of all species mentioned in the synopsis had been written by Trewavas, but they were never published. One of the new genera in the synopsis is *Petrotilapia* Trewavas which was represented by one species, *P. tridentiger*. A combination of two characteristics, tooth shape and mouth position, distinguishes this genus from other Lake Malawi cichlid genera. Trewavas (1935) observed that all teeth are tricuspid, movable and have expanded crowns and slender shafts. In only one other genus, *Labeotropheus* Ahl, are all the teeth tricuspid but the position of the mouth, tooth insertion, tooth shaft shape and dental arcade differ considerably in the two genera.

P. tridentiger is represented by a syntype collection at the British Museum (Natural History). The syntype specimens were collected at Deep Bay (=Chilumba) in the north, Monkey Bay in the south and from "Bar to Kudzi" in the extreme south. All specimens examined were considered to be conspecific and hence *Petrotilapia* was regarded as a monotypic genus.

Petrotilapia is one of ten genera of rock-frequenting cichlids considered to be more closely related to each other than to any other genus in the lake (Trewavas, 1935; Oliver & Loiselle, 1972). This closely related group of species is characterized by having small scales on the nape, chest and cheek. In general they are very colourful fishes and are known collectively by the Chitonga name Mbuna. *Petrotilapia tridentiger* (*sensu* Trewavas) is one of the largest Mbuna, attaining a total length of 250 mm (Jackson, 1961).

The first ecological study on an Mbuna community was conducted by Fryer (1959). His work consisted mainly of stomach content analyses of the fish communities at Nkhata Bay on the mid-western shore of Lake Malawi (Figure 1). Fryer considered *P. tridentiger* to be an enigmatic species. In the first instance it is one of a group of Mbuna species whose diet consists entirely of loosely attached epilithic algae (loose aufwuchs*). This group, in particular *P. tridentiger* and *Pseudotropheus zebra* (Boulenger), apparently shared an identical diet as well as habitat and consequently appeared to defy the competitive exclusion principle. Fryer (1959) concluded that these two species managed to coexist as they did not compete for food due to a superabundance of aufwuchs. The hypothesis that food is superabundant was not tested as there were no data at the time to support or reject Fryer's theory.

The second enigmatic aspect concerning *P. tridentiger* is that it apparently exhibits a random and "bewildering diversity" of colour phases (Fryer, 1959). As a general rule Fryer contended that colour was very important as a means of conveying species identity and sex in the Mbuna. In the case of *P. tridentiger*, Fryer concluded that colour could not be important in mate and species recognition and suggested instead that "some other characteristic such as the formation of the mouth and dentition may be important in preventing the successful completion of any interspecific mating behaviour" with other species of Mbuna.

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* The German term *Aufwuchs* has come into common usage in English and is therefore spelt with a lower case 'a' in this thesis.

CHAPTER 2

BASIC BIOLOGY OF THE GENUS PETROTILAPIA

Aspects of the biology of Petrotilapia species which are necessary for an understanding of their systematics, ecology and speciation are described, on the basis of the present work, in this chapter. Much of the following information is typical of the Cichlidae.

BREEDING

Adult males establish territories on the rocky shore. These territories are defended against conspecific males only. Males hold territories throughout the year, but it is not known for how long a particular male remains territorial. By virtue of their territorial instinct males are very sedentary, while females and non-territorial males are more mobile. Pair bonds are not formed between sexes and all Petrotilapia species are both polyandrous and polygynous. Frequently a female will move from territory to territory and be courted by each occupant in turn. Males likewise attempt to court any apparently gravid female which moves into their territory. Petrotilapia species are maternal mouth-brooders i.e. the female broods eggs and young in its mouth. Petrotilapia species have the elaborate behavioural repertoires typical of most cichlids (Baerends & Baerends-van Roon, 1950; Ribbink, 1971). Some of these behaviour patterns are important to this thesis and are discussed and illustrated in the following section.

Agonistic behaviour

When an adult male enters a conspecific male's territory, the resident male responds aggressively towards the intruder and attempts to chase it out of the territory (Figure 3). As the intruder (i) approaches, the

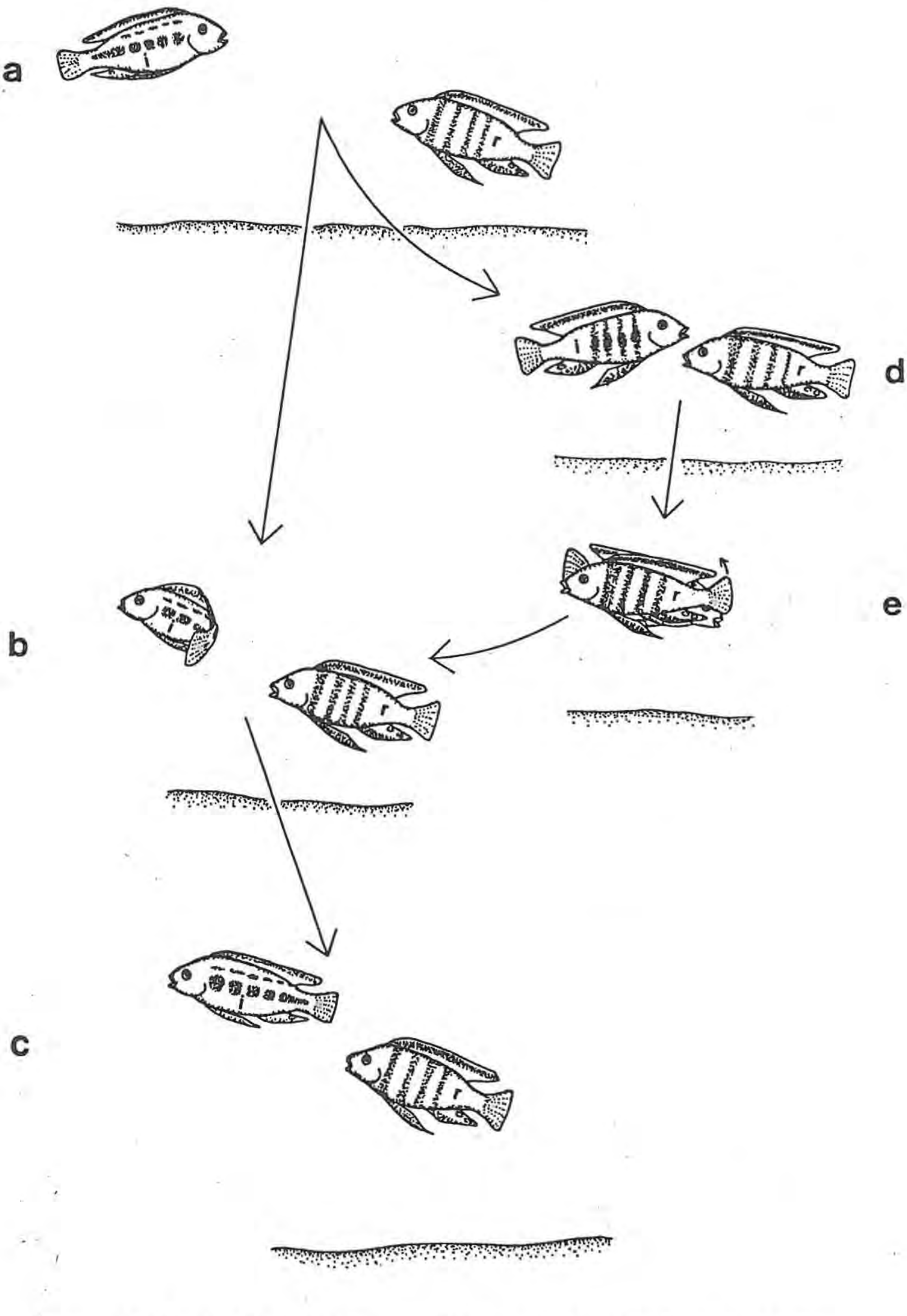

Figure 3. Agonistic behaviour: (a) the resident male (r) adopts a 'lateral display' as the intruder male (i) approaches the territory boundary; (b) the intruder turns to flee; (c) the resident male escorts the intruder across the territory boundary; (d) the intruder, having entered the territory, responds aggressively by adopting a 'lateral display' and changing colour; (e) 'tail beating' by the resident male towards the intruder.

resident (r) extends its median fins, depresses the pelvic fins and remains motionless in a 'lateral display' (Figure 3a). Usually, when confronted in this manner, the intruder retreats (3b) and the resident escorts the intruder until it crosses the territory boundary (3c). Occasionally the intruder responds aggressively to the resident male's challenge by going into 'lateral display' and emphasizing male coloration. The resident responds by remaining in 'lateral display' and intensifying its dominance coloration (3d). The two adversaries then orientate themselves in a parallel head-to-tail position and while remaining in 'lateral display' the resident powerfully beats its tail ('tail beating') towards the head of the intruder (3e). The intruder then turns and flees (3b) and the resident escorts the intruder until it crosses the territory boundary (3c).

Courtship behaviour

As a female (f) draws near to a territory the resident male (m) approaches the female in 'lateral display' (Figure 4a). The male performs a 'side-shake' by adopting an arched position antero-ventral to the female and sending a series of rapid undulations through the fins, especially the dorsal fin (4b). The male then faces away from the female towards the territory centre and performs a 'follow-shake' by wagging its caudal fin from side to side (4c). The male then performs a 'lead-swim' by swimming with exaggerated caudal movements towards the territory centre and the female follows (4d).

If the female is not receptive the behaviour pattern can break down at any one of these stages and the male will respond by chasing the female out of the territory (4e). If the female is receptive the male leads her into a cavern beneath the rocks (out of sight of divers) where spawning presumably occurs. The male sometimes repeats the courtship repertoire if the female does not respond initially to any one of its signals.

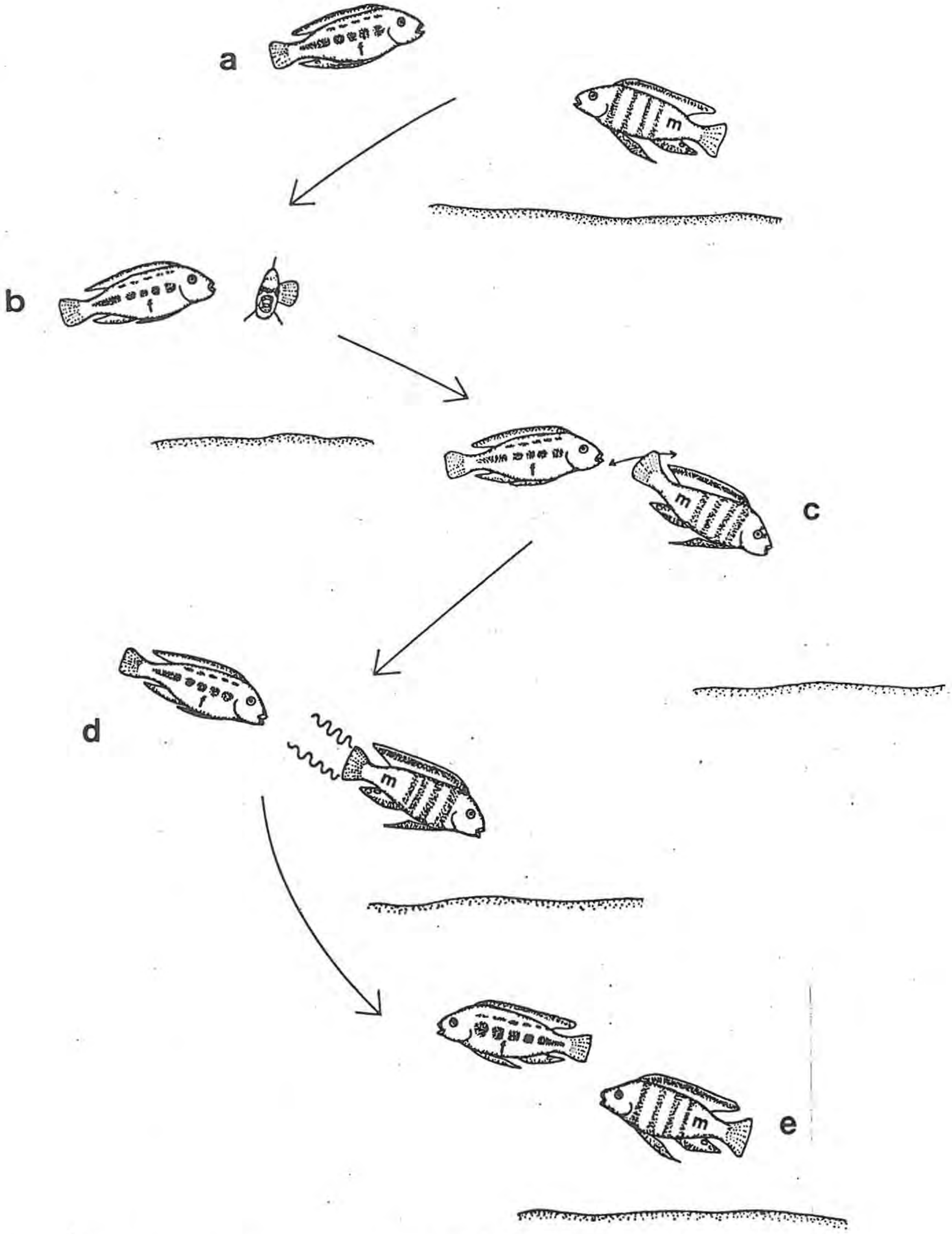

Figure 4. Courtship: (a) the male (m) adopts a 'lateral display' as the female (f) approaches; (b) the male gives a 'side shake'; (c) the male gives a 'follow shake'; (d) a 'lead swim' by the male, with the female following; (e) the male chases the female from the territory.

FEEDING

Fryer (1959) considered P. tridentiger to be a stenotypic feeder subsisting entirely on loose aufwuchs (loosely attached, epilithic algae). As Fryer suggested, the teeth of Petrotilapia species are designed for the efficient collection of loosely attached epilithic algae. When grazing, the individual orientates itself vertically to the rock surface and firmly presses its mouth against the substrate while making a series of rapid open-close movements with its jaws (Figure 5). Thus the bands of teeth act as combs, the gaps between each cusp and tooth permitting the free passage of firmly attached algal strands, while the cusps scrape up any loosely attached and unattached matter. Due to the mobility of the jaws and the movable nature of the slender teeth, the tooth bands accommodate themselves to any irregularities in the rocky surface and thus form a continuous and efficient scraping band.

Recent evidence has shown that Petrotilapia species are capable of ingesting a wide range of prey and in the laboratory will feed on zooplankton, loosely attached benthic prey, food floating on the surface, fish fry, scales and fins from live fishes and loose aufwuchs (Liem, 1980). Recent field work has shown that juvenile Petrotilapia species regularly switch between feeding on epilithic algae and feeding on plankton (McKaye & Marsh, in prep.). Occasionally females and subadult males feed on zoo- and phytoplankton and during dense phytoplankton blooms territorial males, as well as females and juveniles use this transient but rich resource. Plankton feeding in Petrotilapia species is discussed in Chapter 8.

Figure 5. A group of 'Orange *Petrotilapia*' females grazing on algae. The fish in the lower left hand corner and the fish on the extreme right are not *Petrotilapia* species. The 'Orange *Petrotilapia*' form is described as a new species in Chapter 4.

CHAPTER 3

THE EXISTENCE OF A COMPLEX OF SIBLING SPECIES OF PETROTILAPIA AT MONKEY BAY

INTRODUCTION

During a survey of the ornamental fish of Lake Malawi (1978-80), it became apparent that there were a variety of differently coloured Petrotilapia forms on most rocky shores. Using SCUBA it was possible to recognize distinct colour forms of territorial males, which often differed from one another in terms of body size and depth distribution as well. By contrast non-territorial individuals, male and female, showed considerable variation in coloration and distinctive colour forms were not obvious initially (but with experience distinct colour forms of all maturation stages could be recognized). From these observations an hypothesis was erected that each colour form of territorial male belongs to a discrete species. For every colour form of male there should be a corresponding female sufficiently distinct from other females to permit specific mate recognition.

All biological definitions of species focus on reproduction. One of the most widely quoted is that of Mayr (1942) who defines species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups".

This section describes the coloration of the three colour forms of Petrotilapia at Monkey Bay and shows that each colour form of territorial male practises non-random courtship. This is implicit evidence that the colour forms mate assortatively and are therefore discrete species. Differences in agonistic behaviour between the three nominal species are also documented.

METHODS

All observations were made in Monkey Bay using a mask and snorkel while floating on the surface, or SCUBA to a depth of 6 m. Observations were recorded underwater on a perspex slate using a lead pencil. Good visibility, ranging from 4-10 m, ensured that the Petrotilapia forms could be observed from a reasonable distance (not less than 2 m) and at this distance diver disturbance was not noticeable. Mbuna appear to be less disturbed by divers than many other lacustrine, riverine and marine fishes (M.N. Bruton, pers.comm.).

RESULTS

Coloration

Notes on live coloration were recorded in the field and from photographs taken both in the field and in aquaria. Although in the initial phases of the research non-territorial individuals appeared to have no distinctive colour forms, with experience three distinctive forms of adult non-territorial male as well as three female and subadult male colour forms could be recognized. For convenience the three colour forms will be referred to here as 'Blue Petrotilapia', 'Orange Petrotilapia' and 'Black Petrotilapia'. The names refer to the distinguishing colour of the territorial males.

'Blue Petrotilapia' (Figures 6 & 7)

Live territorial males have a pale blue background colour with seven to nine darker blue vertical bars below the dorsal fin. The belly and gular regions are whitish-blue. The dorsal fin is pale blue with dark blue to black bars in the posterior interray membranes. The caudal fin trailing

Figure 6. Territorial male 'Blue Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

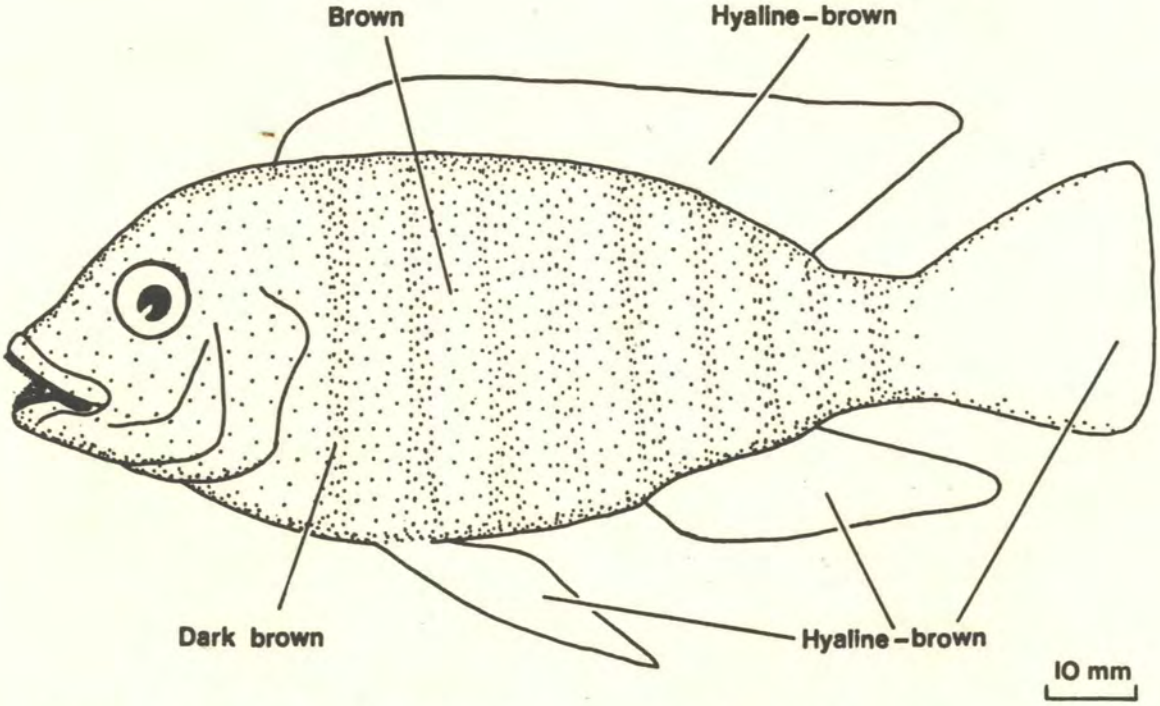

Figure 7. Adult female 'Blue Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

edge is pale orange-brown, the rays are dark blue to black and the membrane between the rays is sky blue. The anal fin is pale blue with dark blue to black stripes in the posterior membranes and one to five bright orange to yellow ocelli on the posterior angle membrane. The leading and ventral edge of the anal fin is whitish-blue. The pelvic fins have a whitish-blue leading edge and pale blue rays and membranes. The pectoral fins are hyaline.

Adult non-territorial males are darker than territorial males and their overall colour tends towards purple. The background colour of live adult females and juveniles varies from dark brown to pale grey-brown. All have seven to ten dark brown vertical bars below the dorsal fin although in darker individuals these markings are partially obscured. The dorsal, caudal, anal and pelvic fins are a semi-transparent brown and match the background colour of the fish. The pectoral fins are hyaline.

'Orange *Petrotilapia*' (Figures 8 & 9)

Live territorial males have a bluish-grey background colour with four to six dark grey vertical bars below the dorsal fin from the first dorsal spine to the base of the caudal fin. The four anteriormost bars are invariably distinct but the posterior ones are often partially faded and sometimes completely absent. There are two dark grey stripes on the head, one extending from the tip of the snout to the orbit and the other between the orbits. The 'cheek' region, below the orbit extending from the snout to the posterior margin of the operculum, and the gular are an orange-brown rust colour. This rust area may extend variably beyond the operculum below the pectoral fins from the base of the pelvic fins to midway between the pelvic fins and vent. The rust colour fades posteriorly and the remainder of the belly is dark bluish-grey. Dorsal

Figure 8. Territorial male 'Orange Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

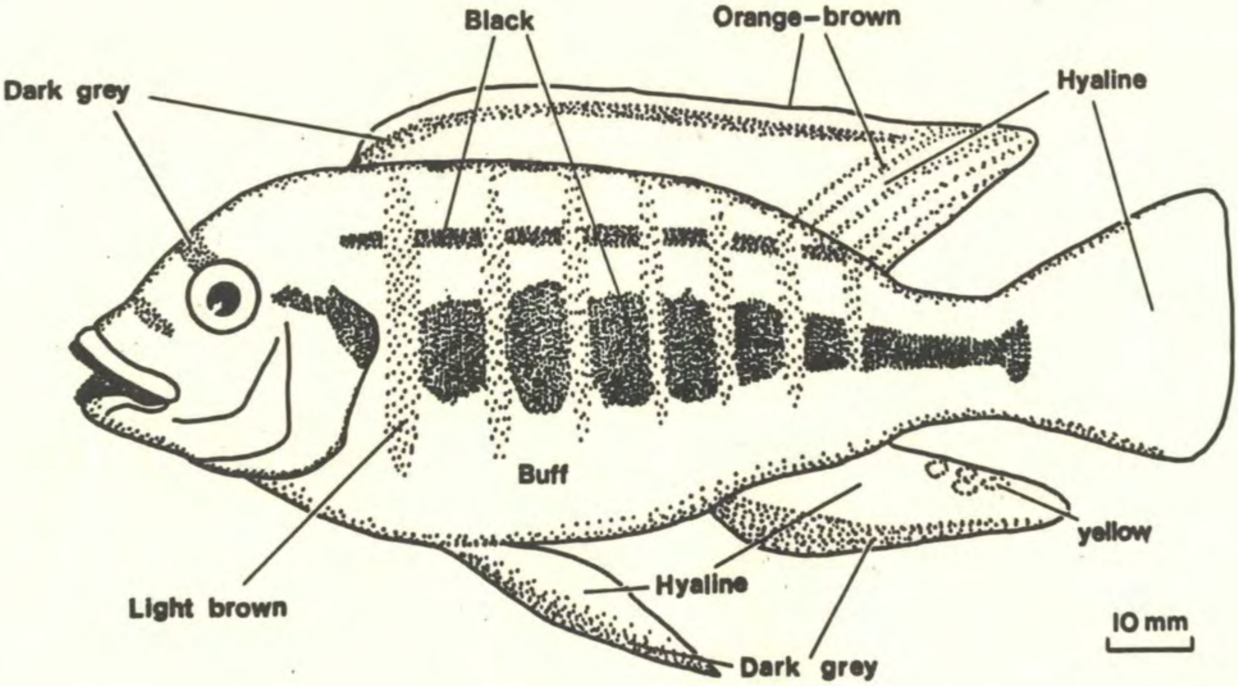

Figure 9. Adult female 'Orange Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

fin lappets are variable in coloration, in some specimens they are pale orange-yellow, sometimes fading posteriorly and giving way to a pale blue, in others the lappets are entirely pale blue. Immediately below the dorsal fin lappets is a very thin light blue band followed by a black submarginal longitudinal stripe, approximately one half of the dorsal fin depth and extending the entire length of the dorsal fin in most specimens. Directly below this black stripe is another thin light blue stripe. Below this stripe the dorsal fin is a semi-transparent grey with orange-brown oval blotches on the interspine and interray membranes of some specimens. The posterior few interray membranes are black. The caudal fin trailing edge is orange, the rays are black and the interray membranes are a semi-transparent pale blue. The anal fin is semi-transparent grey with a thick black bar on the distal edge extending from the base of the first anal spine to the posterior angle. One to four bright yellow ocelli occur on the interray membranes on the posterior angle. The pelvic fins have a whitish-blue leading edge, including the spine, the rays are black and interray membranes are an orange-brown. The pectoral fins are hyaline.

The background coloration of live non-territorial individuals is off-white to pale yellow-brown with a white belly. A series of thick dark brown to black mid-lateral blotches extend from just posterior to the operculum to the base of the caudal fin. The blotches are normally close together and often fuse, particularly posteriorly, to form a continuous stripe. Another series of thin dark brown to black dorso-lateral blotches runs above and parallel to the thick blotches to the posterior base of the dorsal fin. Nine to ten pale brown vertical bars occur on the flanks and caudal peduncle. The dorsal fin is hyaline except for orange-brown tips on the lappets, a thin dark grey to black submarginal longitudinal stripe and orange-brown posterior rays. The anal fin and pelvic fins are hyaline except for dark grey stripes on their distal edges. Small pale yellow ocelli occur on the anal fin angle in some specimens. Adult non-territorial males have a yellow to orange flush on their 'cheeks' and gular region.

'Black *Petrotilapia*' (Figures 10 & 11)

Live territorial males have a dark grey-blue background colour with seven to nine black vertical bars below the dorsal fin. The head, gular and caudal peduncle are black except for a dark blue interorbital bar. Dorsal fin lappets are normally orange but may be pale blue in some specimens. Immediately beneath the dorsal fin lappets is a thin band of sky blue followed by a thick black longitudinal stripe. The black stripe covers most of the dorsal. Below the stripe the dorsal fin is dark grey with orange flecks in some specimens. The caudal fin trailing edge is orange-brown, the rays are black and the interray membranes are sky blue. The anal fin is predominantly black with a pale blue distal edge and one to four bright yellow ocelli on the posterior angle membrane. The pelvic fins have a whitish-blue leading edge, black rays and dark brown interray membranes. The trailing edges of the pelvic fins are often hyaline. The pectoral fins have black rays and hyaline interray membranes.

Non-territorial adult individuals have a pale brown background colour. Superimposed on the flanks are two longitudinal dark brown to black stripes which are segmented by seven to ten grey-brown vertical bars. The ground colour of the fins is hyaline and the dorsal fin has pale orange lappets and a thin dark grey to black longitudinal submarginal stripe. The anal and pelvic fins have pale blue distal borders with a

Figure 10. Territorial male 'Black Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

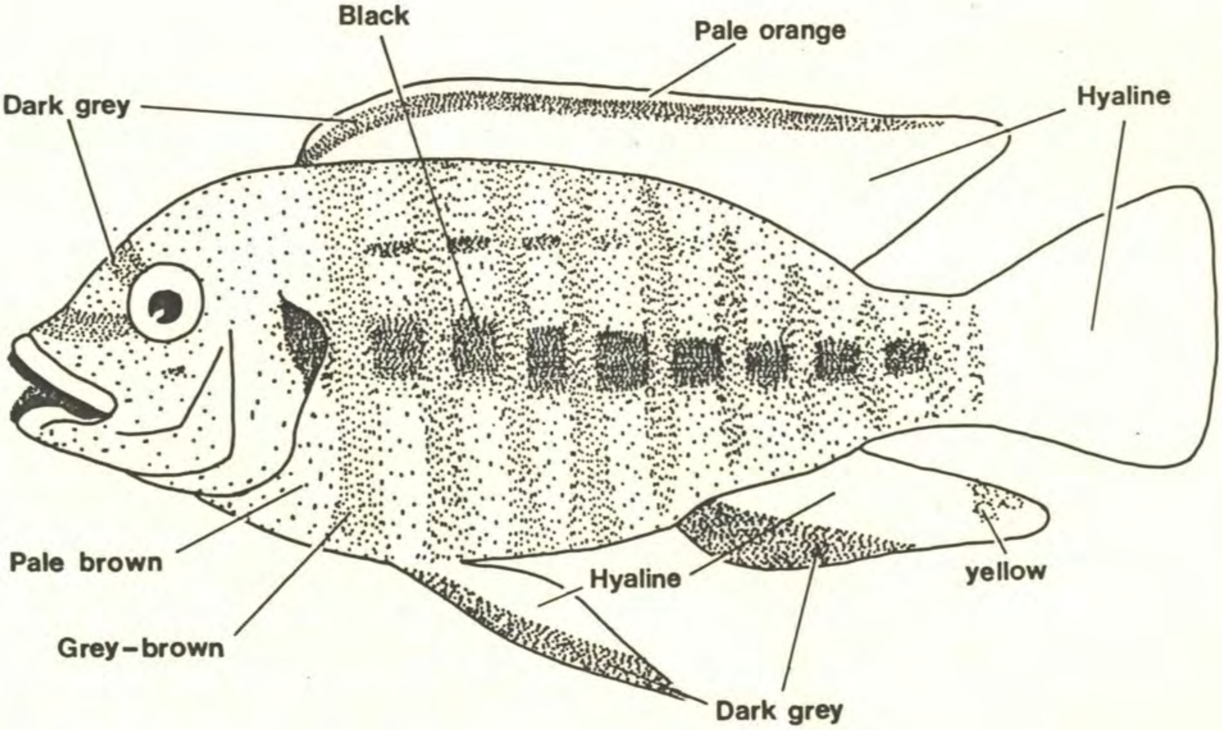

Figure 11. Adult female 'Black Petrotilapia' from Monkey Bay (refer to Chapter 4 for species description).

thin brown to black stripe adjacent to this. The anal fin sometimes has a few yellow ocelli on the posterior angle membrane. Juveniles are uniform pale brown with hyaline fins. Adult markings are faintly visible in some juvenile specimens.

Mate selection

If the three colour forms at Monkey Bay are distinct species then there should be no interbreeding between these forms. Initially it was difficult to detect any consistent differences in the coloration of 'Black Petrotilapia' and 'Orange Petrotilapia' females but by following individual females it became apparent that a particular female would be courted by one male colour form only.

During the 600 hours spent under water in Monkey Bay, approximately 3 600 courtships between Petrotilapia forms were observed and notes were taken on 639 of these courtships. With two exceptions, the colour forms courted in a non-random manner. Of the 639 courtships, 257 were between 'Orange Petrotilapia', 194 were between 'Black Petrotilapia' and 186 were between 'Blue Petrotilapia'. The two exceptions involve courtship of 'Orange Petrotilapia' females by 'Black Petrotilapia' males. In the first attempt a 'Black Petrotilapia' male directed a very brief courtship display towards an 'Orange Petrotilapia' female which was simultaneously being courted by an 'Orange Petrotilapia' male. The 'Black Petrotilapia' male swam up to the female, turned around and gave a brief 'follow shake', but the female did not respond at all. At this point the 'Orange Petrotilapia' male chased the 'Black Petrotilapia' male away. On the second occasion a 'Black Petrotilapia' rose up in the water column to meet a passing 'Orange Petrotilapia' female, gave a brief 'follow shake' and immediately returned to its territory. The female did not respond to the male. Apart from these two unsuccessful attempts it is evident that mate recognition within a colour form is good and that courtship is non-random.

Not every female that passed its corresponding male was courted. Some females were completely ignored whereas others were responded to repeatedly by numerous males in the space of a few minutes. Furthermore males responded vigorously towards certain females and courtships were prolonged but in other instances the courtships were very brief. Prolonged courtships only ensued if females responded positively to the male's 'follow shake'. From the foregoing it seems possible that males can distinguish between gravid and non-gravid females. Furthermore, although males initiate courtship the success of the courtship depends upon both male and female giving the correct responses to the other's signals. Unfortunately males often lead responsive females into caverns beneath rocks which makes further observations difficult and despite the period spent on underwater observations, no spawning of Petrotilapia forms was seen.

Aggression

The males of many Mbuna species hold breeding territories which they defend against conspecifics only (Sharp, in prep.). If the colour forms at Monkey Bay are distinct species then differences in the frequency of aggression expressed by the Petrotilapia colour forms towards one another may be expected. In order to obtain quantitative data on aggression, two kinds of observations were made at Monkey Bay: (a) continuous observations of non-territorial males and (b) continuous observations of territorial males.

(a) Continuous observations of non-territorial males

Non territorial males of all three colour forms were followed as they moved about the rocky shore. The response of all territorial males within 75 cm (estimated) of the path of the non-territorial male was noted. A total of 47 non-territorial males were observed in this way (14 'Blue *Petrotilapia*', 15 'Orange *Petrotilapia*' and 18 'Black *Petrotilapia*'). The number of aggressive responses by territorial males of the three colour forms relative to the number of approaches by non-territorial males was noted and expressed as a percentage (Table I). A Chi-square test was performed on these data.

It is evident from Table 1 that territorial individuals invariably respond aggressively toward non-territorial males of the same colour form as themselves. Territorial males only occasionally respond aggressively towards non-territorial males of different colour forms to themselves ($p < 0.001$). Non-territorial males of a different colour form to the territory holder were only responded to when they were less than 30 cm (estimated) from the territorial male.

Table 1. Percentage of encounters between territorial males and non-territorial males of the Monkey Bay *Petrotilapia* colour forms which were aggressive. Data based on the responses of territorial males towards 14 'Blue *Petrotilapia*', 15 'Orange *Petrotilapia*' and 18 'Black *Petrotilapia*' non-territorial males. (n) represents the number of encounters between non-territorial males and territorial males.

		Territorial male *Petrotilapia* colour forms		
		'Blue' %(n)	'Orange' %(n)	'Black' %(n)
non-territorial male *Petrotilapia* colour forms	'Blue'	88 (44)	6 (39)	21 (47)
	'Orange'	6 (22)	96 (95)	0 (45)
	'Black'	19 (23)	23 (29)	93 (65)

The response normally consisted of a brief 'lateral display' and ended as the intruder moved away. Males of the same colour form as the territory occupant elicited a response as they entered the territory. The territorial male in these situations often moved 2 to 3 m to confront the intruder. A prolonged 'lateral display' was followed by a vigorous chase until the intruder left the territory. In certain cases 'tail beating' accompanied the 'lateral display'.

(b) Continuous observations of territorial males

Individual territorial males were observed for a continuous period of 20 minutes and all aggression was recorded. Observations were made on 12 individuals of each colour form between 0800 and 1000 hours over a 10 day period in late October 1979. The percentage frequency of aggression by the territorial males of each colour form towards (1) male and (2) female and juvenile *Petrotilapia* of each colour form is expressed in Figure 12. A chi-square test was used to determine significant differences in response of territorial males towards the three *Petrotilapia* colour forms. As the colour forms do not occur in equal numbers at the study site the expected values were adjusted according to the ratios of occurrence. The ratios were derived by counting all *Petrotilapia* of each colour form while swimming at random within the study site ('Blue *Petrotilapia*' 30 males, 48 females; 'Orange *Petrotilapia*' 20 males, 40 females; 'Black *Petrotilapia*' 40 males, 40 females). The Chi-square test indicated that territorial males respond most frequently towards their own colour forms irrespective of sex or maturity ($p < 0.001$).

Although it was not possible to quantify the degree of aggression of each encounter there were some obvious and consistent trends. Territorial

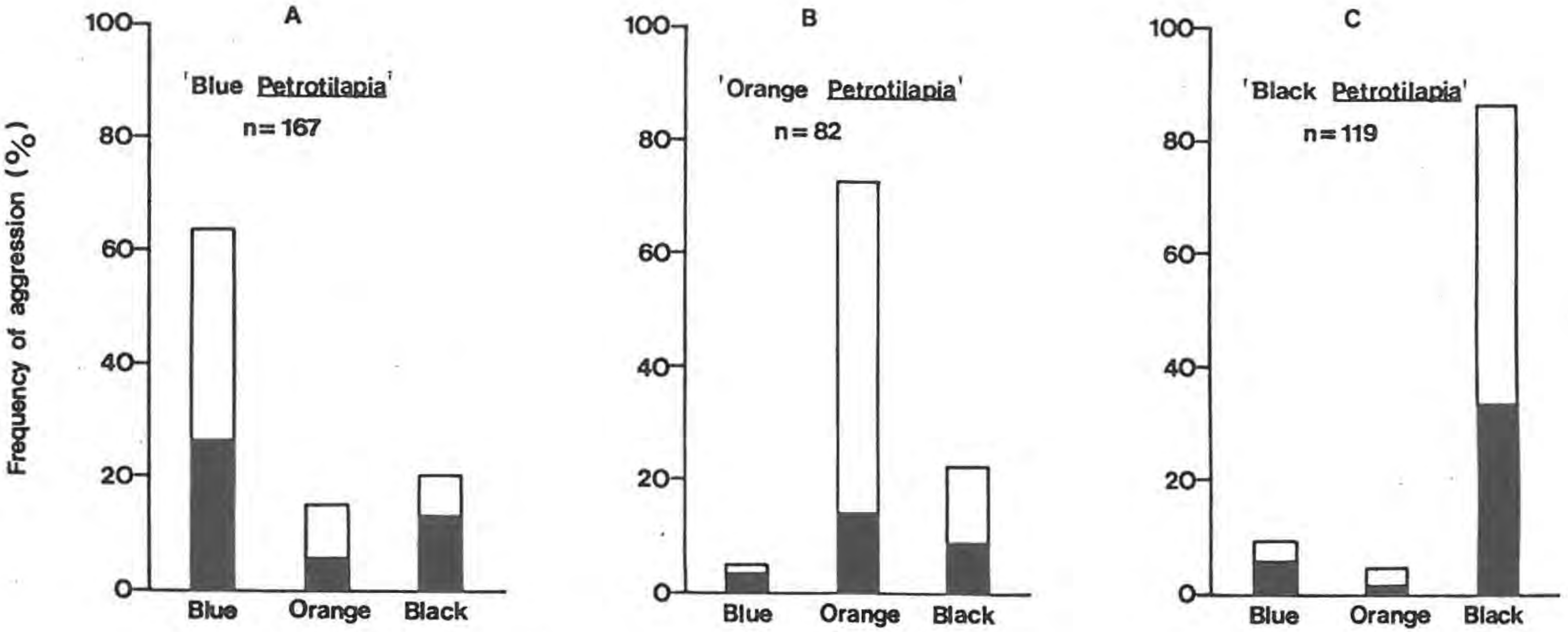

Figure 12. Percentage frequency of aggression directed by territorial male *Petrotilapia* towards male (shaded area) and female and juvenile (unshaded area) conspecifics and congeners. (a) response by 'Blue *Petrotilapia*' territorial males, (b) response by 'Orange *Petrotilapia*' territorial males, (c) response by 'Black *Petrotilapia*' territorial males. 'n' represents the total number of aggressive encounters.

males responded most vigorously towards males of their own colour form. Females and juveniles of all colour forms were normally responded to if they were less than 30 cm (estimated) from the territory occupant when the latter was feeding or courting. The male, in these circumstances, usually responded by darting briefly toward the intruder which would normally move a short distance away but was permitted to remain within the confines of the territory. Occasionally females and juveniles of the same colour form as the territorial male were chased and escorted out of the territory.

DISCUSSION

The results presented above indicate that the three colour forms at Monkey Bay represent three distinct gene pools and should therefore be considered as separate species. In view of the lack of obvious morphological distinctness between these fishes (see Chapter 4), they should be regarded as sibling species (*sensu* Mayr, 1963).

Numerous authors (Noble & Curtis, 1939; Baerends & Baerends-van Roon, 1950; Fryer, 1959, 1977; Greenwood, 1965, 1974; Eccles & Lewis, 1979; Lewis, in prep. a & b) believe that male coloration is important in species recognition and that it facilitates intraspecific mating in the Cichlidae.

Although it is beyond the scope of this thesis to demonstrate conclusively that coloration is an important component in the specific mate recognition system (SMRS) of *Petrotilapia* species, there is implicit evidence to this effect. While diving it is possible to distinguish between adults of the different species of *Petrotilapia* on the basis of colour, as shown above. Among young individuals there is considerable variation in colour, but at maturity intraspecific variation diminishes and concomitantly interspecific differences increase. This applies particularly to males where there is also an intensification of species specific coloration during courtship. It is a well established fact that cichlids have good vision and that visual communication is important in this family (Noble & Curtis, 1939). Recently Muntz (1976) has shown that the absorbance curves of the retinal pigments of some Lake Malawi cichlids match the spectral quality of the water so as to maximize the number of quanta collected. This underlines the importance of colour vision to these fish. Although Muntz (1976) did not investigate *Petrotilapia* species, the results obtained for other cichlid species, irrespective of their natural environment, were consistent. Furthermore a number of Mbuna species were studied by Muntz (1976) and thus it is reasonable to assume that *Petrotilapia* species have good colour vision as well.

Female coloration also appears to play an important role in species and mate recognition. The observations presented above suggest that males recognize conspecific females as it is the male which initiates courtship. In order for the courtship to culminate in spawning, recognition of conspecific males by the female is essential and it is in this regard that male coloration is important. Therefore, although the male initiates courtship, it is the female which finally selects the male as a mating partner.

On the basis of differences in live coloration and positive assortative mating it is easy to differentiate between sympatric species of *Petrotilapia*. The definition of allopatric species in this genus is not as straight forward. Lewis (in prep. a), referring to Lake Malawi cichlids, has pointed out that "no means has been devised for ascertaining whether morphologically similar allopatric forms are specifically distinct". An analysis of the specific mate recognition systems (SMRS) of allopatric populations may resolve this problem.

Paterson (1978) states that "members of a species share a common specific mate recognition system". Throughout a species' existence the SMRS remains fairly constant as it is subject to intense stabilizing selection. The reason for this is that mate recognition comprises a number of co-adapted stages whereby every signal from one partner results in an appropriate response from the other, following reception of the signal and interpretation by the specifically coded central nervous system (Paterson, 1978). This recognition concept of species is theoretically the key to species definition in sibling species complexes. If one population has an identical SMRS to another they must be conspecific. The practical problem is to identify the essential components of a species SMRS and to record it in a manner which can readily be compared to other SMRS's.

In the case of Petrotilapia species, and other Mbuna (Fryer & Iles, 1972), there is implicit evidence that coloration of sexually mature individuals is one of the most important components of the SMRS of each species. Although other aspects of behaviour are also likely to be important SMRS components, the first important signal in mate recognition in Petrotilapia species is that of colour. The initial acceptance or rejection of a mating partner depends on the coloration of the potential mate. As an SMRS is a co-adapted species feature, there must be agreement between both sexually mature male and sexually mature female coloration for two populations to be conspecific. Any colour differences between one or both sexes will probably cause a breakdown in recognition and therefore act as a barrier to reproduction. Thus where coloration is very different it is safe to assume that the species are distinct from one another. Caution is required in situations where colour differences are subtle.

CHAPTER 4

A TAXONOMIC DESCRIPTION OF THREE SPECIES OF PETROTILAPIA FROM MONKEY BAY

INTRODUCTION

The systematic history of the genus Petrotilapia is reviewed in Chapter 1 where it is mentioned that a detailed description of this genus has never been published. In this chapter the generic characteristics presented by Trewavas (1935) are reassessed, P. tridentiger is redescribed and two new species, P. genalutea and P. nigra, are described. In Chapter 3, P. tridentiger has been referred to as 'Blue Petrotilapia', P. genalutea as 'Orange Petrotilapia' and P. nigra as 'Black Petrotilapia'. The live coloration of these three species is described in Chapter 3.

METHODS

Live coloration is the most reliable feature distinguishing the three sibling species. Although it is easy to recognize adults of the three species under water, it is very difficult to identify preserved specimens reliably. Consequently it was necessary to base the species descriptions on specimens which had been identified in the field, and then captured. Specimens were collected individually by SCUBA divers who herded the fish into a fine mesh net. Morphometrics and meristics were taken of Monkey Bay specimens and observations and limited collections were made at other sites in the lake.

Morphometrics

Measurements were taken with vernier calipers reading to 0.1 mm using the technique of Eccles & Lewis (1977). The specimen is placed on a measuring board with its head touching the head block and with its body axis at right angles to the block. The perpendicular distance from the block to the appropriate point is then measured (Figure 13).

Total length is measured with the tail closed so that the outer rays are parallel to the axis. *Standard length* is taken as the distance from the tip of the snout to the posterior edge of the hypurals. *Length to dorsal end* and *length to anal end* is the axial distance from the posterior base of the dorsal and anal fins respectively to the tip of the snout. *Head length* is measured from the tip of the longer jaw to the most posterior margin of the bony operculum. *Snout length* is measured from the anterior edge of the snout (pressed against the head block of the measuring board) to the anterior border of the orbit. *Body depth* is the greatest depth, taken at right angles to the axis of the body. *Body width* is the greatest width of the fish taken along the transverse plane. *Caudal peduncle length* is the distance from the posterior tip of the hypurals to a vertical line from the posterior base of the dorsal fin. *Caudal peduncle* depth is the minimum vertical depth.

Eye diameter is the horizontal distance between the anterior and posterior border of the orbit. *Interorbital width* is the minimum distance between the dorsal bony margins of the two orbits. *Preorbital depth* is taken as the length of a line bisecting the lachrymal bone. *Premaxillary pedicel length* is the distance between the dorsal tip of the premaxillary pedicel and the ventral margin of the premaxilla, excluding the premaxillary teeth. *Premaxillary length* is the projected distance

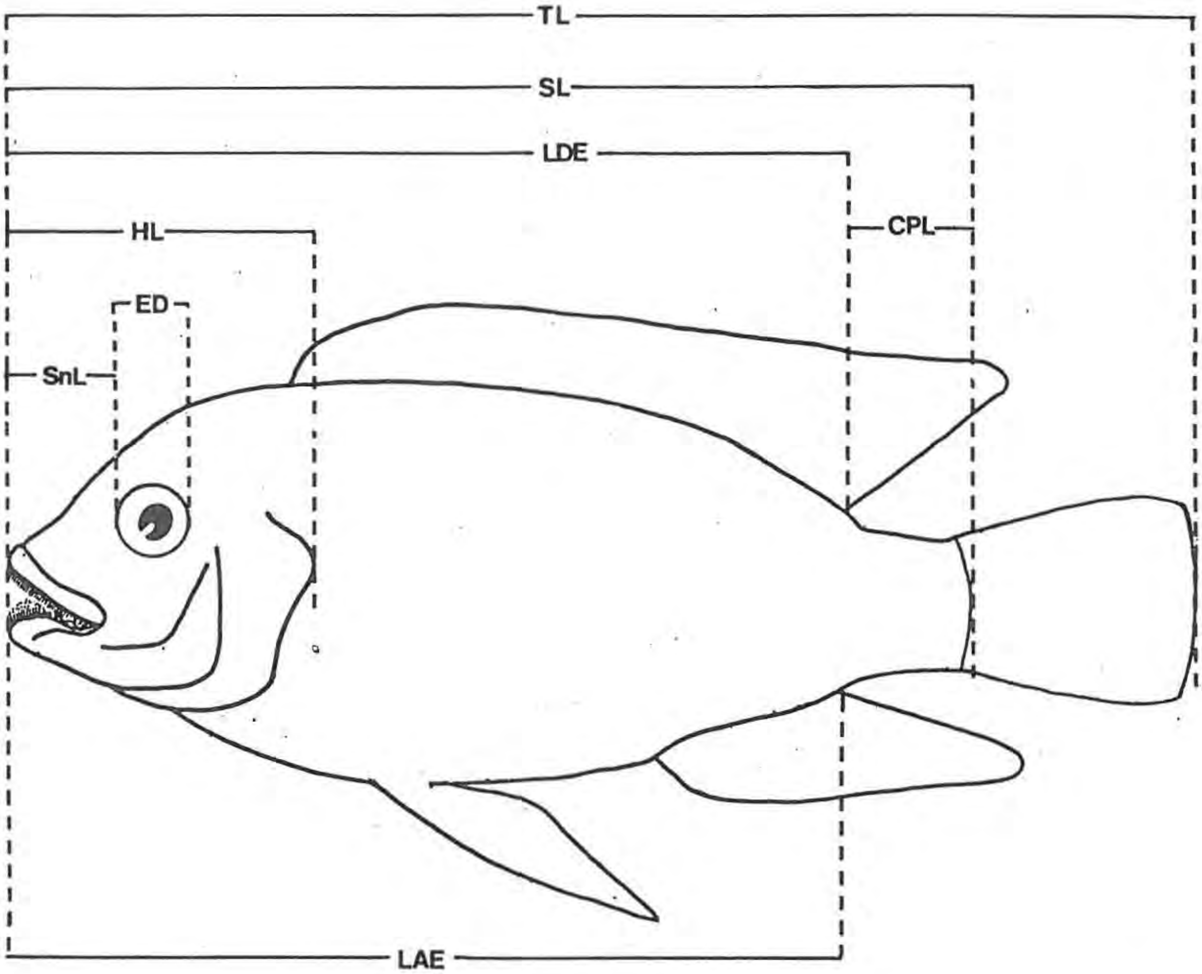

Figure 13. An outline of a Petrotilapia species in lateral view showing the perpendicular distances from the head block to appropriate points on the body used in the morphometric study. TL = total length; SL = standard length; LDE = length to dorsal end; LAE = length to anal end; HL = head length; ED = eye diameter; SnL = snout length; CPL = caudal peduncle length.

between the posterior tip of the premaxillary arm and the anterior tip of the premaxillary symphysis. *Premaxillary width* is the horizontal distance between the lateral tips of the premaxillary arms. *Lower jaw length* is the distance from the angle to the symphysis of the dentary. *Lower jaw width* is the widest point between the two dentary arms in ventral view.

Dorsal spine length is measured along the posterior border of the last dorsal spine. *Anal spine length* is measured along the posterior border of the third anal spine. *Length of pectoral fin* is taken from the upper part of the axilla to the tip of the longest ray. *Pelvic spine length* and *pelvic ray length* are measured from the point of articulation of the spine to the tip of the spine and longest ray respectively.

The following measurements refer to the lower pharyngeal bone: *Pharyngeal fork length* is the length along the median suture. *Pharyngeal total length* is the distance between the anterior tip of the pharyngeal bone and a horizontal line between the tips of the horns. *Pharyngeal width* is the distance between the horns. *Pharyngeal depth* is the greatest depth of the bone including the teeth. *Pharyngeal blade length* is the distance from the tip of the blade to the anterior tip of the dentigerous portion. *Pharyngeal blade depth* is the greatest depth transverse to the axis of the blade.

Meristics

The *pored scales* in both the upper and lower lateral lines are counted, with the exception of any pored scales which occur posterior to the hypurals. The *total lateral line* count reflects the number of scales in a longitudinal series as defined by Trewavas (1935): "at the end of the upper lateral line, one proceeds to the scale of the lower lateral line next behind the transverse row that includes the last scale of the upper lateral line and slopes downwards and forwards from it".

All *gill-rakers* that occurred on the outer edge of the anterior gill arch were counted. Counts are given for gill rakers on the epibranchial, on the region of articulation between the epibranchial and ceratobranchial, and on the ceratobranchial.

Vertebrae were counted from X-rays using the technique of Barel *et al.* (1977) to differentiate the caudal vertebrae from the abdominal vertebrae. The first caudal vertebra is taken as the one to which the first anal pterygiophore points. The last hypural bearing vertebra was included in the caudal vertebral count.

The illustrations and text in Barel *et al.* (1977) were used as the standard for the description of nonquantified form characters, such as the degree of curvature of the dorsal head profile.

Abbreviations used are as follows:

BMNH - British Museum (Natural History)
RUSI - J.L.B. Smith Institute of Ichthyology, Grahamstown
USNM - United States National Museum
L - length
D - depth
W - width
SL - standard length

Petrotilapia Trewavas, 1935

In general the diagnostic characters of the genus presented by Trewavas (1935) distinguish this genus from all other Lake Malawi cichlids. It should be noted, however, that contrary to the definition of Trewavas (1935), the teeth of Petrotilapia species are not all tricuspid and every specimen examined for this study had some distinctly unicuspid teeth. There is usually a single or double lateral series of stout unicuspid teeth along the proximal arms of the dentary and premaxilla, although some of these teeth may be weakly tricuspid. The broad bands of closely set teeth which occur on the major dentigerous area are usually all tricuspid but in some specimens the posterior row has a few unicuspid teeth. Trewavas' definition (1935) should be modified to include those Lake Malawi cichlids with predominantly tricuspid teeth on the major dentigerous area of the jaws excluding the proximal areas of the premaxilla and dentary.

A feature which distinguishes the species in this genus from other Mbuna is their relatively large size. The only other Mbuna which is approximately the same size as the Petrotilapia species is Pseudotropheus williamsi (Günther). P. williamsi is readily distinguished from Petrotilapia species in that it has typical Pseudotropheus dentition with an outer row of bicuspid teeth and a few inner regular rows of short shafted tricuspid teeth.

Petrotilapia tridentiger Trewavas, 1935 (Figure 14)

MATERIAL EXAMINED

The measurements are based on 45 specimens including 2 unsexed (97 and 99 mm SL), 31 males (99-137 mm SL), and 11 females (85-116 mm SL).

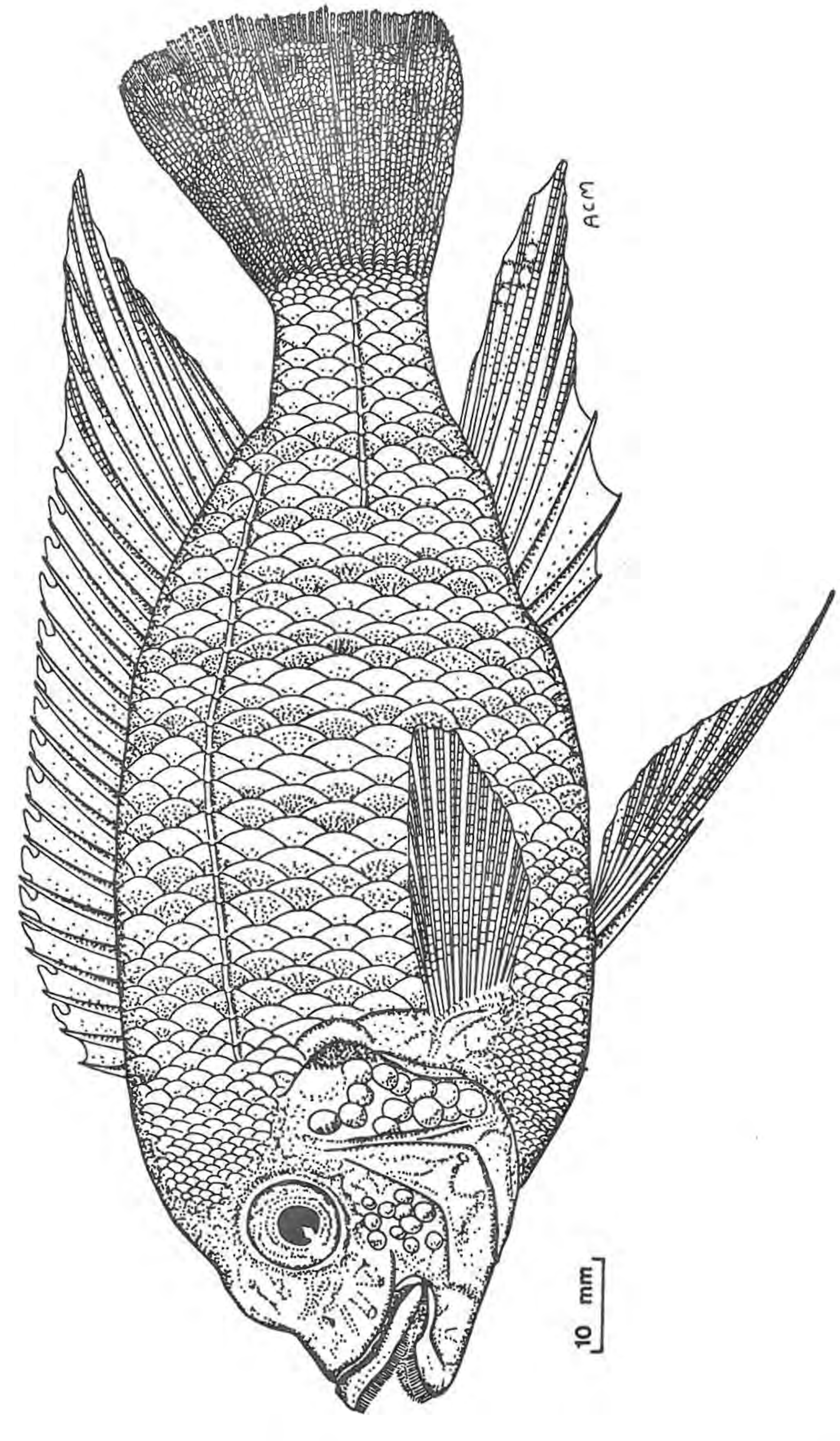

Figure 14. Petrotilapia tridentiger. Male.

All specimens are from Monkey Bay (14°3' S; 34°55' E) and were captured in 0-4 m deep water over rock.

The syntype collection was examined by D.S.C. Lewis. The collection comprises three adult specimens greater than 100 mm SL and two subadult specimens of approximately 81 mm from Monkey Bay; two moderately sized specimens of 89 and 75 mm SL and numerous very small specimens from the extreme south of the lake from "Bar to Kudzi"; and three very small specimens of approximately 30 mm SL from Chilumba. D.S.C. Lewis compared specimens of the three species mentioned in this chapter with the type series from Monkey Bay and concluded that the type series is polytypic but was able to match one of the syntypes with one of the specimens from Monkey Bay. This syntype specimen has been examined and is herein designated as the lectotype. Unfortunately the lower pharyngeal bone of this specimen was not in the specimen when it was examined. From correspondence with P.H. Greenwood it appears that the bone cannot be traced at the British Museum (Natural History), London, and that it must be assumed lost. Nevertheless in view of the fact that this is the only specimen in the syntype collection that can be confidently matched with one of the three Monkey Bay species it must be accepted as the lectotype. The lectotype is shown in Figure 15.

With the exception of the lectotype, all specimens were collected during 1980 by A.C. Marsh.

LECTOTYPE : BMNH 1935-6-14 : 244-248B, male, 125 mm SL.

FURTHER SPECIMENS : RUSI 13394, male, 137 mm SL, 10 September 1980; RUSI 13395-13396, two males, both 130 mm SL, 4 August 1980; RUSI 13397, male, 144 mm SL, 24 February 1980; RUSI 13398, male, 137 mm SL, 10 September 1980; RUSI 13399-13400, two females, 116 and 111 mm SL, 10 September 1980; RUSI 13401-13402, two unsexed, 99 and

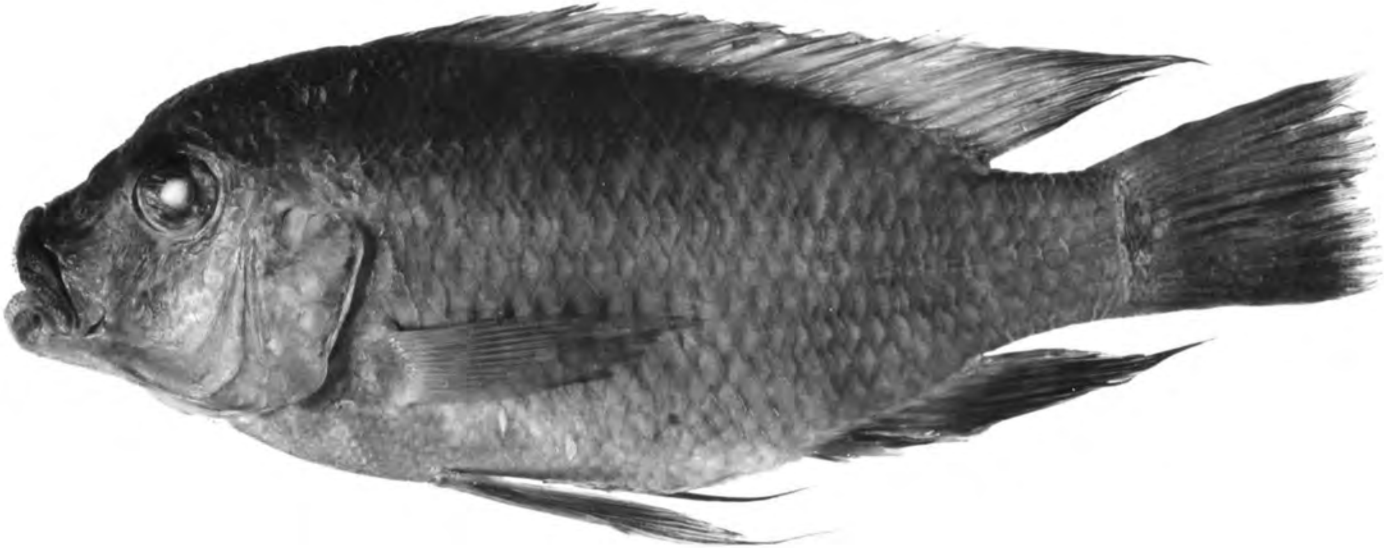

Figure 15. *Petrotilapia tridentiger*. Lectotype - male, 125 mm standard length.

97 mm SL, 10 September 1980; RUSI 13403-13404, two males, 127 and 111 mm SL, 10 September 1980; BMNH 1981-2-2 : 212-220, eight males, 132, 130, 128, 125, 123, 115, 113 and 99 mm SL and one female, 114 mm SL; USNM 228, 443, four males, 123, 121, 112 and 104 mm SL and two females 107 and 102 mm SL, 10 September 1980.

DESCRIPTION

This is one of the largest Mbuna, attaining a standard length of 141 mm at Nkhata Bay (n=7), and 126 mm at Monkey Bay (n=45). The body is deep and wide with the greatest depth occurring between the second and fourth dorsal spines. Snout length is approximately equal to eye diameter. The head profile is variable, in small specimens and some adults the profile forms a smooth curve between the snout and the first dorsal spine whereas other adults have an interorbital gibbosity of variable size. Figure 16 illustrates the extremes of head profile. Although there is no clearcut correlation between the size of the interorbital gibbosity and standard length, the large gibbosities are normally found in large males. The mouth is isognathous with numerous irregular bands of closely set teeth visible in the closed jaws.

As there are a number of significant proportional differences between males and females in this species (Table 2), the sexes are represented separately in Table 3.

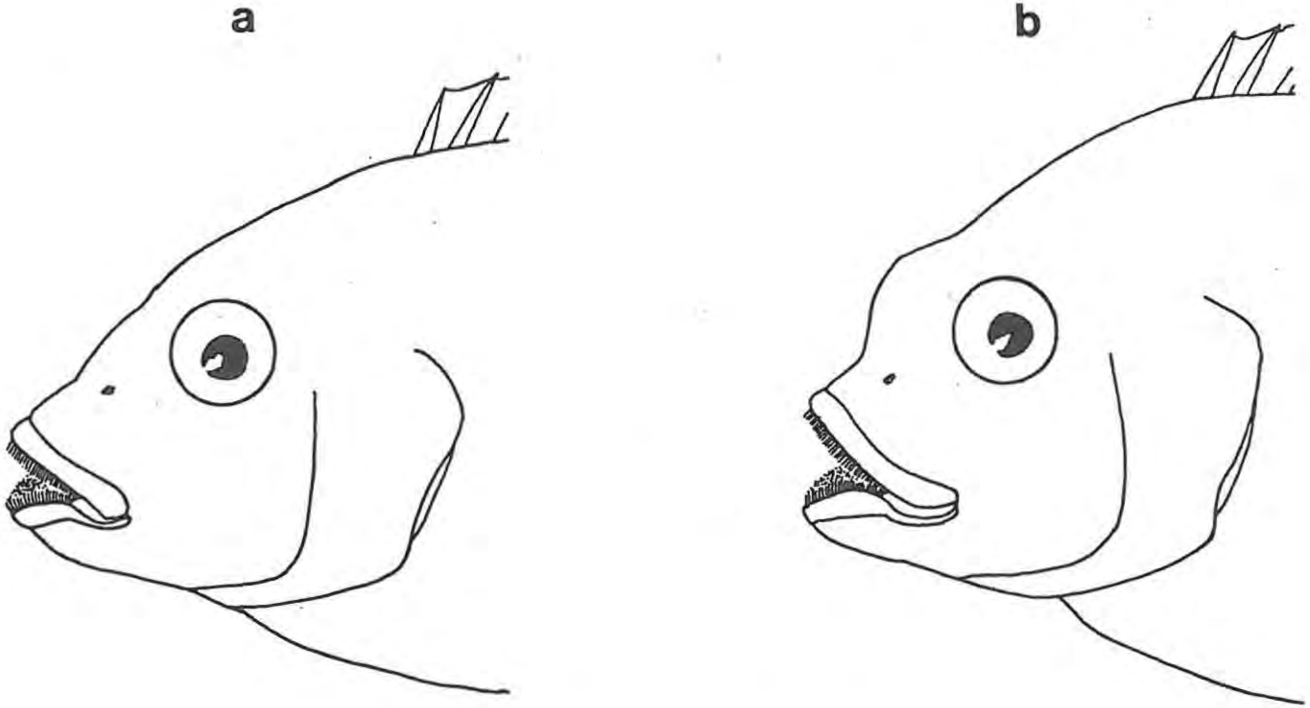

Figure 16. *Petrotilapia tridentiger.* Variation in head profile; (a) male, 132 mm standard length; (b) male, 130 mm standard length.

Table 2. Significant proportional differences between male and female *P. tridentiger* from Monkey Bay. Level of significance (p) determined using t-test for two means. Mean = X, standard deviation = SD, range in brackets. Unless otherwise indicated n = 30 males and 13 females.

	MALE			FEMALE			
PROPORTION	X	SD	RANGE	X	SD	RANGE	P
SL/head L	3.2	0.1	(2.9 - 3.3)	3.1	0.1	(3.0 - 3.2)	< 0.05
SL/caudal fin L	4.3	0.2	(3.7 - 4.8)	4.5	0.4	(4.1 - 5.3)	< 0.02
SL/pelvic fin ray L	2.9	0.3	(2.5 - 3.7)	3.4	0.2	(3.1 - 3.7)	< 0.001
Head L/eye diameter	3.4	0.1	(3.2 - 3.7)	3.3	0.1	(3.0 - 3.5)	< 0.05
Head L/lower jaw L	3.7	0.2	(3.3 - 4.1)	3.9	0.3	(3.4 - 4.5)	< 0.05
Head L/premaxillary L	3.4	0.4	(2.7 - 4.1)	3.7	0.5	(2.9 - 4.5)	< 0.05
Head L/interorbital W	2.6	0.2	(2.3 - 2.8)	2.8	0.2	(2.6 - 3.2)	< 0.01
Head L/preorbital D	4.2	0.3	(3.5 - 4.6)	4.5	0.3	(4.0 - 4.9)	< 0.01
Eye diameter/interorbital W	0.8	0.1	(0.7 - 0.9)	0.9	0.1	(0.8 - 1.0)	< 0.001
Eye D/preorbital D	1.2	0.1	(1.0 - 1.6)	1.4	0.1	(1.3 - 1.5)	< 0.001
* Pharyngeal fork L/blade D	4.2	0.5	(2.6 - 5.1)	4.6	0.4	(4.2 - 5.5)	< 0.02
Pelvic fin ray L/pelvic fin spine L	2.2	0.3	(1.6 - 2.8)	1.8	0.1	(1.7 - 2.0)	< 0.001
Body W/premaxillary W	1.4	0.1	(1.2 - 1.7)	1.5	0.1	(1.3 - 1.7)	< 0.02

* n = 29 males and 10 females

Table 3. Proportional measurements for *P. tridentiger* (lectotype in bold)

	Males (n=31)	Females (n=11)
In standard length:		
Body D	2.5 - **2.7** - 2.9	2.6 - 3.0
Head L	2.9 - **3.2** - 3.3	3.0 - 3.2
Caudal peduncle L	6.5 - **7.9** - 8.7	6.4 - 8.3
Caudal fin L	3.7 - **4.4** - 4.8	4.1 - 5.3
Pectoral fin L	3.5 - **3.7** - 4.2	3.6 - 4.3
Pelvic fin spine L	5.8 - **6.2** - 7.2	5.7 - 7.1
Pelvic fin ray L	2.5 - **2.6** - 3.7	3.1 - 3.7
L to dorsal fin end	1.1 - **1.2**	1.1 - 1.2
L to anal fin end	1.1 - **1.2**	1.1 - 1.2
In head length:		
Eye diameter	3.2 - **3.6** - 3.7	3.0 - 3.5
Snout L	**2.7** - 3.8	2.7 - 4.0
Preorbital D	3.5 - **4.2** - 4.6	4.0 - 4.9
Interorbital W	2.3 - **2.8**	2.6 - 3.2
Lower jaw L	3.3 - **3.6** - 4.1	3.4 - 4.5
Premaxillary L	2.7 - **3.3** - 4.1	2.9 - 4.5
Premaxillary pedicel L	4.0 - **4.8** - 6.3	4.3 - 6.5
In fork length of lower pharyngeal bone: ✱		
Total L of pharyngeal	0.8 - 0.9	0.9
Pharyngeal W	0.8 - 1.0	0.9 - 1.0
Pharyngeal D	2.6 - 3.6	2.6 - 3.5
Pharyngeal blade L	2.0 - 4.2	2.3 - 3.6
Pharyngeal blade D	2.6 - 5.1	4.2 - 5.5
In eye diameter:		
Interorbital W	0.7 - **0.8** - 0.9	0.8 - 1.0
Preorbital D	1.0 - **1.4** - 1.6	1.3 - 1.5
Premaxillary pedicel L	1.2 - **1.3** - 1.9	1.3 - 1.9
Miscellaneous proportions:		
Caudal peduncle L/caudal peduncle D	0.8 - **0.9** - 1.1	0.9 - 1.2
Pelvic fin ray L/pelvic fin spine L	1.6 - **2.3** - 2.8	1.7 - 2.0
Body W/premaxillary W	1.2 - **1.4** - 1.7	1.3 - 1.7
Interorbital W/premaxillary W	0.9 - **1.0** - 1.1	0.9 - 1.1
Premaxillary W/premaxillary D	1.1 - **1.2** - 1.5	1.1 - 1.7
Body D/Caudal peduncle D	2.6 - **2.8** - 3.0	2.6 - 3.0

✱ pharyngeal bone missing from lectotype

FINS

Dorsal **XVI**-XVIII, 7-**8**-9; anal **111**, 6-**7**-8 (lectotype in bold). The dorsal fin has well developed lappets and the longest rays extend posteriorly in males to between one third and mid-way along the caudal fin, and in females from beyond the base of the caudal fin to one third along the caudal fin. The anal fin extends backwards to a position slightly less than or equal to that of the dorsal fin. The pelvic fin rays are moderately filamentous. In adult males the pelvic fins extend variably from the base of the first anal fin spine to just beyond the base of the third anal fin spine. In females the pelvic fins extend to between the vent and base of the first anal fin spine. The pectoral fin length is 71.6-91.0 % of the head length. The caudal fin is subtruncate and densely scaled except on the extreme trailing edge.

SQUAMATION *

The scales on the head and anterior two thirds of the dorsum are cycloid. The remainder of the body, including the caudal fin (except on the extreme trailing edge) but excluding all other fins, is covered in moderately ctenoid scales. Upper lateral line 19-**21(22)**-24, lower lateral line 7-**10(11)**-13, 29-**31**-33 scales in the longitudinal series, excluding caudal scales.

OSTEOLOGY

Vertebrae were counted from X-rays of nine specimens: abdominal series **14**-15, caudal series 15-**16**. Seven of the specimens had total vertebral counts of 30 and two had total vertebral counts of 31.

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* where left and right hand sides varied on the lectotype both counts are given

DENTITION (Figure 17)

The teeth are closely set in numerous irregular bands. The outermost rows are procumbent. Most of the teeth comprise a long slender, slightly recurved shaft ending in a strongly recurved tricuspid tip. On the proximal arms of the dentary and premaxilla the teeth are arranged in one to three rows and are all unicuspid. The premaxillary unicuspid teeth are approximately two thirds the length of the majority of tricuspid teeth but are considerably stouter. The dentary unicuspid teeth are much smaller, being approximately one third of the length of the tricuspid teeth and of similar shaft diameter. In some specimens the unicuspid teeth occur in the three posteriormost rows of both the premaxilla and the dentary. Many of the teeth in these posterior rows are only weakly tricuspid having two rudimentary cusps on either side of a major cusp.

LOWER PHARYNGEAL BONE (Figure 18)

The lower pharyngeal bone is moderately indented posteriorly with a heart-shaped dentigerous area. The anterior blade is moderately long. The teeth in the anterior half are oval in section and strongly recurved towards the posterior. The teeth in the posterior half are rounded in section basally, becoming oval higher up the shaft with a slight anterior curvature. The teeth in the posterior row are much stouter than those of the penultimate row. The tips of all the teeth are slightly hooked and blunt.

GILL RAKERS

2-$\underline{3}$-4; $\underline{1}$; 7-$\underline{9}$-11 on the anterior arch. Individual rakers are stout and triangular and have blunt tips. The rakers become larger and stouter towards the dorsal end of the ceratobranchial. The first one or two

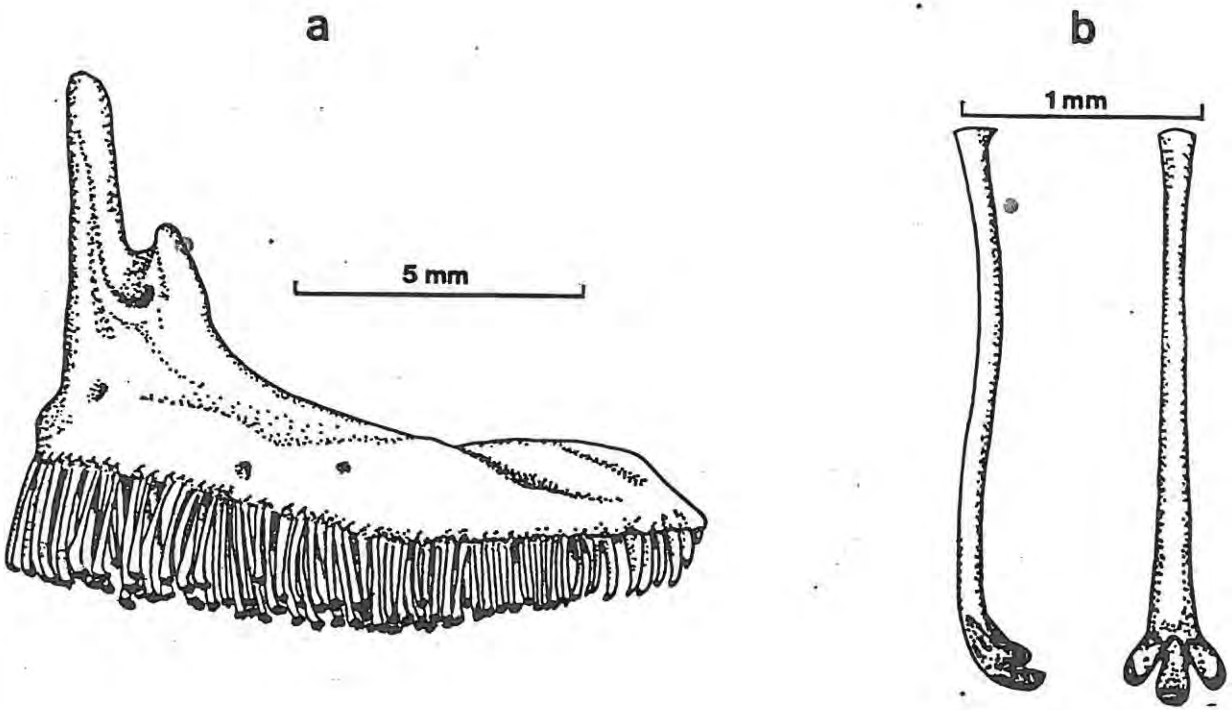

Figure 17. *Petrotilapia tridentiger* (a) lateral aspect of left premaxillary; (b) lateral aspect and frontal aspect of a single tricuspid tooth.

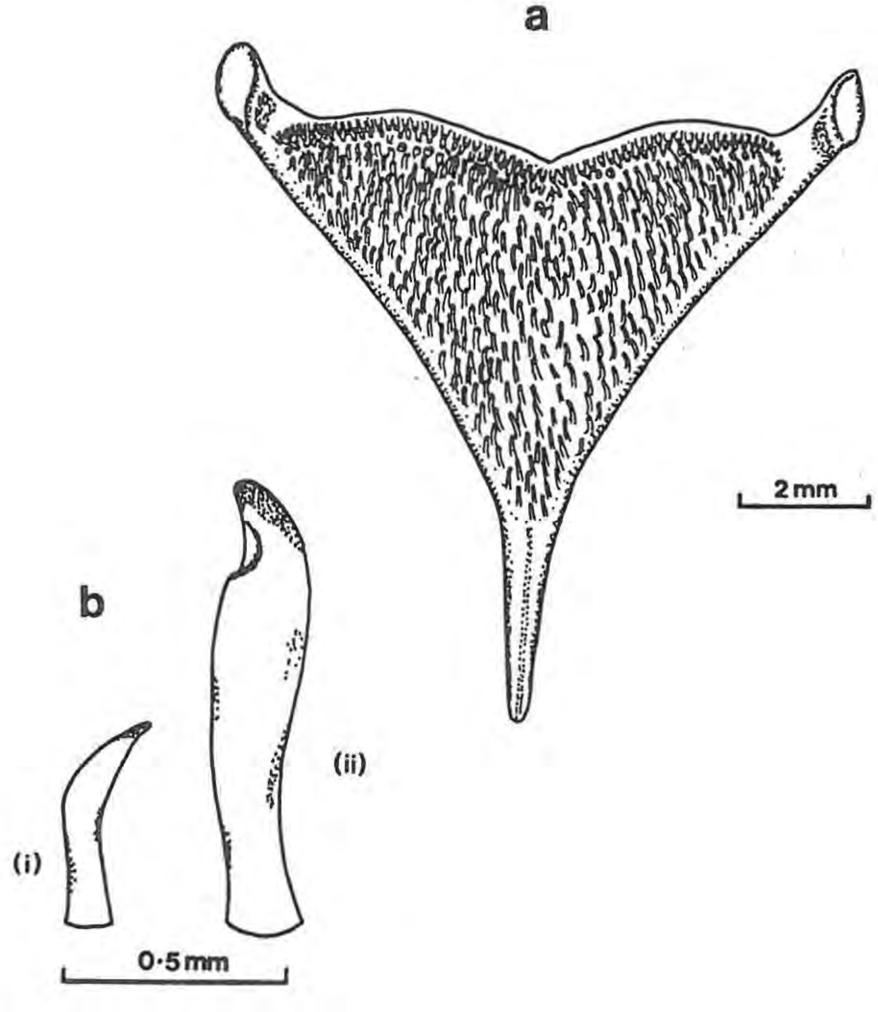

Figure 18. *Petrotilapia tridentiger*. (a) Dorsal aspect of lower pharyngeal bone; (b)(i) Lateral aspect of typical lower pharyngeal bone tooth; (ii) Lateral aspect of tooth from posterior row.

ceratobranchial rakers on the lower arch are often reduced.

COLORATION (Figures 6 & 7)

Details on live coloration are presented in Chapter 3. Preserved specimens are a uniform and dull dark brown to grey. There are no dark bands on any of the fins.

ECOLOGY

A detailed account of the ecology of this species is presented in Chapter 8. It is a lithophilous species which feeds predominantly on epilithic algae and the benthic invertebrates which occur in the algal mat. In general it is a shallow water species being confined to the upper 8 m of water although at Boadzulu Island (14°15' S; 35°8' E) it penetrates to 20 m. P. tridentiger is a widespread species with a disjunct distribution (Figures 21(a) and 21(b)). In particular it does not occur at any of the sites surveyed between Otter Point in the south and Nkhata Bay in the central region of the lake (a distance of approximately 240 km). Most of the intervening shore is sandy and therefore the species could at most be represented by small populations on scattered reefs. At the two sites where there are substantial rocky shores (Senga Point and Bandawe Point) this species did not occur, suggesting that it may not occur in this part of the lake at all. The shores of Mocambique and Tanzania were not visited and therefore the distribution between Chilumba and Makanjila is not known.

DIAGNOSIS

A large species attaining a standard length of 141 mm at Nkhata Bay and 126 mm at Monkey Bay. Morphologically it differs from P. nigra and

P. genalutea in that it has a broader head and a relatively long and narrow caudal peduncle. The most pronounced differences are in coloration and markings. In particular, the dorsal fin has no submarginal stripe and lappet coloration is no different from the rest of the fin. Adult males are normally uniform blue and females and juveniles are normally uniform brown. Faint vertical bars slightly darker than the ground colour may be present. Preserved specimens are distinguishable from the other two Monkey Bay Petrotilapia species in that the dorsal fin does not have a submarginal stripe.

Petrotilapia genalutea sp.nov. (Figure 19)

MATERIAL EXAMINED

The measurements are based on 38 specimens including 1 unsexed (106 mm SL), 18 males (95-124 mm SL) and 19 females (92-126 mm SL). All specimens are from Monkey Bay (14°3' S; 34°55' E) and were captured in 0-4 m deep water over rock during 1980 by A.C. Marsh.

HOLOTYPE : BMNH 1981-2-2: 221, male, 121 mm SL.

PARATYPES : RUSI 492, male, 123 mm SL, 6 August 1980; RUSI 494-495, two males, 113 and 110 mm SL, 6 August 1980; RUSI 496-498, three females, 118, 95 and 92 mm SL, 16 September 1980; RUSI 499, male, 96 mm SL, 16 September 1980; BMNH 1981-2-2 : 222-226, two males, 115 and 108 mm SL and three females, 115, 105 and 95 mm SL; USNM 228, 444 three males, 122, 121 and 120 mm SL, 6 August 1980 and three females, 107, 101 and 99 mm SL, 16 September 1980.

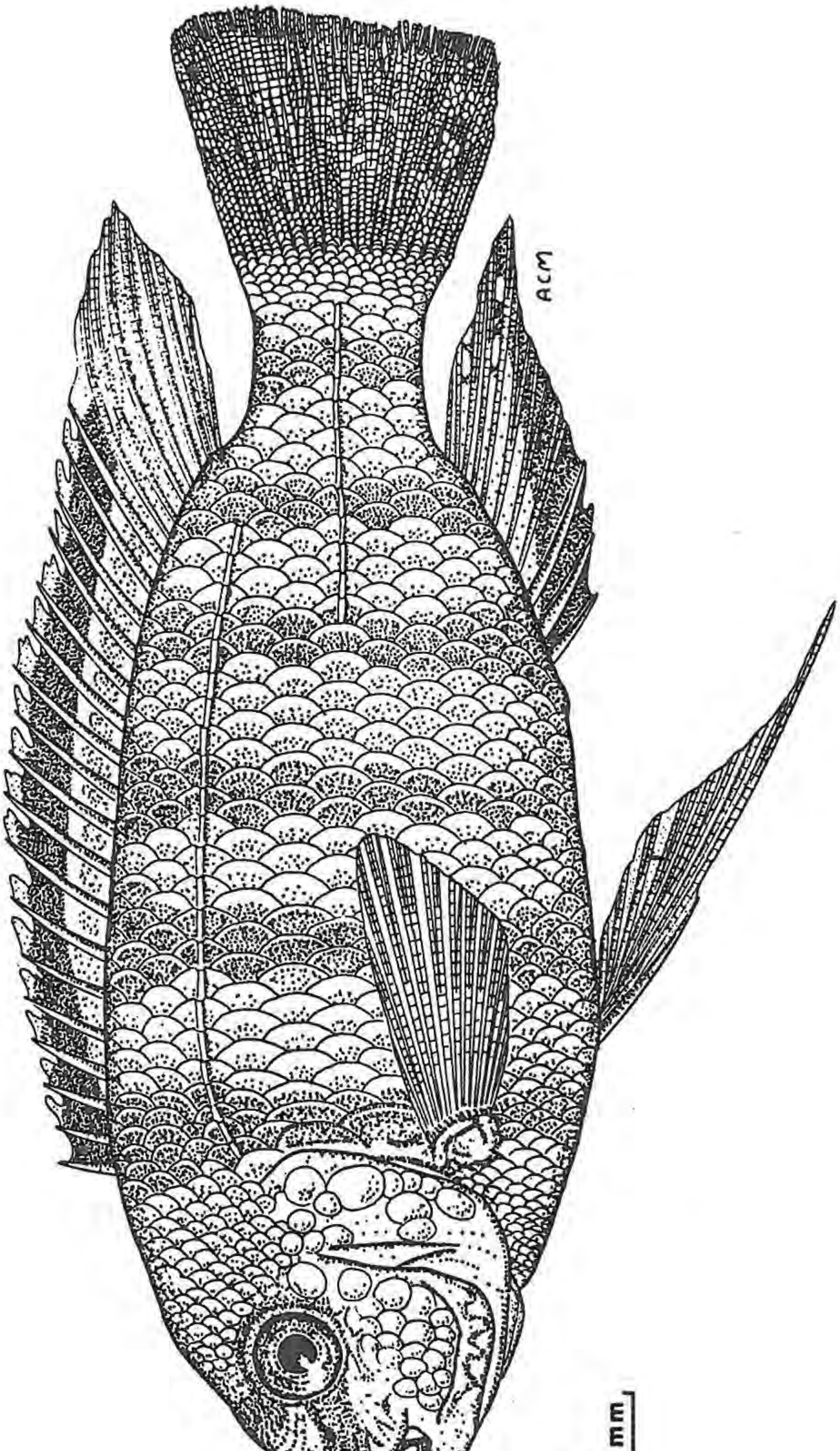

Figure 19. *Petrotilapia genalutea*. Holotype.

DESCRIPTION

A relatively large Mbuna, attaining a standard length of 131 mm at Nkhata Bay (n=8) and 122 mm at Monkey Bay (n=38). The body is deep and wide with the greatest depth occurring between the second and fourth dorsal fin spines. Snout length is approximately equal to eye diameter. The dorsal head profile varies from being weakly incurved between the eye and the first dorsal fin spine in many specimens (n=18) to moderately and smoothly curved from the snout to the first dorsal fin spine in others (n=20).

Some specimens, irrespective of sex or size, have a small interorbital gibbosity. The mouth is isognathous (n=28) to weakly prognathous (n=10) with numerous irregular bands of closely set teeth visible in the closed jaws.

As there are a number of significant proportional differences between males and females in this species (see Table 4), the sexes are represented separately in Table 5.

FINS

Dorsal XVII-**XVIII**-XIX, **8**-9; anal **III**, 6-**7**-9 (holotype in bold). The dorsal fin has well developed lappets and the longest rays extend posteriorly in males to between one third and midway along the caudal fin and in females from the base of caudal fin to one third along the caudal fin. The anal fin extends backwards to a position equal to that of the dorsal fin. The pelvic fin rays are moderately filamentous. In adult males the pelvic fin extends variably from the base of the first anal fin spine to just beyond the base of the third anal fin spine. In females the pelvic fin extends to between the vent and the base of the second anal fin spine. The pectoral

Table 4. Significant proportional differences between male and female P. genalutea from Monkey Bay. Level of significance (p) determined using t-test for two means. Mean = X, standard deviation = SD, range in brackets. Unless otherwise indicated, n = 18 males and 19 females.

	MALE			FEMALE			
PROPORTION	X	SD	RANGE	X	SD	RANGE	P
SL/pelvic fin spine L	6.6	0.4	(5.8 - 7.5)	6.3	0.3	(5.7 - 6.7)	<0.01
SL/pelvic fin ray L	2.8	0.4	(2.2 - 3.6)	3.4	0.2	(3.1 - 3.7)	<0.001
Head L/premaxillary L	3.4	0.5	(2.8 - 4.2)	3.8	0.4	(3.0 - 4.2)	<0.02
Caudal peduncle L/caudal peduncle D	1.0	0.1	(0.8 - 1.1)	0.9	0.1	(0.8 - 1.0)	<0.02
Premaxillary W/premaxillary L	1.3	0.2	(1.0 - 1.6)	1.5	0.2	(1.1 - 2.1)	<0.01
* Pharyngeal fork L/pharyngeal blade L	2.6	0.3	(2.1 - 3.5)	2.3	0.2	(2.0 - 2.7)	<0.01
Pelvic fin ray L/pelvic fin spine L	2.4	0.5	(1.6 - 3.3)	1.9	0.1	(1.7 - 2.1)	<0.001
Body D/caudal peduncle D	2.8	0.1	(2.5 - 3.0)	2.7	0.1	(2.5 - 2.9)	<0.02

* n = 18 males and 18 females

Table 5. Proportional measurements of *P. genalutea* (holotype in bold)

In standard length:	Males (n=18)	Females (n=19)
Body D	2.6 - **2.8** - 3.0	2.6 - 3.0
Head L	3.1 - **3.3** - 3.4	3.0 - 3.5
Caudal peduncle L	6.9 - **8.5** - 8.8	7.5 - 9.3
Caudal fin L	3.6 - **4.2** - 4.5	3.4 - 4.4
Pectoral fin L	3.7 - **4.1** - 4.2	3.4 - 4.3
Pelvic fin spine L	5.8 - **6.3** - 7.5	5.7 - 6.7
Pelvic fin ray L	2.2 - **2.6** - 3.6	3.1 - 3.7
L to dorsal fin end	**1.1**	1.1
L to anal fin end	1.1 - **1.2**	1.1 - 1.2
In head length:		
Eye diameter	3.0 - **3.2** - 3.4	3.0 - 3.4
Snout L	2.8 - **2.9** - 3.7	2.8 - 3.4
Preorbital D	3.9 - **4.6** - 5.2	4.0 - 5.0
Interorbital W	2.5 - **2.7** - 3.2	2.6 - 3.2
Lower jaw L	3.4 - **3.7** - 4.0	3.0 - 4.0
Premaxillary L	2.8 - **4.0** - 4.2	3.0 - 4.2
Premaxillary pedicel L	4.3 - **4.5** - 6.6	4.5 - 7.0
In fork length of lower pharyngeal bone:		
Total L of pharyngeal	0.8 - **0.9** - 1.0	0.8 - 0.9
Pharyngeal W	**0.9** - 1.0	0.8 - 1.0
Pharyngeal D	2.3 - **2.4** - 4.0	2.8 - 3.4
Pharyngeal blade L	2.1 - **3.2** - 3.5	2.0 - 2.7
Pharyngeal blade D	4.1 - **5.0** - 5.8	3.3 - 5.5
In eye diameter:		
Interorbital W	**0.8** - 1.1	0.8 - 1.1
Preorbital D	1.3 - **1.5** - 1.7	1.2 - 1.6
Premaxillary pedicel L	**1.4** - 1.9	1.4 - 2.4
Miscellaneous proportions:		
Caudal peduncle L/caudal peduncle D	0.8 - **0.9** - 1.1	0.8 - 1.0
Pelvic fin ray L/pelvic fin spine L	1.6 - **2.4** - 3.3	1.7 - 2.1
Body W/premaxillary W	1.2 - **1.7**	1.0 - 1.8
Interorbital W/premaxillary W	0.9 - **1.0**	0.7 - 1.1
Premaxillary W/premaxillary D	1.0 - **1.5** - 1.6	1.1 - 2.1
Body D/caudal peduncle D	2.5 - **2.7** - 3.0	2.5 - 2.9

fin length is 75-92% of the head length excluding one exceptional female with a pectoral fin length of only 45% of the head length. The caudal fin is subtruncate and is densely scaled except on the extreme trailing edge.

SQUAMATION *

The scales on the head and anterior two thirds of the dorsum are cycloid. The remainder of the body including the caudal fin (except on the extreme trailing edge) but excluding all other fins, is covered in ctenoid scales. Upper lateral line 19-22(23)-25, lower lateral line 9-11(12)-14, 29-31(32)-35 scales in longitudinal series, excluding caudal scales.

OSTEOLOGY

Vertebrae were counted from X-rays of nine specimens: abdominal series 15, caudal series 16. All specimens had total vertebral counts of 31.

DENTITION

Indistinguishable from *P. tridentiger*.

LOWER PHARYNGEAL BONE

Although the lower pharyngeal bone of *P. genalutea* is very similar to that of *P. tridentiger*, the blade of the lower pharyngeal bone is significantly deeper in *P. tridentiger*.

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* where left and right hand sides varied on the holotype, both counts are given.

GILL RAKERS *

2-3-4; 1; 9(10)-12 on the anterior arch. Individual rakers are stout, triangular and have blunt tips. The rakers become longer and stouter towards the dorsal end of the ceratobranchial. The first one or two ceratobranchial rakers on the lower arch are often reduced.

COLORATION (Figures 8 & 9)

Details on live coloration are presented in Chapter 3. Preserved adult males have a dark grey background colour with four to six vertical flank bars visible in some specimens. The dorsal, pelvic and anal fins retain their dark submarginal stripes in preservative. The orange-brown rust colour that occurs on the cheeks of live males is not present in preserved specimens. Females are dark grey dorsally becoming pale grey ventrally. Dark grey to black mid-lateral blotches and a submarginal stripe in the dorsal are present in preservative.

ECOLOGY

A detailed account of the ecology of this species is presented in Chapter 8. Like *P. tridentiger*, *P. genalutea* is a lithophilous species which feeds predominantly on epilithic algae and on the benthic invertebrates which occur in the algal mat. In general it is a shallow water species occurring in the upper 8 m of water although at Boadzulu Island (14°15' S; 35°8' E) it penetrates to 18 m. *P. genalutea* is a widespread species (Figures 21(a) & 21(b)) occurring on most rocky shores and islands on the western side of Lake Malawi south of Ruarwe and as far north as Makanjila on the eastern side of the lake. It is not known whether it occurs north of Makanjila or between Senga Point and Bandawe Point.

* where left and right hand sides varied on the holotype, both counts are given

ETYMOLOGY

The trivial name, from the Latin gena = cheek and lutea = orange, refers to the characteristic orange 'cheeks' of adult males of this species.

DIAGNOSIS

A moderately large species attaining a standard length of 131 mm at Nkhata Bay and 122 mm at Monkey Bay. Certain specimens are quite different from the other two species in that their dorsal head profile is incurved but others are not distinguishable in this respect. The interorbital width is narrower and the caudal peduncle stouter than in *P. tridentiger*. *P. genalutea* differs markedly from *P. tridentiger* in that it has a submarginal stripe in the dorsal fin. It is morphologically very similar to *P. nigra* and the main differences are in terms of colour. *P. genalutea* males have distinctive orange cheeks, a blue-grey ground colour and obvious flank bars whereas *P. nigra* males are a relatively uniform black. Female differences are subtle. *P. genalutea* females generally have a paler and yellower ground colour and consequently very obvious flank blotches. The mid-lateral blotches normally fuse posteriorly to form a thick black stripe. *P. nigra* females are darker in ground colour and the mid-lateral blotches rarely fuse together.

Petrotilapia nigra sp.nov. (Figure 20)

MATERIAL EXAMINED

The measurements are based on 45 specimens including 24 males (99-122 mm Sl) and 21 females (83-114 mm SL). All specimens were collected from Monkey Bay (14°3' S; 34°55' E) in 0-10 m deep water over rock during 1980 by A.C. Marsh.

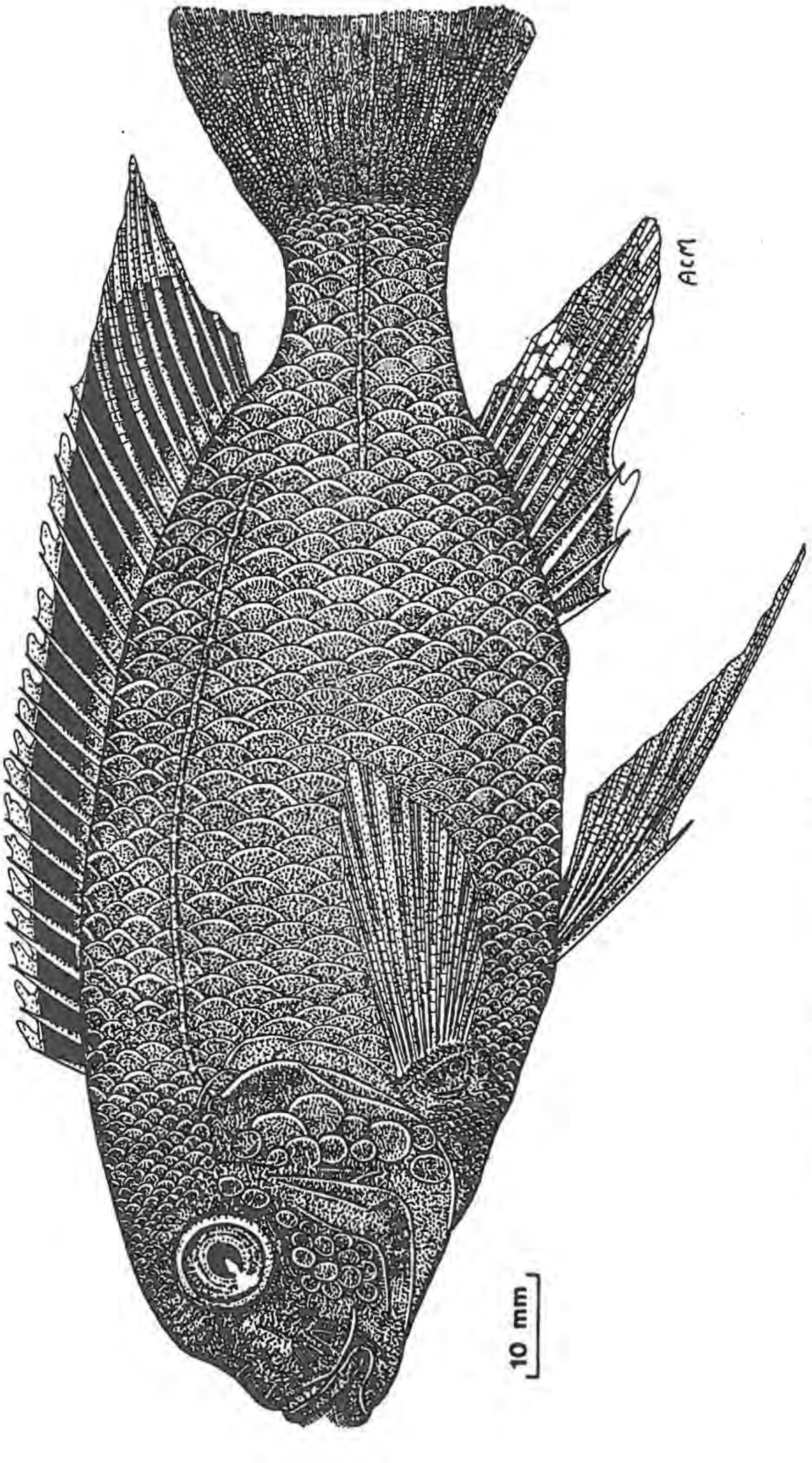

Figure 20. Petrotilapia nigra. Holotype.

HOLOTYPE : BMNH 1981-2-2 : 206, male, 122 mm SL.

PARATYPES : RUSI 500-501, two males, 118 and 115 mm SL, 27 August 1980; RUSI 502, male, 113 mm SL, 11 September 1980; RUSI 503, male, 107 mm SL, 27 August 1980; RUSI 504-508, five females, 111, 108, 106, 102 and 99 mm SL, 11 September 1980; RUSI 509, male, 102 mm SL, 11 September 1980; RUSI 510, male, 99 mm SL, 27 August 1980; BMNH 1981-2-2 : 207-211, two males, 120 and 111 mm SL and three females, 113, 108 and 95 mm SL; USNM 228, 442, one male, 116 mm SL, 27 August 1980, one male, 103 mm SL and two females, 107 and 105 mm SL, 11 September 1980.

DESCRIPTION

A fairly large Mbuna, attaining a standard length of 122 mm at Monkey Bay (n=45). The body is deep and wide, the greatest depth occurring between the second and fourth dorsal fin spines. The snout length is generally slightly longer than the eye diameter. The dorsal head profile is variable and in most specimens the profile between the orbit and the first dorsal fin spine is a gentle smooth curve to an almost straight line. Some specimens have a slightly incurved dorsal head profile. A small interorbital gibbosity is present in some individuals but there is no obvious relationship between the occurrence of an interorbital gibbosity and size or sex. The mouth is generally isognathous to slightly prognathous. One specimen, a male of 103 mm SL, had a slightly retrognathous mouth. The jaws contain numerous irregular bands of closely set teeth which are visible in the closed jaws.

As there are a number of significant proportional differences between males and females (see Table 6), the sexes are represented separately in Table 7.

Table 6. Significant proportional differences between male and female *P. nigra* from Monkey Bay. Level of significance (P) determined using t-test for two means. Mean = X, standard deviation = SD, range in brackets. n = 24 males and 21 females.

	MALE			FEMALE			
PROPORTION	X	SD	RANGE	X	SD	RANGE	P
SL/pelvic fin spine L	6.0	0.2	(5.6 - 6.5)	6.3	0.4	(5.7 - 6.9)	< 0.01
SL/pelvic fin ray L	2.6	0.3	(2.2 - 3.2)	3.3	0.2	(2.9 - 3.7)	< 0.001
Head L/eye diameter	3.3	0.2	(3.0 - 3.7)	3.2	0.1	(2.9 - 3.4)	< 0.05
Head L/lower jaw L	4.0	0.4	(3.2 - 4.7)	3.7	0.3	(3.1 - 4.3)	< 0.02
Head L/premaxillary L	3.4	0.4	(2.8 - 4.3)	3.8	0.4	(3.0 - 4.7)	< 0.01
Head L/interorbital W	2.8	0.2	(2.5 - 3.1)	2.9	0.2	(2.4 - 3.2)	< 0.01
Eye diameter/interorbital W	0.8	0.1	(0.8 - 1.0)	0.9	0.1	(0.8 - 1.0)	< 0.001
Eye diameter/preorbital D	1.3	0.1	(0.9 - 1.6)	1.4	0.1	(1.3 - 1.6)	< 0.01
Pelvic fin ray L/pelvic fin spine L	2.3	0.3	(0.9 - 2.7)	1.9	0.1	(1.8 - 2.2)	< 0.001

Table 7. Proportional measurements for *P. nigra* (holotype in bold)

In standard length:	Males (n=24)	Females (n=21)
Body D	2.5 - **2.8** - 2.9	2.6 - 3.1
Head L	3.0 - **3.4**	3.0 - 3.5
Caudal peduncle L	7.6 - **7.9** -10.1	7.2 - 9.5.
Caudal fin L	3.7 - **4.4** - 4.5	3.5 - 5.1
Pectoral fin L	3.4 - **3.7** - 4.5	3.5 - 4.5
Pelvic fin spine L	5.6 - **6.1** - 6.5	5.7 - 6.9
Pelvic fin ray L	2.2 - **2.5** - 3.2	2.9 - 3.7
L to dorsal fin end	1.1 - **1.2** - 1.2	1.1 - 1.2
L to anal fin end	1.1 - **1.2**	1.1 - 1.2
In head length:		
Eye diameter	3.0 - **3.3** - 3.7	2.9 - 3.4
Snout L	2.6 - **3.2** - 3.6	2.8 - 3.8
Preorbital D	2.8 - **3.8** - 4.8	3.9 - 5.0
Interorbital W	2.5 - **2.6** - 3.1	2.4 - 3.2
Lower jaw L	3.2 - **3.5** - 4.7	3.1 - 4.3
Premaxillary L	2.8 - **3.6** - 4.3	3.0 - 4.7
Premaxillary pedicel L	4.0 - **4.5** - 5.7	4.1 - 5.3
In fork length of lower pharyngeal bone:		
Total L of pharyngeal	0.8 - **0.9**	0.9
Pharyngeal W	0.8 - **0.9** - 1.0	0.8 - 1.1
Pharyngeal D	2.7 - **2.9** - 3.8	2.9 - 3.5
Pharyngeal blade L	**2.2** - 3.0	2.2 - 3.0
Pharyngeal blade D	4.1 - **4.5** - 5.0	4.1 - 5.7
In eye diameter:		
Interorbital W	**0.8** - 1.0	0.8 - 1.0
Preorbital D	0.9 - **1.2** - 1.6	1.3 - 1.6
Premaxillary pedicel L	1.2 - **1.4** - 1.9	1.3 - 1.8
Miscellaneous proportions:		
Caudal peduncle L/caudal peduncle D	0.7 - **1.0**	0.8 - 1.1
Pelvic fin ray L/pelvic fin spine L	0.9 - **2.4** - 2.7	1.8 - 2.2
Body W/premaxillary W	1.3 - **1.6**	1.2 - 1.8
Interorbital W/premaxillary W	0.8 - **1.0** - 1.1	0.8 - 1.0
Premaxillary W/premaxillary D	1.1 - **1.4** - 1.7	1.0 - 1.8
Body D/caudal peduncle D	2.5 - **2.8** - 3.0	2.5 - 3.0

FINS

Dorsal XVII-**XVIII**-XIX, 7-**9**; anal **111**, 6-**7**-9 (holotype in bold). The dorsal fin has well developed lappets and the longest rays extend posteriorly in males to between one quarter and midway along the caudal fin and in females to approximately one third along the caudal fin. The anal fin extends posteriorly in males to the same extent or slightly more than that of the dorsal fin whereas in females the anal fin extends one quarter to one third along the caudal fin. The pelvic rays are moderately filamentous. In adult males the pelvic fin extends variably from just beyond the vent to just beyond the base of the third anal fin spine. In females the pelvic fin extends variably from just anterior to the vent to just posterior to the base of the first anal fin spine. The pectoral fin length is 70-94% of the head length. The caudal fin is subtruncate and is densely scaled except on the extreme trailing edge.

SQUAMATION

The scales on the head and anterior two thirds of the dorsum are cycloid. The remainder of the body including the caudal fin (except on extreme trailing edge) but excluding all other fins, is covered in moderately ctenoid scales. Upper lateral line 20-**23**-24, lower lateral line 8-**9**-13, 29-**32**-33 in longitudinal series, excluding caudal scales.

OSTEOLOGY

Vertebrae were counted from X-rays of nine specimens: abdominal series **15**-16, caudal series 15-**16**. Seven of the specimens, including the holotype, had total vertebral counts of 31, one had a count of 30 and another a count of 32.

DENTITION

Indistinguishable from *P. tridentiger*.

LOWER PHARYNGEAL BONE

The pharyngeal bone is indistinguishable from that of the other two species to the naked eye. Measurements with vernier calipers revealed, however, that the pharyngeal blade of *P. nigra* is not proportionally as deep as that of *P. tridentiger*, and is proportionally longer than that of *P. genalutea*. The pharyngeal bone of *P. nigra* is not as deep proportionally as that of *P. genalutea*.

GILL RAKERS *

2(3)-4, 1, 8-11 on the anterior arch. Individual rakers are stout and triangular and have blunt tips. The rakers become longer and stouter towards the dorsal end of the ceratobranchial. The first one or two ceratobranchial rakers on the lower arch are often reduced.

COLORATION (Figures 10 & 11)

Details of live coloration are presented in Chapter 3. Preserved territorial males are uniform black. Preserved non-territorial specimens are dark brown-grey becoming light brown ventrally with a variable amount of flank markings visible. The black submarginal dorsal fin stripe is always visible.

ECOLOGY

A detailed account of the ecology of this species is presented in Chapter 8. *P. nigra* is a lithophilous species which feeds predominantly on epilithic

* where left and right hand sides varied on the holotype, both counts are given

algae and benthic invertebrates which occur in the algal mat. It has a very limited distribution in the south-east arm of Lake Malawi (Figure 21(b)) and a broad depth range. At Monkey Bay it occurs from the shallows down to 30 m and at Thumbi West Island (14°1' S; 34°49' E) it penetrates to 35 m.

ETYMOLOGY

The trivial name is from the Latin nigra = black, and refers to the dominant colour of territorial males.

DIAGNOSIS

P. nigra is a relatively small species from this genus, attaining a standard length of 122 mm at Monkey Bay. Relative to P. tridentiger, P. nigra has a narrower interorbital width and a stouter caudal peduncle. P. nigra is also distinguishable from P. tridentiger by the possession of a dark submarginal stripe in the dorsal fin. Morphologically P. nigra is very similar to P. genalutea. The most important differences are in terms of live coloration and markings. P. nigra males are a uniform black whereas P. genalutea males have a blue-grey ground colour, flank bars and an orange 'cheek'. The dorsal fin submarginal bar is thicker in P. nigra males than in P. genalutea males. P. nigra females are generally darker than P. genalutea females and therefore there is less contrast between the flank blotches and ground colour. Unlike P. genalutea, the mid-lateral flank blotches in P. nigra females rarely fuse together posteriorly.

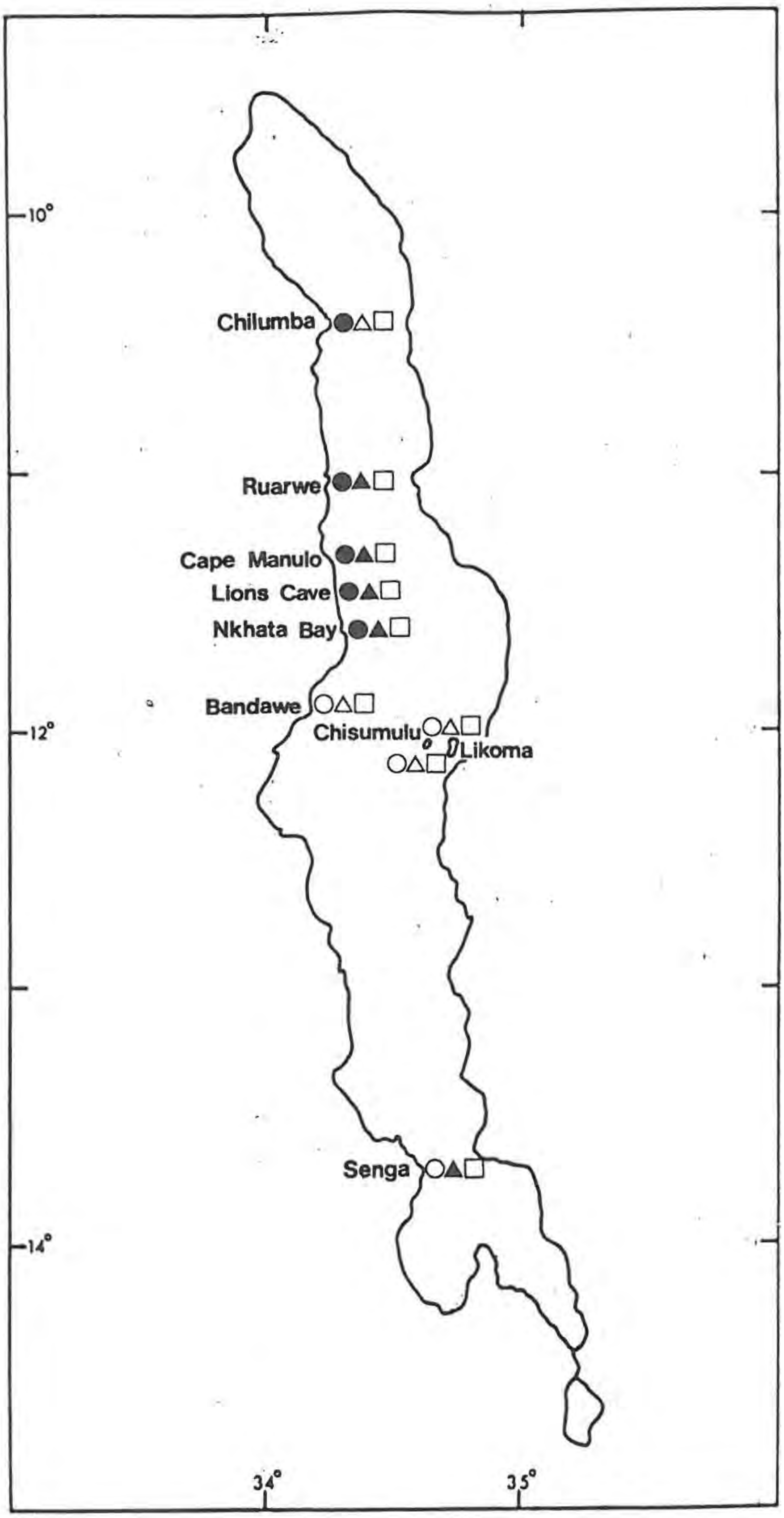

Figure 21(a). Map of Lake Malawi showing distribution of <u>P. tridentiger</u>, <u>P. genalutea</u> and <u>P. nigra</u> north of Senga. <u>P. tridentiger</u> present ●, absent ○. <u>P. nigra</u> present ■, absent □. <u>P. genalutea</u> present ▲, absent △ .

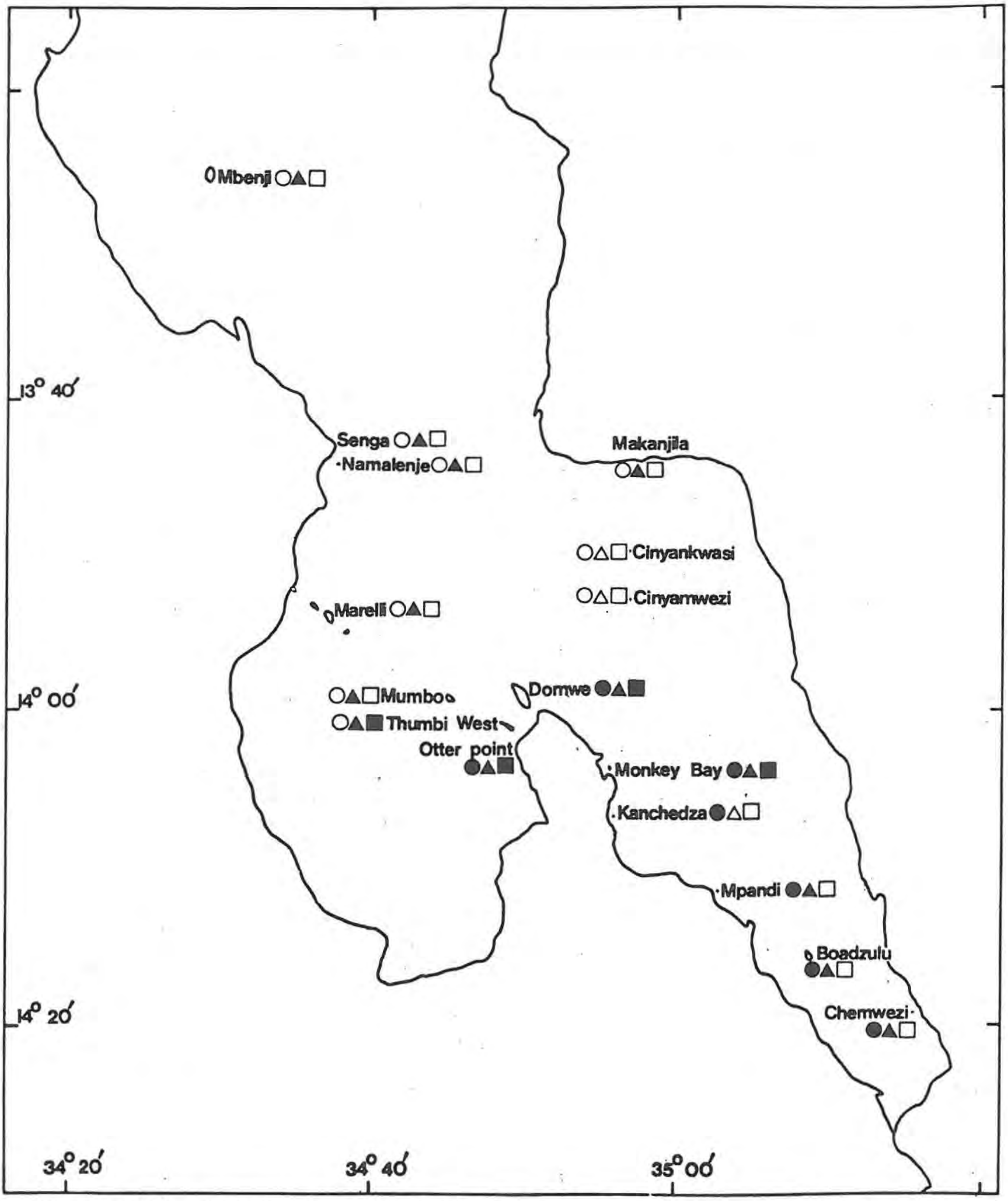

Figure 21(b). Distribution of P. tridentiger, P. nigra and P. genalutea in southern Lake Malawi. P. tridentiger present ● , absent ○ . P. nigra present ■ , absent □. P. genalutea present ▲ , absent △ .

DISCUSSION

The difficulty in distinguishing the three species of Petrotilapia dealt with in this chapter focuses attention on one of the major problems facing biologists working on the cichlids of the Great Lakes of Africa, namely the existence of sibling species complexes. The difficulties encountered when attempting to separate the species on morphological grounds are in part attributable to intraspecific variation. Tables 2, 4 and 6 highlight some of the sexual differences within each species and the descriptive information presented for each species shows that even for a given sex, characters may vary considerably.

An examination of Tables 8-12 reveals that there is considerable interspecific overlap in all characters. Of the three species, P. tridentiger is morphologically most distinctive. This species has a mode of 17 dorsal fin spines, while the mode for P. genalutea and P. nigra is 18 (Table 8). P. tridentiger also differs from the other two species in terms of the total number of vertebrae (Table 9).

As a consequence of their similar morphologies and intraspecific character variation, no one character has been found whose dimensions are completely distinctive for each species. Morphometric differences only become apparent if the information is subject to statistical analysis. Using a t-test for two means, numerous significant morphometric differences exist between territorial males of the three species ($p < 0.05$) (Table 12). Nevertheless in only four characters are all three species significantly different from one another. Although statistical tests may aid in resolving morphological differences in sibling species, proportional differences which can only be detected with the aid of statistics are unlikely to be of any diagnostic value.

Table 8. Frequency distribution of dorsal fin spine and ray counts and anal fin ray counts for the three species of Petrotilapia.

'n' represents the number of specimens examined.

Species	Dorsal fin spines				Dorsal fin rays			Anal fin rays				
	16	17	18	19	7	8	9	6	7	8	9	n
P. tridentiger	3	25	6	0	1	21	12	2	14	1	0	45
P. genalutea	0	7	27	2	0	27	9	1	15	1	1	38
P. nigra	0	7	35	1	1	30	12	4	16	2	1	45

Table 9. Frequency distribution of vertebral counts for the three species of <u>Petrotilapia</u>. These data from from nine specimens of each species.

Species	Abdominal series			Caudal series		Total vertebral count		
	14	15	16	15	16	30	31	32
<u>P. tridentiger</u>	4	5	0	3	6	7	2	0
<u>P. genalutea</u>	0	9	0	0	9	0	9	0
<u>P. nigra</u>	0	8	1	2	7	1	7	1

Table 10. Frequency distribution of pored scale counts in the three species of <u>Petrotilapia</u>. Pored scales posterior to the hypurals are not counted. 'n' represents the number of specimens examined.

Species	Upper lateral line							Lower lateral line								Longitudinal series							n
	19	20	21	22	23	24	25	7	8	9	10	11	12	13	14	29	30	31	32	33	34	35	
P. tridentiger	2	3	8	19	27	6	0	0	4	15	25	14	4	1	0	6	5	20	26	5	0	0	45
P. genalutea	3	4	10	15	23	14	1	1	1	8	26	23	8	1	1	3	4	11	27	18	4	1	38
P. nigra	0	4	11	25	37	8	0	0	3	12	22	35	13	1	0	1	8	21	40	15	0	0	45

Table 11. Frequency distribution of gill rakers from the anterior gill arch for the three species of *Petrotilapia*. All specimens had one gill raker in the region of articulation between the epibranchial and the ceratobranchial. 'n' represents the number of specimens examined.

Species	Epibranchial gill rakers			Ceratobranchial gill rakers						n
	2	3	4	7	8	9	10	11	12	
P. tridentiger	13	44	1	1	3	19	37	8	0	45
P. genalutea	21	49	2	0	0	12	44	14	2	38
P. nigra	25	58	3	0	2	19	50	15	0	45

Table 12. A comparison of the proportional measurements of territorial male *Petrotilapia* species from Monkey Bay (*P. tridentiger*, n = 31; *P. genalutea*, n = 18; *P. nigra*, n = 24). All measurements in millimetres. Mean (X) followed by range in brackets. Significant differences ($P < 0.05$) determined using t-test for two means. Means underlined indicates that all three means are significantly different from one another. One mean underlined indicates that this mean is significantly different from the others which are not different from each other. Two means underlined indicates that these means are significantly different from one another but not from the unmarked mean. If all three means are unmarked, they are not significantly different.

	P. tridentiger		*P. genalutea*		*P. nigra*	
Proportion	X	Range	X	Range	X	Range
Standard L (mm)	$\underline{126}$	(114 - 137)	$\underline{122}$	(108 - 124)	$\underline{112}$	(102 - 122)
SL/body D	$\underline{2.7}$	(2.5 - 2.9)	$\underline{2.8}$	(2.6 - 3.0)	2.7	(2.5 - 2.9)
SL/head L	3.2	(2.9 - 3.3)	$\underline{3.3}$	(3.1 - 3.4)	3.2	(3.0 - 3.4)
SL/caudal peduncle L	$\underline{7.6}$	(6.5 - 8.7)	8.0	(6.9 - 8.8)	$\underline{8.2}$	(7.6 -10.1)
SL/caudal fin L	$\underline{4.3}$	(3.7 - 4.8)	4.0	(3.6 - 4.5)	4.1	(3.7 - 4.5)
SL/pectoral fin L	3.9	(3.5 - 4.2)	4.0	(3.7 - 4.2)	$\underline{3.7}$	(3.4 - 4.5)
SL/pelvic fin spine L	$\underline{6.3}$	(5.8 - 7.2)	$\underline{6.6}$	(5.8 - 7.5)	$\underline{6.0}$	(5.6 - 6.5)
SL/pelvic fin ray L	2.7	(2.5 - 3.7)	2.7	(2.2 - 3.6)	2.6	(2.2 - 3.2)
SL/L to dorsal end	$\underline{1.2}$	(1.1 - 1.2)	1.1	(1.1)	1.1	(1.1 - 1.2)
SL/L to anal fin end	1.2	(1.1 - 1.2)	1.2	(1.1 - 1.2)	1.2	(1.1 - 1.2)
Head L/eye diameter	$\underline{3.4}$	(3.2 - 3.7)	$\underline{3.2}$	(3.0 - 3.4)	$\underline{3.3}$	(3.0 - 3.7)
Head L/snout L	3.2	(2.7 - 3.8)	3.2	(2.8 - 3.7)	3.1	(2.6 - 3.6)
Head L/preorbital D	$\underline{4.1}$	(3.5 - 4.6)	4.4	(3.9 - 5.2)	4.3	(2.8 - 4.8)
Head L/interorbital W	$\underline{2.5}$	(2.3 - 2.8)	2.7	(2.5 - 3.2)	2.7	(2.5 - 3.1)
Head L/lower jaw L	3.6	(3.3 - 4.1)	3.7	(3.4 - 4.0)	$\underline{3.9}$	(3.2 - 4.7)
Head L/premaxillary L	3.2	(2.7 - 4.1)	3.4	(2.8 - 4.2)	3.3	(2.8 - 4.3)
Head L/premaxillary pedicel L	4.8	(4.0 - 6.3)	5.1	(4.3 - 6.6)	4.8	(4.0 - 5.7)
Pharyngeal fork L/pharyngeal total L	0.9	(0.8 - 0.9)	0.9	(0.8 - 1.0)	0.9	(0.8 - 0.9)
Pharyngeal fork L/pharyngeal W	0.9	(0.8 - 1.0)	0.9	(0.9 - 1.0)	0.9	(0.8 - 1.0)
Pharyngeal fork L/pharyngeal D	3.0	(2.6 - 3.6)	$\underline{2.9}$	(2.3 - 4.0)	$\underline{3.2}$	(2.7 - 3.8)
Pharyngeal fork L/pharyngeal blade L	2.5	(2.0 - 4.2)	$\underline{2.7}$	(2.1 - 3.5)	$\underline{2.4}$	(2.2 - 3.0)
Pharyngeal fork L/pharyngeal blade D	$\underline{4.2}$	(2.6 - 5.1)	4.7	(4.1 - 5.8)	4.6	(4.1 - 5.0)
Eye diameter/interorbital W	$\underline{0.8}$	(0.7 - 0.9)	0.9	(0.8 - 1.1)	0.8	(0.8 - 1.0)
Eye diameter/preorbital D	$\underline{1.2}$	(1.0 - 1.6)	$\underline{1.4}$	(1.3 - 1.7)	$\underline{1.3}$	(0.9 - 1.6)
Eye diameter/premaxillary pedicel L	$\underline{1.4}$	(1.2 - 1.9)	$\underline{1.6}$	(1.4 - 1.9)	1.5	(1.2 - 1.9)
Caudal peduncle/L/caudal peduncle D	1.0	(0.8 - 1.1)	1.0	(0.8 - 1.1)	0.9	(0.7 - 1.0)
Pelvic fin ray L/pelvic fin spine L	2.3	(1.6 - 2.8)	2.5	(1.6 - 3.3)	2.4	(0.9 - 2.7)
Body W/premaxillary W	1.4	(1.2 - 1.7)	1.4	(1.2 - 1.7)	1.4	(1.3 - 1.6)
Interorbital W/premaxillary W	1.0	(0.9 - 1.1)	1.0	(0.9 - 1.0)	1.0	(0.8 - 1.1)
Premaxillary W/premaxillary D	1.3	(1.1 - 1.5)	1.3	(1.0 - 1.6)	1.3	(1.1 - 1.7)
Body D/caudal peduncle D	2.7	(2.6 - 3.0)	2.8	(2.5 - 3.0)	2.7	(2.5 - 3.0)

Similar situations exist for other species complexes in Lake Malawi as well as in Lakes Tanganyika and Victoria. Barel *et al.* (1977) suggest that accurate species diagnosis in Lake Victoria cichlids is normally possible only if a number of taxonomic characters are considered together. Eccles & Lewis (1977) also found that for a reliable separation of three Lake Malawi cichlids, *Lethrinops stridei* Eccles & Lewis, *L. micrentodon* (Regan), and *L. microdon* Eccles & Lewis, it is necessary to use a number of characters in conjunction. In the Lake Malawi genus *Labidochromis* Trewavas, all species display considerable variation in most taxonomic characters and, owing to the degree of interspecific overlap, these taxonomic characters have little diagnostic value (Lewis, in prep. b).

In the case of the *Petrotilapia* species complex, the species cannot be reliably separated using morphological characters alone. The most obvious difference between the three species of *Petrotilapia* is live coloration, particularly of territorial males (i.e., sexually mature males). Although Barel *et al.* (1977) suggest that as a rule the diagnostic value of live coloration is of limited use in cichlid taxonomy, in the case of sibling species it is often the only reliable diagnostic character. There are indications that the importance of coloration in cichlid taxonomy will increase as more field research is conducted on the cichlids of the Great Lakes of Africa. Besides certain ecological differences, the most important character separating the four endemic sibling species of *Sarotherodon* in Lake Malawi is the coloration of sexually active males (Trewavas, 1947; Lowe, 1952). In Lake Victoria, as a rule, the morphological characters separating species are slight and male breeding colour is considered to be the most distinctive specific feature. Furthermore, with the exception of male breeding colour there is a high degree of individual variation in morphological characters (Greenwood, 1974).

In their discussion of the taxonomy of some Lethrinops species from Lake Malawi, Eccles & Lewis (1979) suggest that the coloration of living fish is of considerable taxonomic value. Furthermore, Lewis (in prep. b) concludes that the most useful diagnostic character in the genus Labidochromis is the coloration of sexually active males.

Before the diagnostic value of colour can be accepted, it is necessary to establish that the various colour forms are distinct species and not colour morphs of the same species. There are numerous examples where the systematic status of certain fishes is in doubt due to the existence of numerous colour forms. One of the most interesting examples is the marine genus Hypoplectrus (Walbaum). In this genus there are nine nominal species and in the absence of any other morphological differences the species descriptions are based almost exclusively on colour patterns (Graves & Rosenblatt, 1980). In addition to the nine nominal species there are a further three distinctive unnamed colour forms (Thresher, 1978). Barlow (1975) has shown that the Hypoplectrus species mate non-assortatively and an electrophoretic analysis of their enzyme systems indicates that there is probably only one highly polymorphic Hypoplectrus species (Graves & Rosenblatt, 1980).

The South American cichlid Cichlasoma citrinellum (Günther) is a polychromatic species. In Lake Jiloa, Nicaragua, the two colour morphs of C. citrinellum generally mate assortatively but a certain amount of interbreeding has been reported (McKaye & Barlow, 1976). McKaye (1980) believes that the two morphs are incipient species undergoing sympatric speciation, but at present they share a common gene pool.

Polymorphic African cichlid species have been reported from Lake Malawi, Lake Victoria, Lake Kivu and Lake Kioga (Fryer & Iles, 1972). With the exception of Lake Malawi no information has been presented on assortative mating in any of these examples. In Lake Malawi, Fryer (1959) noted that polymorphism occurs in five species of Mbuna, *Labeotropheus fuelleborni* Ahl, *L. trewavasae* Fryer, *Pseudotropheus tropheops* Regan, *P. zebra* (Boulenger) and *Genyochromis mento* Trewavas. In most of these species the male is monochromatic, and the female occurs in two forms, a 'normal' type and a 'blotched' type. At Nkhata Bay, *P. zebra* has five different colour forms, two male and three female (Fryer, 1959). Using evidence of positive assortative mating amongst these five colour forms of *P. zebra*, as well as other ecological differences, Holzberg (1978) suggested that the nominal species, *P. zebra*, comprises two discrete gene pools. Both gene pools are sexually dimorphic and one of the females is also dimorphic, thus accounting for the five colour forms. The nominal species, *P. zebra*, is therefore both polymorphic and polytypic. Furthermore, Holzberg (1978) suggested that a third *P. zebra*-like species occurs in deep water in Nkhata Bay.

Evidence of positive assortative mating within the genus *Petrotilapia*, presented in Chapter 3, provides another instance in which a so-called polychromatic species is shown to be a complex of species. The *Petrotilapia* species are sexually dimorphic but none are polymorphic.

In the Great Lakes of Africa where 'explosive speciation' has occurred, there are likely to be numerous sibling species complexes in which live coloration is the most distinctive specific feature. In a situation such as this, traditional taxonomic methods are inadequate unless they are combined with sound field observations, particularly on mate selection. Furthermore, if sibling species are found which differ mainly in live coloration, careful and systematic collections should be made by identifying, capturing and labelling specimens in the field, prior to a systematic study.

If this method were not adopted, a preserved collection representing all three species of Petrotilapia from Monkey Bay would probably be assigned to one species, or two if the dorsal fin markings were considered.

CHAPTER 5

FURTHER COLOUR FORMS OF PETROTILAPIA

The three colour forms of Petrotilapia which occur at Monkey Bay were shown to be discrete species in Chapter 3 and were formally described in Chapter 4. These results have shown that the three species are extremely similar to one another in gross morphology and that they therefore represent a complex of sibling species. The only reliable character that distinguishes these sibling species is live coloration. There are at least 14 other colour forms of Petrotilapia in Lake Malawi. Most of the rocky shores surveyed in the lake were occupied by two to four of the seventeen colour forms of Petrotilapia. Although it was not possible to do extensive field observations at all of these sites, the colour forms appeared to behave as distinct species in that there was positive assortative mating (see discussion, page 108).

In view of the fact that the three Monkey Bay species form the basis of this thesis they are formally described. A full description of the other 14 forms is not necessary to demonstrate the importance of biological characters to the systematics of this genus and has therefore been left for a later study. In this chapter a description of the coloration of the 14 colour forms is presented to emphasize the importance of this character in the systematics of Petrotilapia.

'Gold' form

The coloration of a territorial male and a typical female from Cinyankwasi Island is shown in Figures 22 and 23. Territorial males are almost completely black. The dorsal fin has sky blue lappets and in some specimens

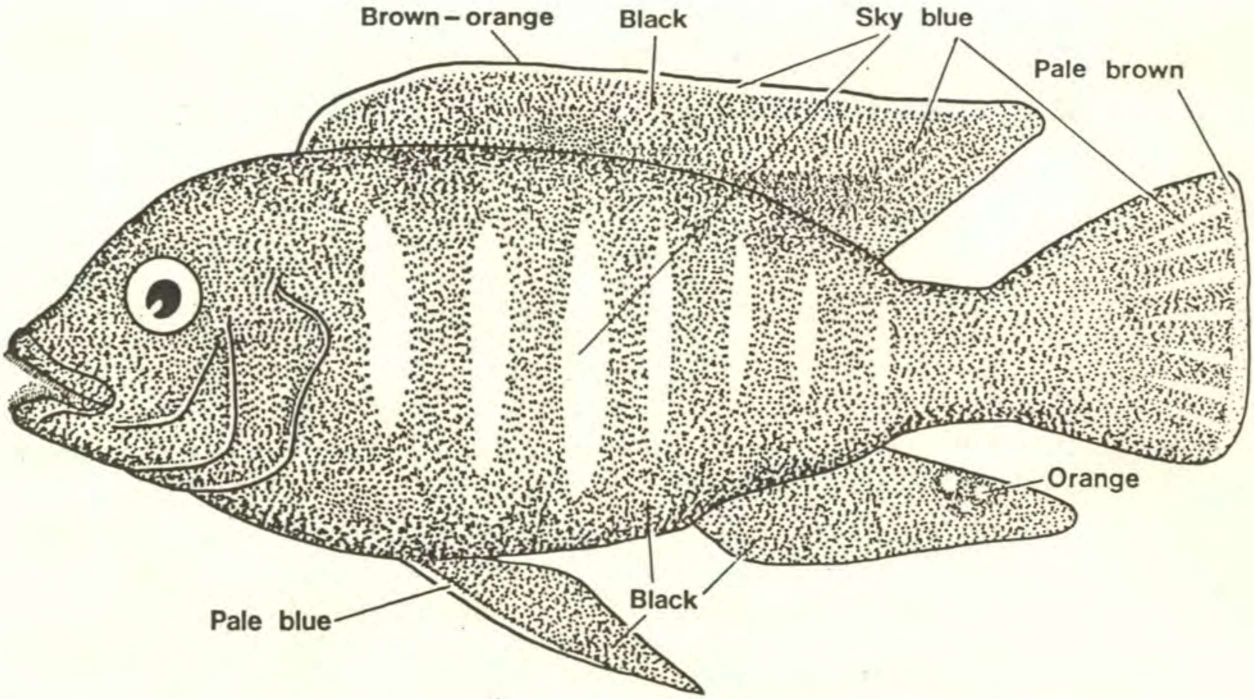

Figure 22. 'Gold' form Petrotilapia - territorial male from Cinyankwasi.

Figure 23. 'Gold' form Petrotilapia - adult female from Cinyankwasi.

the lappets have brown-orange tips. The posterior interray membranes of the dorsal fin and the interray membranes of the caudal fin are sky blue. The trailing edge of the caudal fin is pale brown. The anal fin has up to five bright yellow to orange ocelli on the posterior angle. The leading edge of the pelvic fin, including the spine, is pale blue. The flanks normally have seven narrow, sky blue bars which do not reach the dorsal fin base or belly. The prominence of the bars varies. In some individuals the barring is barely noticeable except during courtship or aggressive displays. During these encounters the blue colour becomes intensified. In water deeper than about 15 m, territorial males are more obviously barred. In these specimens the bars are generally broader and are a pale blue-grey colour.

Adult females and juveniles are generally an intense golden colour, but some individuals are drab brown. The flanks have two parallel rows of dark brown to black blotches. Sub-adults and non-territorial males have a pale blue-grey ground colour with four to eight dark blue blotches on their flanks.

The 'Gold' form is only found on the islands of Cinyankwasi and Cinyamwezi (Figure 24b) where it has a broad depth range (0.1-35 m).

'Mumbo Blue' form

The coloration of a territorial male and an adult female from Mumbo Island is illustrated in Figures 25 and 26. Territorial males are sky blue in ground coloration and have eight to nine dark blue vertical bars on their flanks. The belly is pale blue. The head is dark blue and has a thick dark grey interorbital stripe. Dorsal fin lappets are sky blue and in some specimens the lappet tips are orange. Beneath the lappets

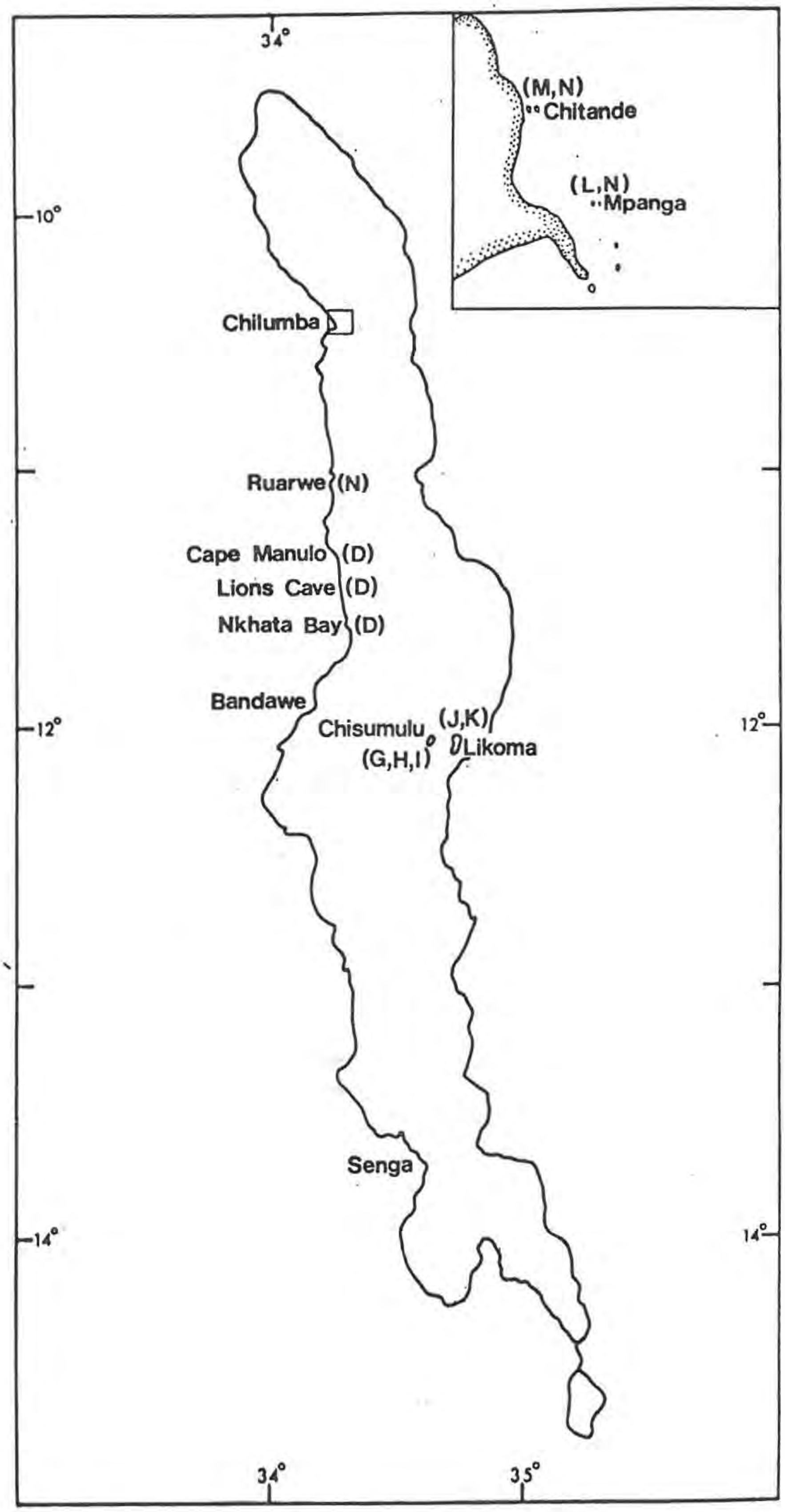

Figure 24(a) Distribution of undescribed Petrotilapia forms in Lake Malawi north of Mbenje Island. 'Small Blue' form = D, 'Orange Pelvic' form = G, 'Retrognathous' form = H, 'Yellow Ventral' form = I, 'Likoma Variable' form = J, 'Likoma Barred' form = K, 'Black Flank' form = L, 'Chitande' form = M and 'Ruarwe' form = N.

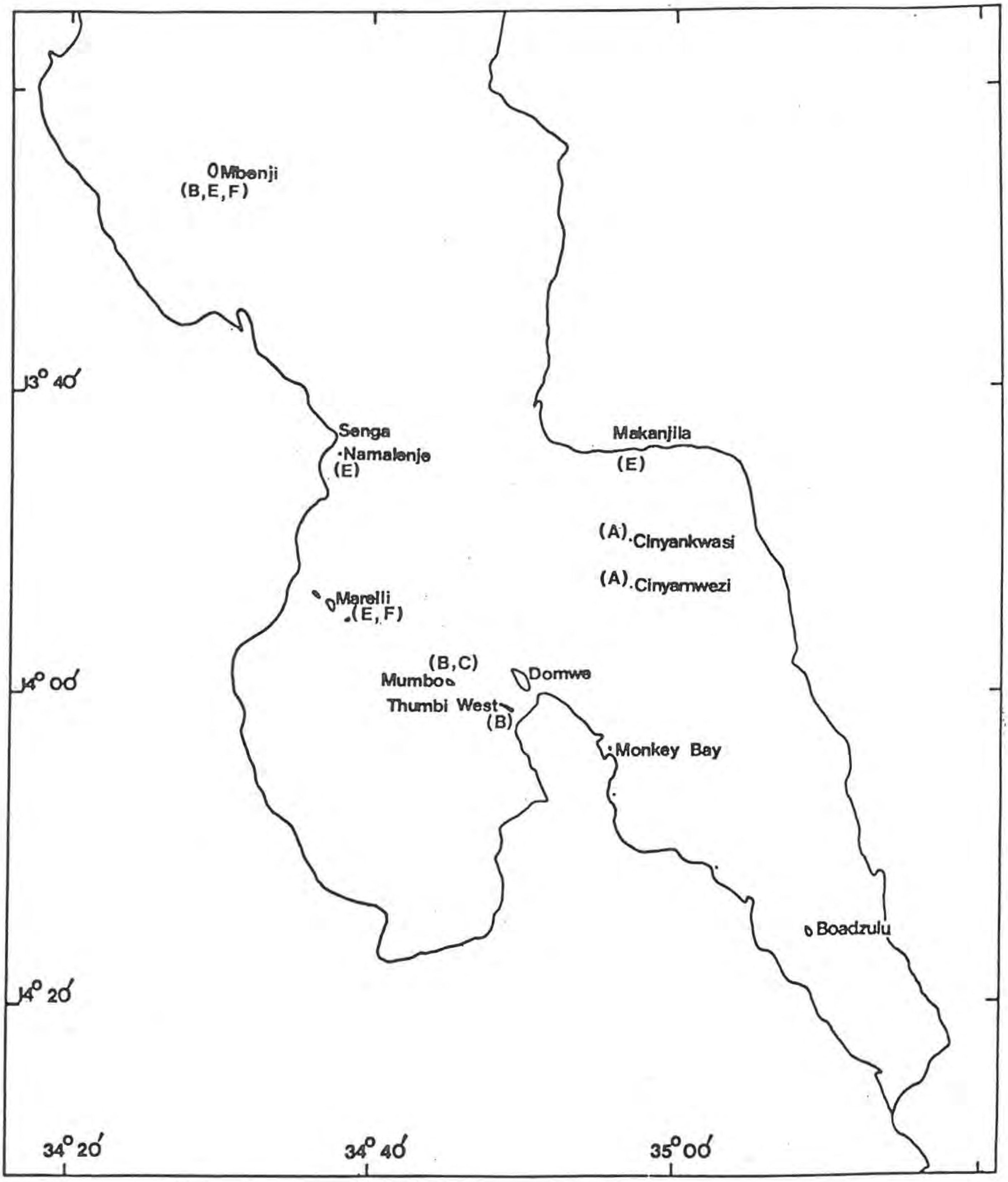

Figure 24(b). Distribution of undescribed Petrotilapia forms in southern Lake Malawi. 'Gold' form = A, 'Mumbo Blue' form = B, 'Mumbo Yellow' form = C, 'Yellow Fin' form = E and 'Fuscous' form = F.

Figure 25. 'Mumbo Blue' form Petrotilapia - territorial male from Mumbo Island.

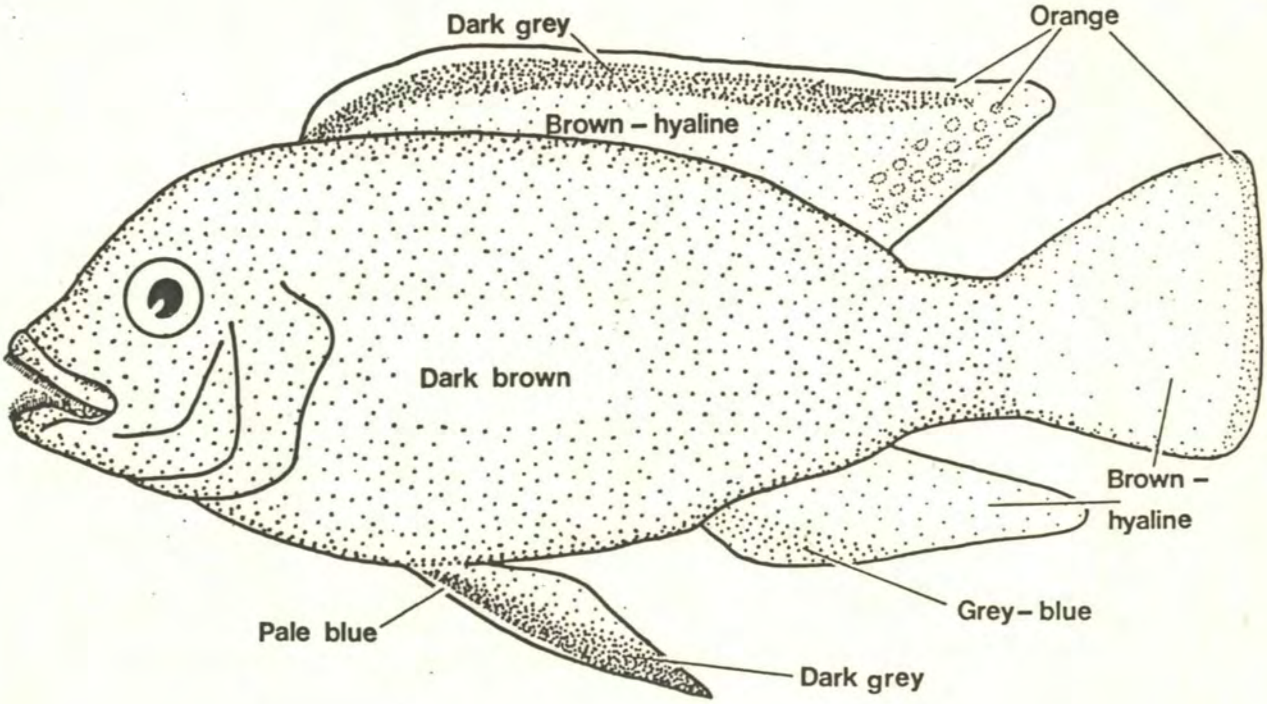

Figure 26. 'Mumbo Blue' form Petrotilapia - adult female from Mumbo Island.

is a black longitudinal stripe. Posteriorly the interray membranes of the dorsal fin have numerous orange spots and the rays are black. The remainder of the dorsal fin is a hyaline blue colour. The caudal fin has an orange trailing edge, the rays are black and the interray membranes are lilac. The anal fin has a pale blue distal edge followed by a black stripe. Proximal to this stripe the fin is a semi-transparent blue-grey and a few bright yellow ocelli are normally present on the posterior angle. The pelvic fins have a pale blue leading edge, followed by a dark grey-black stripe. The rays on the rest of the fin are grey and the interray membranes are hyaline-orange.

Females are generally a uniform dark brown. The dorsal fin has pale orange lappets, a dark grey longitudinal stripe and orange spots on the posterior interray membranes. The ground colour of the dorsal fin is brown-hyaline. The caudal fin is brown-hyaline with the exception of the trailing edge which is orange. The anterior half of the anal fin is dark grey and the remainder is brown-hyaline. Each pelvic fin has a pale blue leading edge, followed by a dark grey stripe which fades gradually towards the midline to a pale orange hue. Non-territorial adult males have a purple ground colour and similar markings to territorial individuals. Due to their dark background, the markings are partially obscured.

The 'Mumbo Blue' form has a disjunct distribution occurring at the islands of Mumbo, Thumbi West and Mbenje (Figure 24b). This form does not occur on the three Marelli Islands, Namalenje Island and the neighbouring mainland, which all lie between Mumbo and Mbenje Islands. The 'Mumbo Blue' form lives in the shallows and has not been recorded below 6 m.

'Mumbo Yellow' form

The coloration of a territorial male and an adult female from Mumbo Island is shown in Figures 27 and 28. The ground colour of territorial males is a slate grey suffused with yellow. Dorsally the head is a greyish-yellow colour becoming bright yellow below the orbit. There is a grey green interorbital stripe. The bright yellow extends ventrally along the belly and pelvic fins. The flanks are slate grey suffused with yellow and may have four to six indistinct grey-green vertical bars. The dorsal fin has orange lappets. Below the lappets is a black longitudinal stripe. The remainder of the dorsal fin is blue-hyaline with patches of yellow. The rays in the posterior part of the dorsal fin are black. The caudal fin has black rays, blue-hyaline interray membranes and an orange trailing edge. The anal fin has a sky blue distal edge followed by a black stripe. The remainder of the anal fin is a bluish-grey hyaline colour. A few bright yellow ocelli occur on the posterior angle.

The ground colour of females is normally a dull, pale grey. The flanks have seven to eight grey vertical bars. In between the stripes are some thick black mid-lateral blotches. Thin black dorso-lateral blotches are also apparent on some specimens. The dorsal fin is hyaline except for pale orange lappets and a thin dark grey longitudinal stripe. The caudal fin has dark grey rays and hyaline interray membranes. The anal fin has a dark grey border and hyaline centre. Pelvic fins are greyish-hyaline. Non-territorial males tend to be much darker than territorial males and most have a brownish rusty flush where territorial males are bright yellow.

The 'Mumbo Yellow' form is restricted to Mumbo Island (Figure 24b) and is common between 3-8 m (rarely 0.1-18 m).

Figure 27. 'Mumbo Yellow' form Petrotilapia - territorial male from Mumbo Island.

Figure 28. 'Mumbo Yellow' form Petrotilapia - adult female from Mumbo Island.

'Small Blue' form

This is the smallest Petrotilapia species known. The largest mature male measured 111 mm SL and the mean SL of 11 mature males was 102 mm (89-111 mm). The coloration of a territorial male and an adult female from Nkhata Bay is shown in Figures 29 and 30. Territorial males have a sky blue ground colour and may have five to nine dark blue vertical bars on the flanks. The gular region and belly are bright yellow. The dorsal fin has bright yellow lappets and a black longitudinal submarginal stripe. Anteriorly the base of the dorsal fin is orange, the rest of the fin is sky blue. The trailing edge of the caudal fin is yellow to orange, the rays are grey and the interray membranes are sky blue. The anal fin has a thick black bar on the distal edge and bright yellow ocelli on the posterior angle. The remainder of the fin is hyaline. Each pelvic fin has a pale blue leading edge and the remainder of the fin is hyaline with occasional orange flecks.

Females and juveniles generally have a brilliant gold ground colour with a series of large black mid-lateral blotches and a series of small black dorso-lateral blotches. The dorsal fin is golden except for a narrow dark submarginal stripe. The caudal fin is golden with the exception of the rays which are brown. The pelvic fin has a dark grey leading edge, golden to bright yellow rays and hyaline interray membranes. There is a certain amount of variation in colour, as some females have a dull pale brown ground colour and there is a gradation of colour between this extreme and the normal golden colour. Flank blotches are variable and in some specimens, particularly juveniles, they are hardly visible and the blotch colour, although normally black, can be dark brown. The submarginal stripe in the dorsal fin is only apparent in adult females.

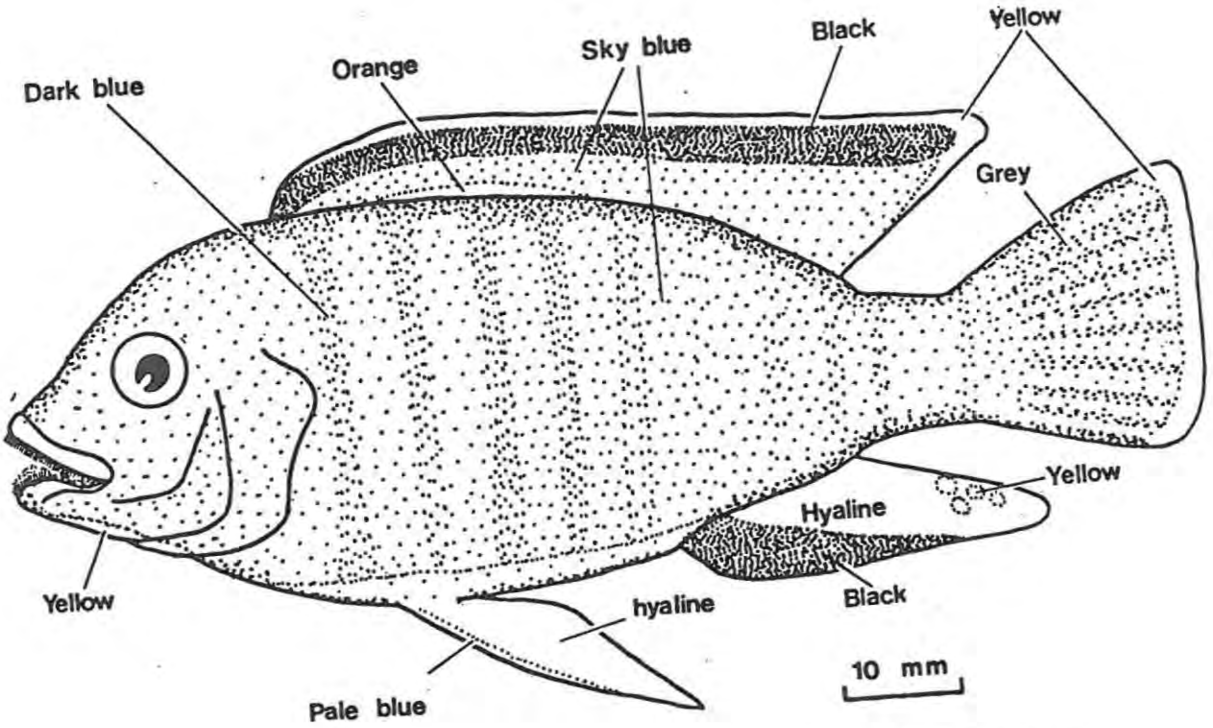

Figure 29. 'Small Blue' form Petrotilapia - territorial male from Nkhata Bay.

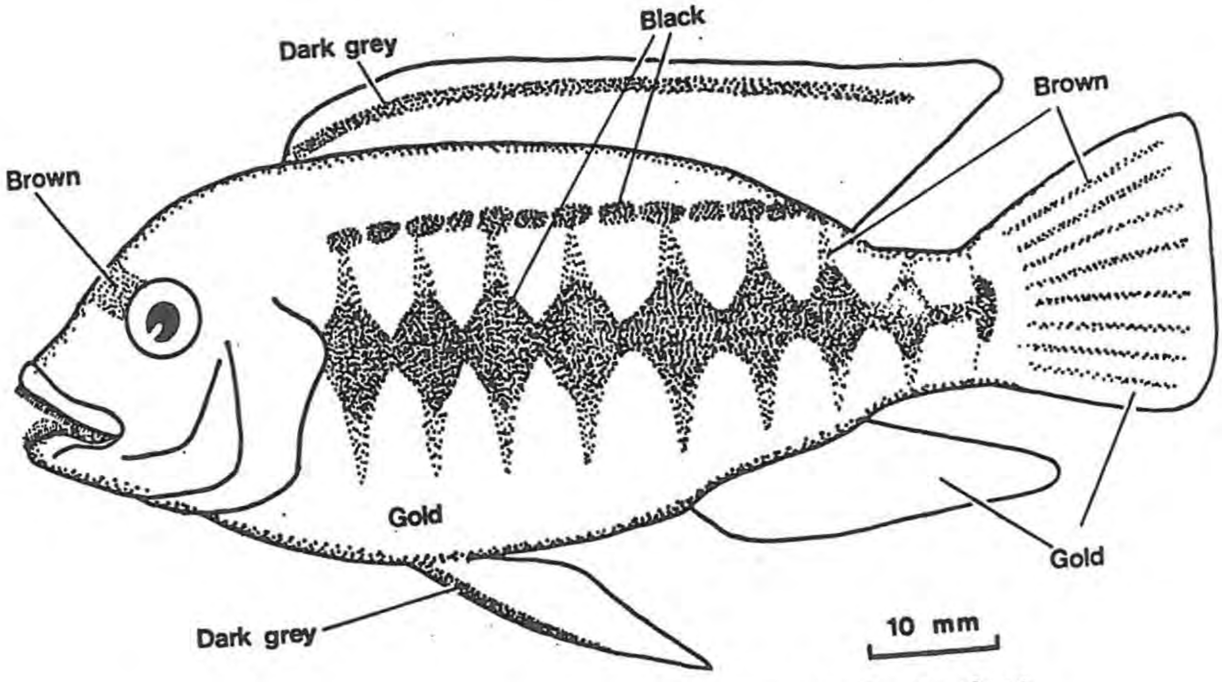

Figure 30. 'Small Blue' form Petrotilapia - adult female from Nkhata Bay.

Non-territorial males are similar to territorial males but have a dark blue ground colour which obscures any flank stripes. The 'Small Blue form occurs at Nkhata Bay, Lions Cave and Cape Manulo (Figure 24a). All of the coastline between Nkhata Bay and Cape Manulo is rocky and this form probably occurs along this entire length of coast. At Nkhata Bay the 'Small Blue' form occurs from 2-42 m but it is not common in water less than 8 m deep.

'Yellow Fin' form

The coloration of a territorial male from Mbenje Island and a female from Makanjila is illustrated in Figures 31 and 32 respectively. Territorial males have a sky blue ground colour with a yellowish hue. Most specimens have seven to nine darker blue vertical flank bars. The cheeks are bright yellow. The yellow extends postero-ventrally to a variable extent. In some specimens it may only reach the pectoral fin, in others it extends as far as the vent. The dorsal fin varies from pale blue (as in Figure 31) to an almost uniform yellow with patches of blue. Variations in dorsal fin colour are not confined to any one locality. Dorsal fin lappets are normally yellow. In certain of the Mbenje specimens there is a faint dusky submarginal stripe. The caudal fin generally has a yellow-orange trailing edge, yellow rays and blue interray membranes suffused with yellow. At Mbenje caudal fin rays are dark grey to black. The anal fin is grey-blue to blue with bright yellow ocelli on the posterior angle. Pelvic fins have a pale blue leading edge, yellow interray membranes and pale grey rays. In some Mbenje specimens there is a dark grey stripe adjacent to the spine. Females and juveniles are a uniform dull brown colour.

The 'Yellow Fin' form is found at Makanjila, the three Marelli Islands,

Figure 31. 'Yellow Fin' form Petrotilapia - territorial male from Mbenje Island.

Figure 32. 'Yellow Fin' form Petrotilapia - adult female from Makanjila.

Namalenje Island and Mbenje Island (Figure 24b). It normally occurs in shallow water as deep as 6m. At Namalenje Island it was not recorded below 3m.

'Fuscous' form

The coloration of a territorial male and a mouth-brooding female, from the Marelli Islands, is shown in Figures 33 and 34. Territorial males have a dark fuscous (brownish-grey) ground colour. The cheek region is brown-orange and this colour extends ventrally to a variable extent. In some specimens the entire belly is brown-orange whereas in others the colour extends only to the base of the pectoral fins. The dorsal fin has prominent lappets which vary from the normal orange to pale blue. A thick black submarginal stripe dominates the dorsal fin. The fin is blue-grey below this stripe. The caudal fin has a yellow-orange trailing edge and the remainder is dark fuscous. The anal fin is dark fuscous but in some specimens the distal edge is paler and the posterior angle is hyaline. There are one to five bright yellow ocelli on the posterior angle. The anterior half of the pelvic fins is dark fuscous to black and the remainder of the fin is yellowish-brown. In many specimens the lips are yellow.

Females and juveniles generally have a pale brown to khaki ground colour although dark brown specimens have occasionally been seen. There are prominent narrow black mid-lateral and dorso-lateral bands. In some specimens these bands are divided into blotches by seven to nine vertical bars. The mid-lateral band extends anteriorly to the orbit and many specimens have a black supraorbital stripe. Dorsal medial blotches are also present. The dorsal fin has pale grey lappets tipped with orange-

Figure 33. 'Fuscous' form Petrotilapia - territorial male from Marelli Islands.

Figure 34. 'Fuscous' form Petrotilapia - adult mouth brooding female from Marelli Islands.

brown. A thin, dark grey submarginal stripe occurs directly below the lappets. The remainder of the fin is hyaline and the posterior interray membranes sometimes have numerous spots. In certain specimens the spots are yellow on a hyaline background whereas other specimens have hyaline spots on a yellow background. The caudal and anal fins are hyaline with numerous small bright yellow spots on the posterior angle of the anal fin. The pelvic fins have a pale whitish leading edge followed by a thin grey stripe. The remainder of the fin is hyaline.

The 'Fuscous' form occurs on all three Marelli Islands and at Mbenje Island (Figure 24b). It does not occur at Namalenje Island or the nearby mainland which lie between Mbenje and the Marelli Islands. It occurs from 2 m to over 20 m and is particularly common between 5 and 10 m.

'Orange Pelvic' form

The coloration of a territorial male and an adult female, from Chisumulu Island is illustrated in Figures 35 and 36. Territorial males have a sky blue ground colour and may have seven faint blue-grey flank bars. The dorsal fin has blue lappets some of which have orange tips. Directly beneath the lappets is a thin black submarginal stripe. The two posteriormost interray membranes of the dorsal fin have numerous orange spots. The remainder of the fin is blue-hyaline. The caudal fin has an orange-brown trailing edge, dark grey rays and lilac interray membranes. The ventral and dorsal margins of the caudal fin are dark blue to black. The anal fin has a black stripe along its distal edge and bright yellow ocelli on the posterior angle. The remainder of the fin is blue-hyaline. Each pelvic fin has a pale blue leading edge followed by a thin black stripe.

Figure 35. 'Orange Pelvic' form Petrotilapia - territorial male from Chisumulu Island.

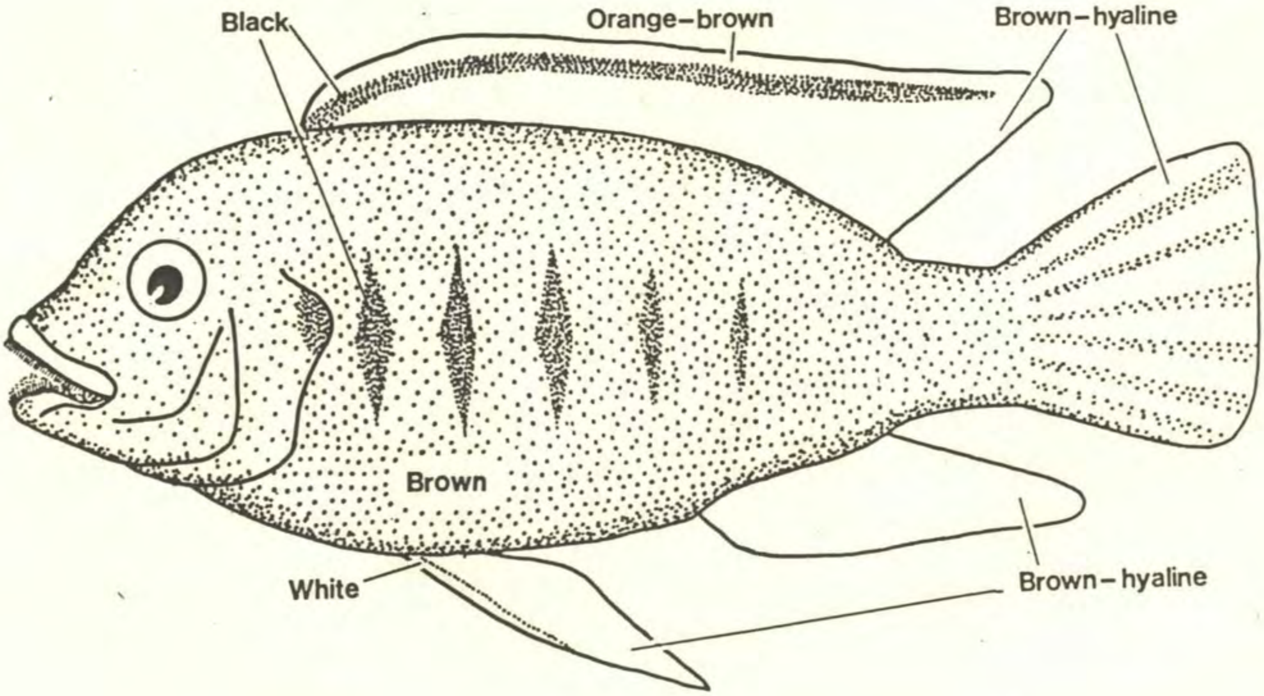

Figure 36. 'Orange Pelvic' form Petrotilapia - adult female from Chisumulu Island.

The remainder of the pelvic fin is bright orange. Most males have a black opercular blotch.

The ground colour of females is normally dark brown but varies from pale brown through to chocolate brown. Situated mid-laterally are a series of black wedge-shaped blotches. Certain specimens also have a series of narrow dorso-lateral blotches. The dorsal fin has orange-brown lappets and a thin black submarginal stripe. The remainder of the fin is brown-hyaline. The caudal fin has brown-hyaline interray membranes and the rays are the same shade of brown as the body. The anal fin is entirely brown-hyaline. Pelvic fins have a white leading edge and the remainder of the fin is brown-hyaline with an orange hue. Females have a black opercular blotch.

The 'Orange Pelvic' form is restricted to Chisumulu Island where it is common in water less than 3 m deep and was not observed deeper than 4m (Figure 24a).

'Retrognathous' form

This is the only Petrotilapia species which has an obvious morphological difference from congeners. In this form the premaxilla extends anteriorly beyond the dentary which results in a ventrally directed gape. The coloration of a territorial male from Chisumulu Island is shown in Figure 37.

Territorial males are sky blue with eight to nine navy blue vertical bars on the body. The head is navy blue dorsally with ocher-brown cheeks. The ocher-brown hue extends variably along the belly. In some specimens

Figure 37. 'Retrognathous' form Petrotilapia - territorial male from Chisumulu Island.

the entire flanks have an ocher-brown hue. This effect is caused by each scale being edged in ocher-brown. The dorsal fin has a sky blue ground colour with a variable amount of ocher anteriorly. The posterior section of the dorsal fin is sky blue and orange spots occur along the trailing edge in certain specimens. The caudal fin has an ocher-brown trailing edge, navy blue rays and sky blue interray membranes. The anal fin has a sky blue ground colour which is suffused with ocher-brown to a variable extent. The posterior angle of the anal fin has one to four bright yellow ocelli. The pelvic fins are sky blue but are normally heavily suffused with ocher-brown.

Females are uniform dark brown and due to their lack of any obvious markings, no illustration has been given. In colour they closely resemble the female of the 'Yellow fin' form.

The 'Retrognathous' form is restricted to the island of Chisumulu (Figure 24a). It occurs from the shallows(0.1 m) down to a depth of approximately 10 m.

'Yellow Ventral' form

The coloration of a territorial male and an adult female from Chisumulu Island is illustrated in Figures 38 and 39. Territorial males have a pale sky blue ground colour with five to six sky blue vertical bars on their flanks. The head below the level of the orbit and the ventral half of the flanks is suffused with yellow. The yellow extends to the posterior base of the anal fin. The dorsal fin is sky blue-hyaline with scattered orange-pink flecks. In some specimens the central third of the posterior rays is black. The caudal fin has yellow rays and lilac

Figure 38. 'Yellow Ventral' form Petrotilapia - territorial male from Chisumulu Island.

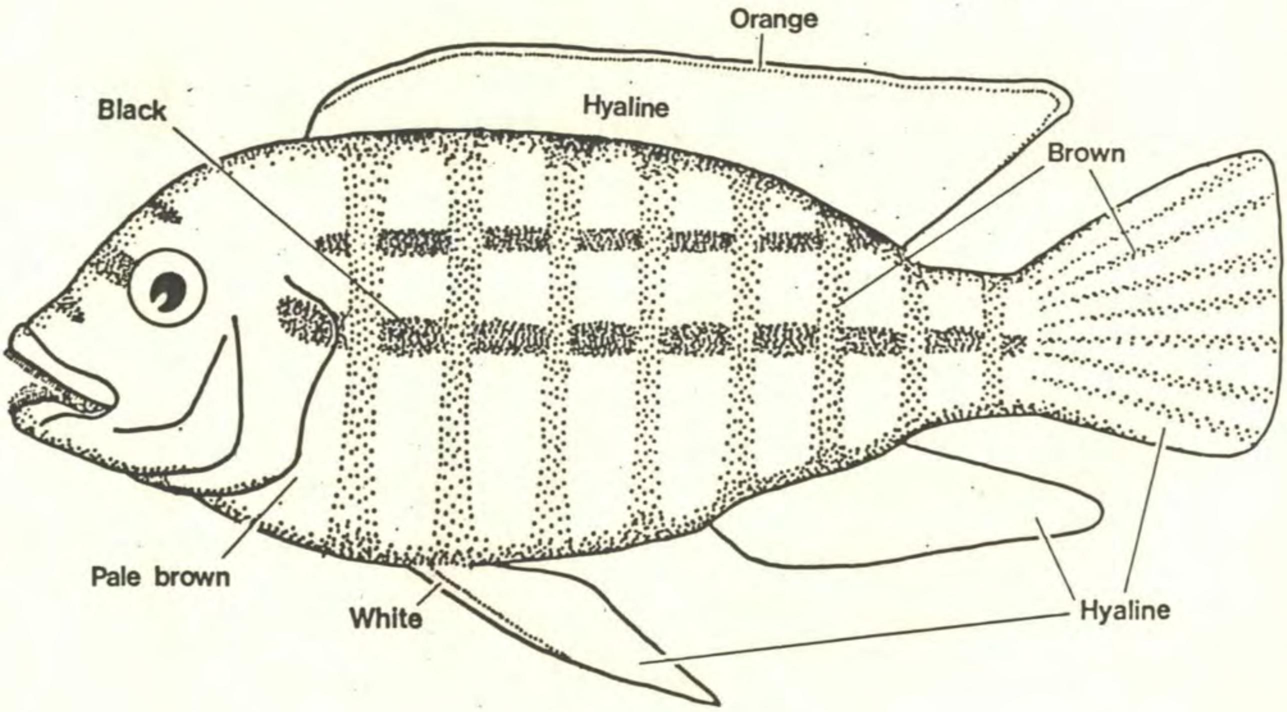

Figure 39. 'Yellow Ventral' form Petrotilapia - adult female from Chisumulu Island.

interray membranes. The anal fin has a black stripe along its distal edge. The remainder of the fin is navy blue with some bright yellow ocelli on the posterior angle. The pelvic fins are yellow.

Females are pale brown with thin black dorso-medial, dorso-lateral and mid-lateral blotches. The mid-lateral blotches are extended anteriorly to form an opercular blotch. The flanks also have eight narrow brown vertical stripes. The dorsal fin is hyaline and has orange lappets. The caudal fin has hyaline interray membranes and brown rays. The anal fin is hyaline and the pelvic fins are hyaline except for a white leading edge.

The 'Yellow Ventral' form is confined to the island of Chisumulu (Figure 24a). It is common in water deeper than 10 m and occurs beyond 20 m. Although this form was not observed in water shallower than 8 m, this may be attributable to insufficient observation time.

'Likoma Variable' form

The coloration of a territorial male and adult female from Likoma Island is illustrated in Figures 40 and 41. Territorial males of this form vary considerably in colour. Ground colour varies from sky blue to navy blue, but always has a metallic sheen. The head region below the orbit normally has an ocher hue but this is absent in some specimens. The ocher may extend onto the belly and in some specimens reaches as far as the vent. The dorsal fin has pale blue lappets anteriorly, posteriorly the lappets are pale blue with an orange hue or uniform orange. The posterior border of the dorsal fin is orange. The remainder of the fin is normally the same colour as the flank but in some specimens it has an ocher hue. The caudal fin has an orange trailing edge, black rays and flank coloured interray membranes. The anal fin is normally flank coloured, the extreme

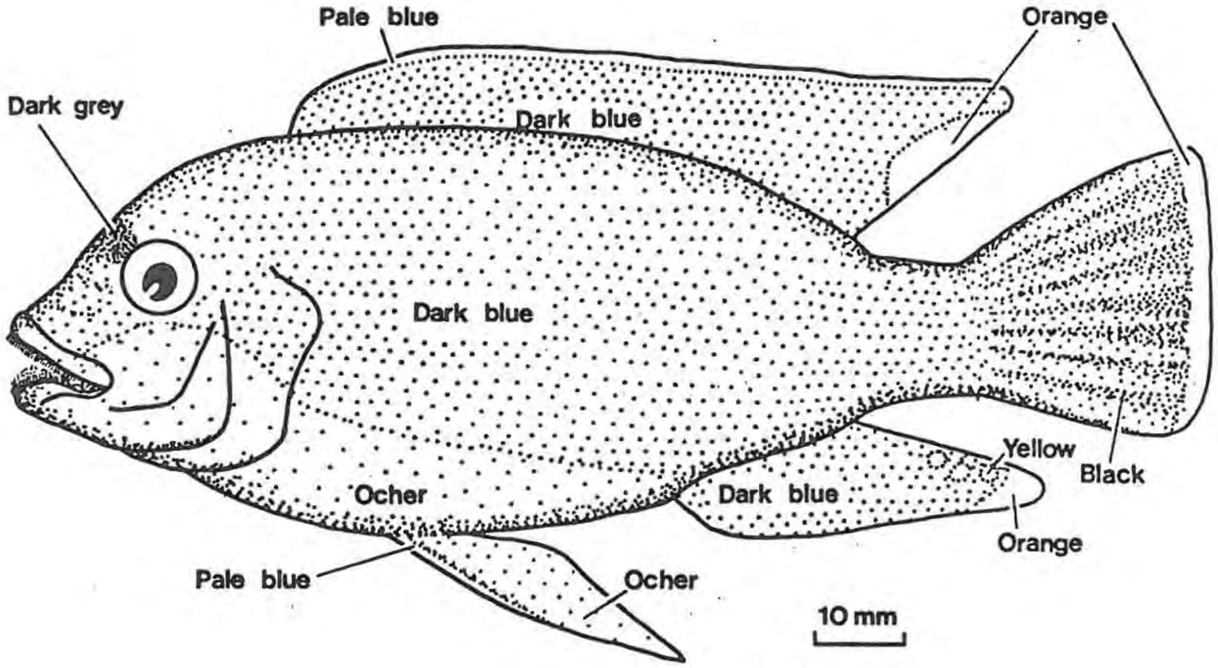

Figure 40. 'Likoma Variable' form Petrotilapia - territorial male from Likoma Island.

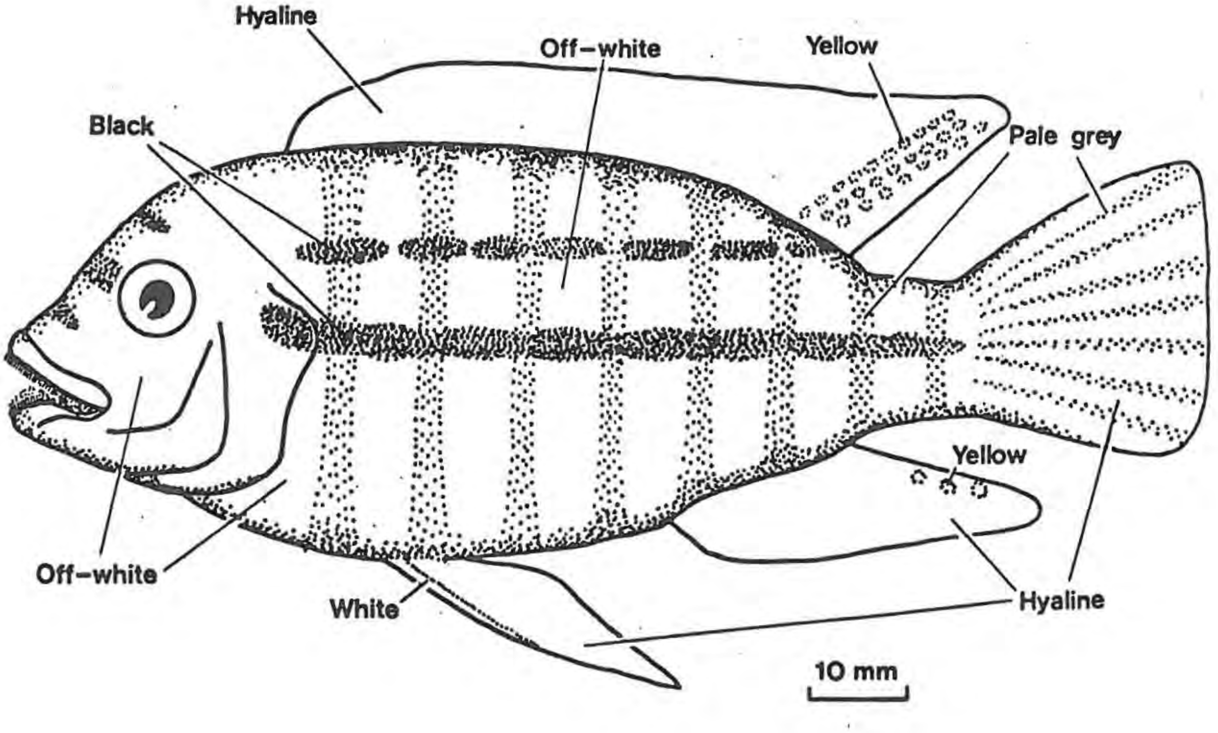

Figure 41. 'Likoma Variable' form Petrotilapia - adult female from Likoma Island.

edge is orange and there are ocelli on the posterior angle. In some specimens the anal fin is ocher. The pelvic fins are ocher but have a pale blue leading edge.

Females generally have an off-white ground colour with eight to nine pale grey vertical stripes. A thin black mid-lateral and dorso-lateral band are characteristic of this form. The mid-lateral band extends anteriorly to form an opercular blotch. Certain specimens are darker in ground colour and in these the longitudinal bands and vertical stripes are less obvious. The dorsal fin is hyaline with columns of yellow spots on the posteriormost interray membranes. The caudal fin has pale grey rays and hyaline interray membranes. The anal fin is hyaline and has a few small yellow spots on the posterior angle in some specimens. The pelvic fins have a white leading edge and the remainder is hyaline. The 'Likoma Variable' form is restricted to Likoma Island and has a broad depth range, occurring from the shallows (0.1 m) down to at least 30 m (Figure 24a).

'Likoma Barred' form

The coloration of a territorial male and a typical female from Likoma Island is illustrated in Figures 42 and 43. The ground colour of territorial males varies from sky blue to navy blue. Superimposed on this are seven to nine vertical bars which vary from navy blue to black. The head is the same colour as the vertical bars. The ventral surface often has a rusty-brown hue. The dorsal fin has prominent lappets which are pale blue or orange or, in most specimens, a mixture of both colours. The posterior edge of the dorsal fin is orange. Directly beneath the lappets is a thick black submarginal stripe. The remainder of the dorsal

Figure 42. 'Likoma Barred' form Petrotilapia - territorial male from Likoma Island.

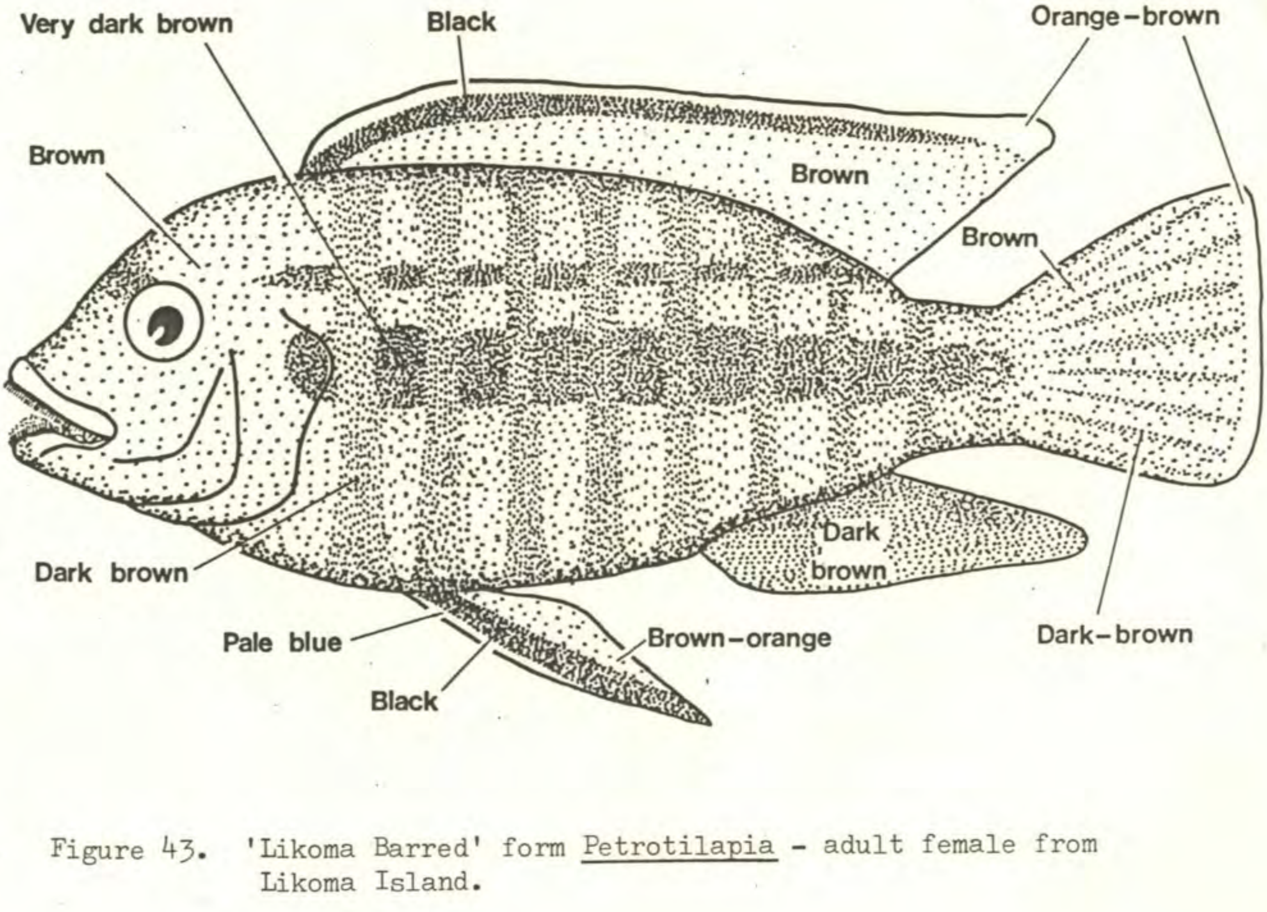

Figure 43. 'Likoma Barred' form Petrotilapia - adult female from Likoma Island.

fin is a dull blue-grey. The caudal fin has an orange-brown trailing edge, dark blue to black rays and lilac interray membranes. The anal fin has a pale blue distal edge followed by a thick black stripe. The posterior angle is hyaline and has one to six bright yellow ocelli. Each pelvic fin has a pale blue leading edge followed by a black stripe which fades progressively into a dull grey-brown.

Females have a brown ground coloration with seven to nine dark brown vertical bars running from the base of the dorsal fin to the belly. In the gaps between the bars are a series of very dark brown to black mid-lateral and dorso-lateral blotches. The mid-lateral blotches extend anteriorly to form an opercular blotch. The posterior edge and lappets of the dorsal fin are orange-brown. Beneath the lappets is a thin black submarginal stripe. The remainder of the dorsal fin is brown. The caudal fin has an orange-brown trailing edge, dark brown rays and brown interray membranes. The anal fin is uniform dark brown. The pelvic fins have a pale blue leading edge followed by a black stripe. The remainder of the pelvic fin is brown-orange.

The 'Likoma Barred' form is restricted to Likoma Island where it is common in water less than 6 m and does not usually occur below 10 m, although at Mazimbwe Rocks, a small rocky outcrop on the southern end of Likoma Island (Figure 24a), it has been recorded at 15 m.

'Black Flank' form

The coloration of a territorial male and adult female from Mpanga Rocks, Chilumba, is shown in Figures 44 and 45. Territorial males are almost entirely deep purple or black. Dorsal fin lappets are orange or pale blue and there is a thick black longitudinal stripe adjacent to the lappets

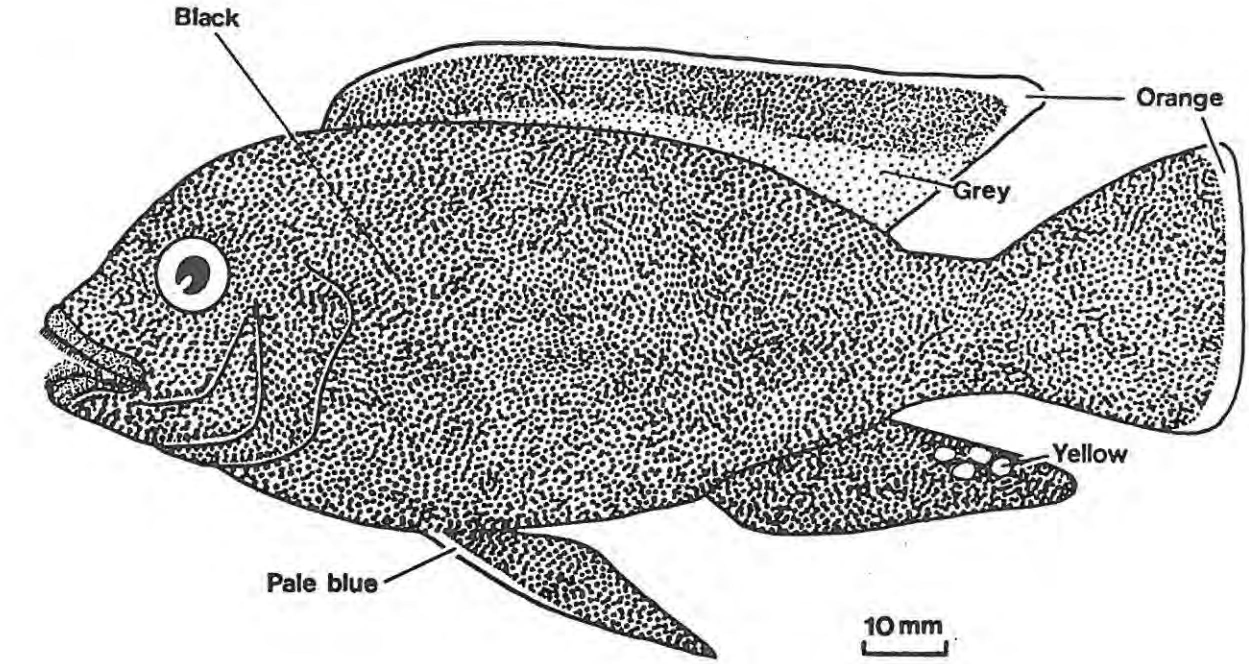

Figure 44. 'Black Flank' form <u>Petrotilapia</u> - territorial male from Mpanga Rocks, Chilumba.

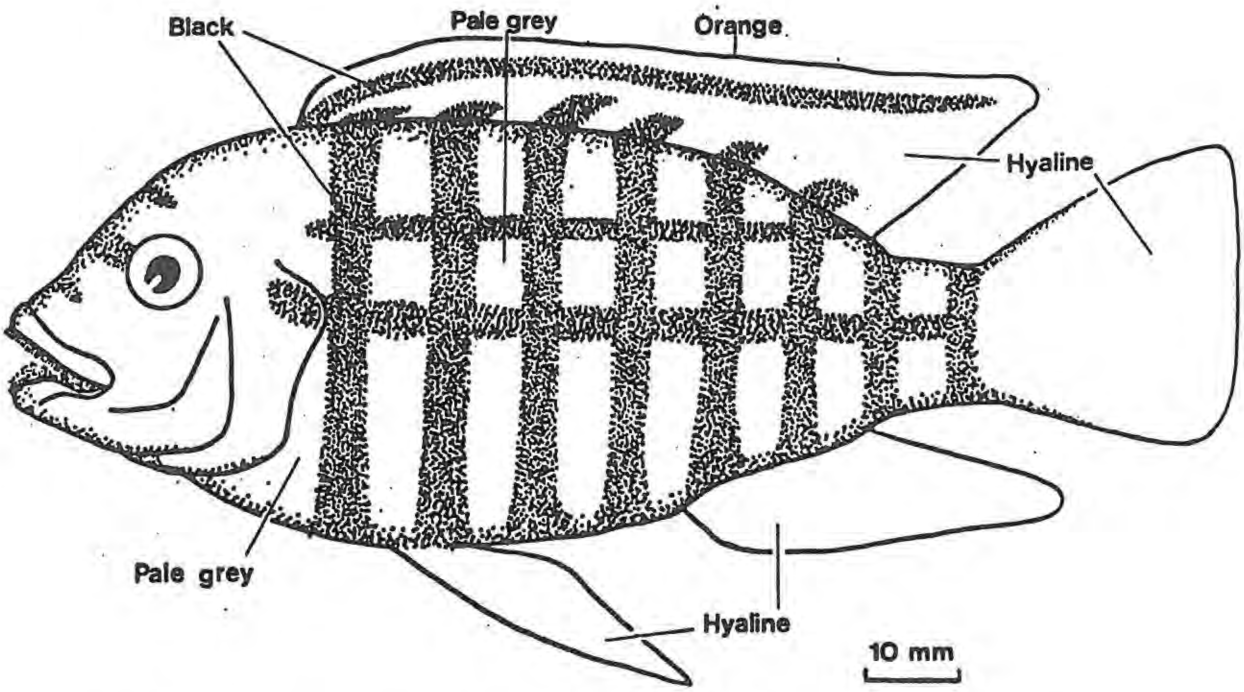

Figure 45. 'Black Flank' form <u>Petrotilapia</u> - adult female from Mpanga Rocks, Chilumba.

followed by a grey basal portion. The trailing edge of the caudal fin is orange. One to five bright yellow ocelli occur on the posterior angle of the anal fin. The leading edge of the pelvic fins is pale blue.

The ground colour of females varies from a pale grey to a dull brown. The flanks have eight black vertical stripes which are criss-crossed by a black mid-lateral and dorso-lateral band. The vertical stripes in many specimens partially penetrate into the dorsal fin. The dorsal fin, with the exception of orange tipped lappets and a thin black submarginal stripe, is hyaline. The caudal, anal and pelvic fins are hyaline.

The 'Black Flank' form has only been recorded at Mpanga Rocks, Chilumba, where it occurs in water 2 m to 8 m deep (Figure 24a).

'Chitande' form

The coloration of a territorial male and a female from Chitande Island. Chilumba is illustrated in Figures 46 and 47. Territorial males are sky blue with five blue-grey vertical stripes on the anterior half of the body. The head region below the orbit and the belly up to the vent are yellow. The dorsal fin has yellow lappets followed by a thin black submarginal stripe. The remainder of the dorsal fin is sky blue with flecks of orange, particularly on the posterior rays. The caudal fin has a yellow-orange trailing edge, orange-brown rays and sky blue interray membranes. The dorsal and ventral edge of the caudal fin is dark grey. The antero-distal edge of the anal fin has a thin black stripe. Bright yellow ocelli occur on the posterior angle of the anal fin and the remainder of the fin is grey-hyaline. The pelvic fin, with the exception of a thin grey stripe on the leading edge, is yellow.

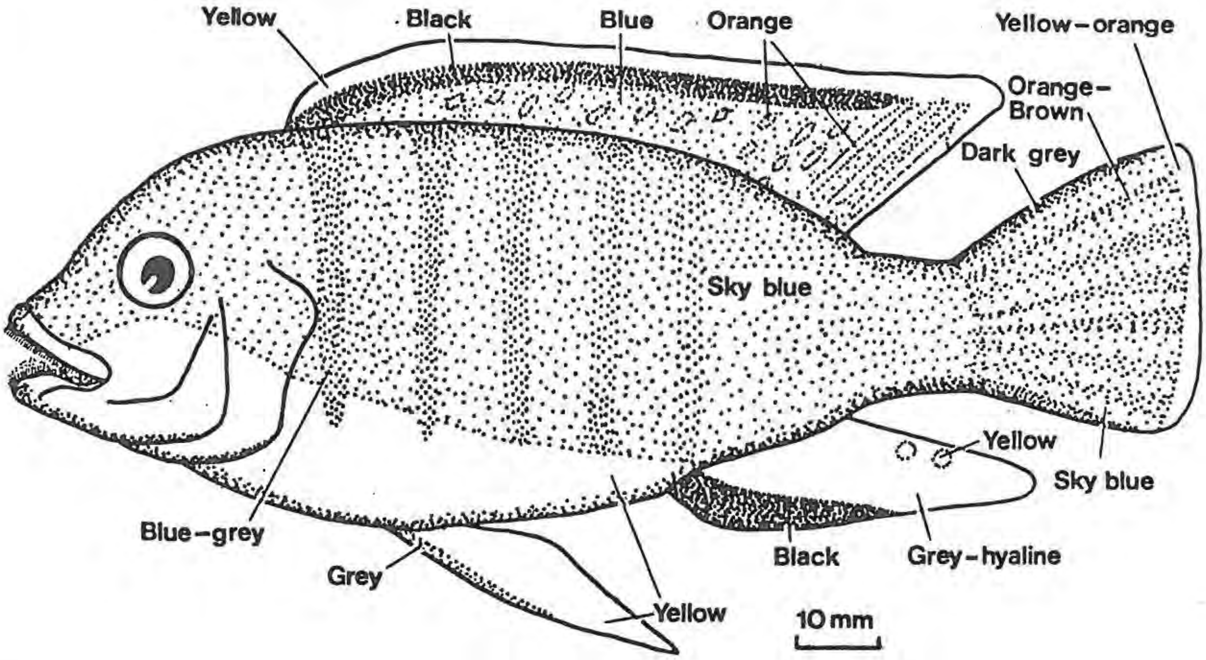

Figure 46. 'Chitande' form Petrotilapia - territorial male from Chitande Island, Chilumba.

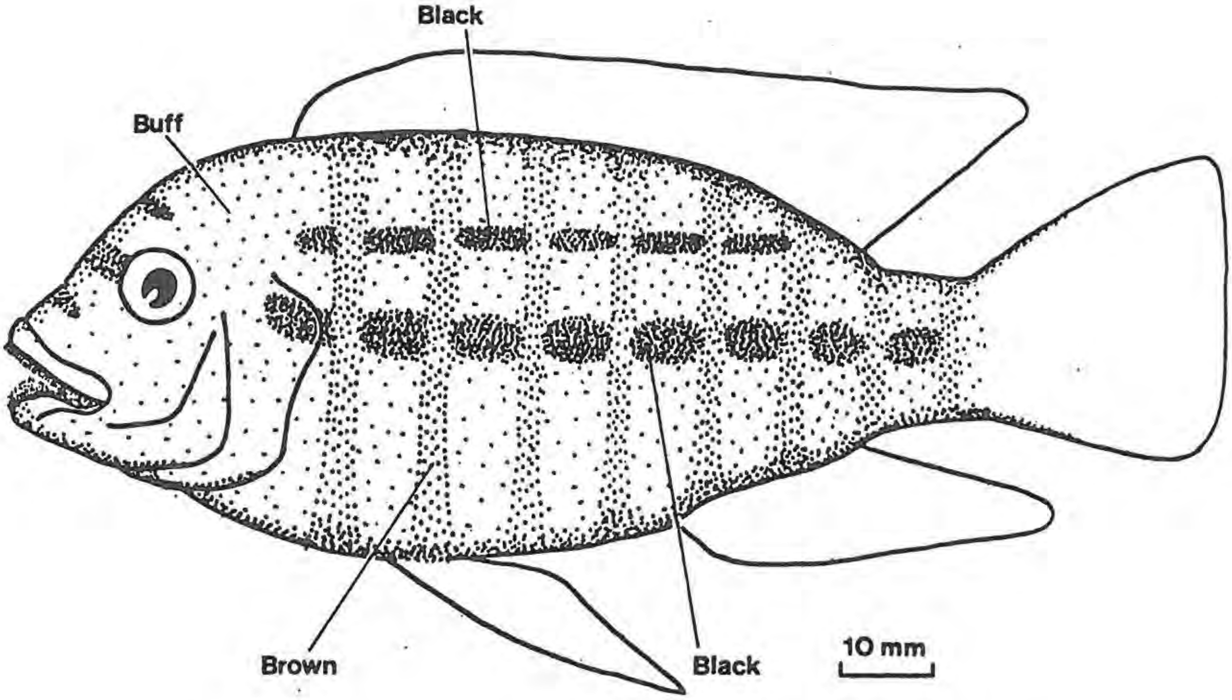

Figure 47. 'Chitande' form Petrotilapia - adult female from Chitande Island, Chilumba.

Females have a yellow-buff ground colour, eight brown vertical stripes and a series of black mid-lateral and dorso-lateral blotches. Detailed observations were not made on fin coloration but they lack any obvious markings and are probably all hyaline. The 'Chitande' form has only been recorded from Chitande Island, Chilumba (Figure 24a), where it occurs in shallow water (0.1 m) to a depth of 6 m.

'Ruarwe' form

The coloration of a female and a territorial male, from Ruarwe is illustrated in Figures 48 and 49. Territorial males have a uniform sky blue ground colour although in some specimens faint darker vertical bars are visible. The gular region and belly are yellow. The yellow extends to just beyond the pelvic fin base but may reach as far as the posterior base of the anal fin in some individuals. The dorsal fin has bright yellow lappets, lilac interray membranes posteriorly and the remainder of the fin is yellow-hyaline with a slight blue hue in some specimens. At Ruarwe the caudal fin has an orange-yellow trailing edge, darker grey-blue rays and lilac interray membranes. At Chilumba the coloration of the caudal fin is similar but the rays are normally orange-brown. The anal fin is yellow-hyaline and has a number of bright yellow ocelli on the posterior angle. The pelvic fins have a pale blue leading edge and the remainder is yellow to orange.

The ground colour of females and juveniles varies. At Ruarwe the ground colour is yellow-buff, whereas at Chilumba the ground colour tends to be darker brown. All have thin black mid-lateral and dorso-lateral bands and dorso-medial blotches. At Ruarwe nine khaki vertical stripes are evident, but in the darker females of Chilumba these stripes are not apparent.

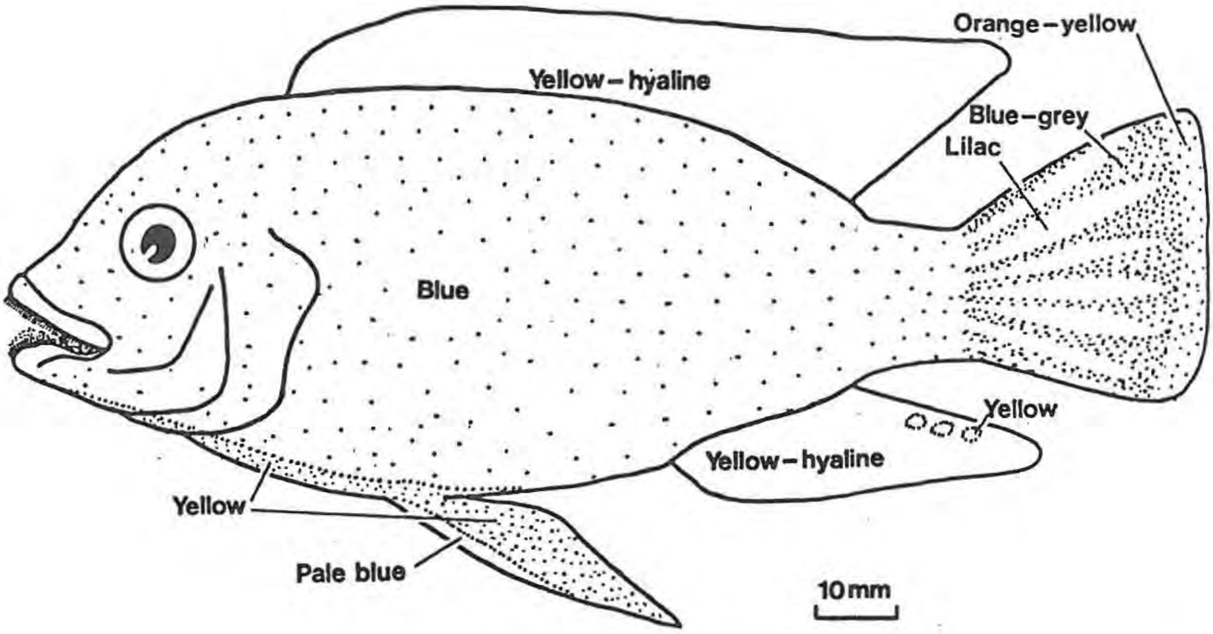

Figure 48. 'Ruarwe' form Petrotilapia - territorial male from Ruarwe.

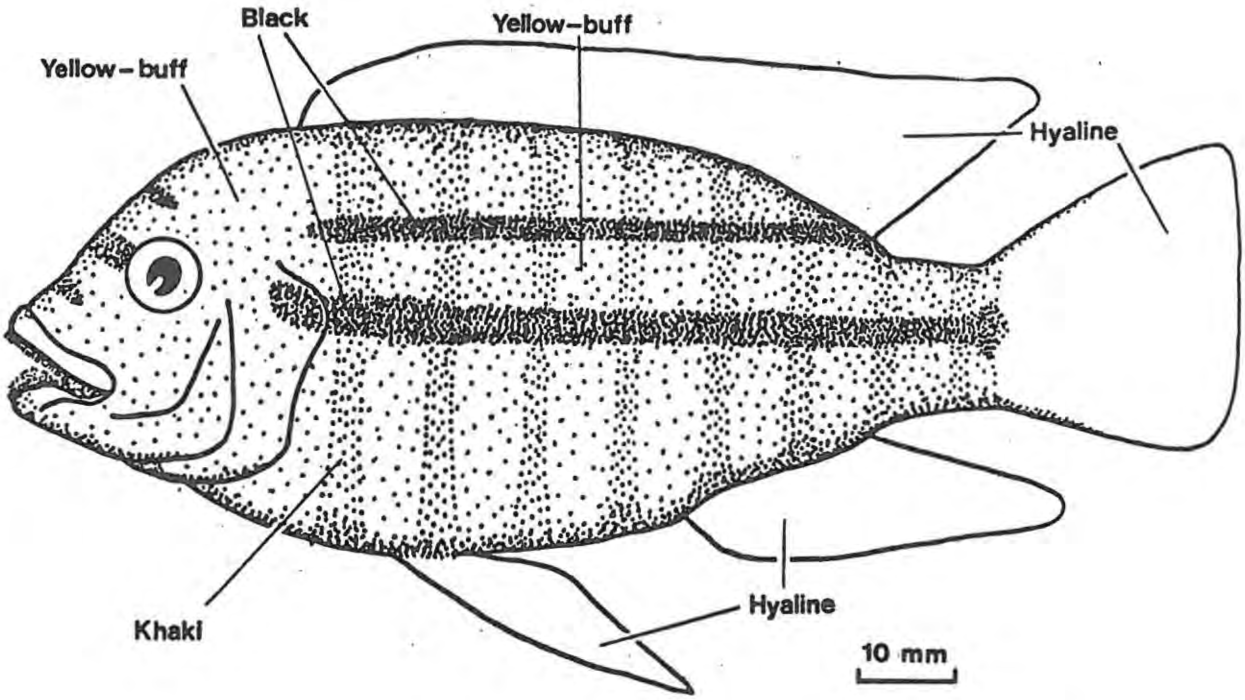

Figure 49. 'Ruarwe' form Petrotilapia - adult female from Ruarwe.

All fins are hyaline, those of Ruarwe fish generally have a yellowish hue whereas those at Chilumba have a brownish hue.

The 'Ruarwe' form occurs at Ruarwe and at Chilumba (at both Chitande Island and at Mpanga Rocks) (Figure 24a). It has a broad depth range occurring from 2 m to 25 m at Mpanga Rocks.

DISCUSSION

Most sites surveyed in the lake are occupied by at least two distinct colour forms of Petrotilapia. Cinyankwasi Island, Cinyamwezi Island and Kanchedza Island are the only sites which are occupied by a single colour form. Cinyankwasi Island is 10 km from Makanjila, the nearest mainland rocky shore (Figure 24b) and is separated from it by 64 m deep water. Cinyamwezi Island is even more isolated being 16 km from Makanjila (Figure 24b) with a depth of 90 m between the two sites. By contrast, Kanchedza Island is only 400 m from the nearest mainland rocky shore and is separated from it by 6 m deep water. All three of these islands are very small and this factor (rather than the degree of isolation) is probably responsible for the presence of only one colour form of Petrotilapia. There are four colour forms of Petrotilapia at Mbenje Island and this is the largest number of sympatric colour forms of Petrotilapia in the lake. In order to match the male and female of each colour form, a minimum of ten courtships was witnessed for each colour form. Without exception the sympatric colour forms courted in a non-random fashion. If the coloration of adult males and females is considered together then each colour form is unique in the genus Petrotilapia. In situations where one sex resembles that of the same sex in another colour form, the opposite sex of each colour form is very distinctive. For example, females of 'Small Blue' form and 'Gold' form are almost identical but males are obviously different. Based on the assumption that coloration of male and female is an important co-adapted component of a species' specific mate recognition system, the 14 colour forms mentioned in this chapter should behave as discrete species.

It is important to stress that while the fourteen colour forms described in this chapter are probably discrete species and not races of the three nominal species, it is not possible, given the available data, to arrive at a firm conclusion concerning their taxonomic status. Extensive research on the specific mate recognition systems of the fourteen colour forms and three nominal species may reveal that the underlying assumptions which suggest that the fourteen colour forms merit the rank of species, are unfounded. Nevertheless, for the remainder of the thesis, the term 'species', when applied to the genus Petrotilapia, embraces all seventeen colour forms described in Chapters 3,4 and 5. This word usage avoids the clumsy language which results if the term 'form' is used for the fourteen undescribed colour forms and 'species' for the three described species. It also reflects an intuitive judgement that they are indeed true biological species.

While it is possible to distinguish between species, and colour morphs of the same species, through careful field observations in a sympatric situation, it is not easy to resolve allopatric affinities. In sibling species reliance on morphological differences is obviously not a realistic method for species definition. Nevertheless any trenchant morphological differences will strengthen the implicit evidence that a particular form is a species. For example the obvious morphological distinctness of the 'Retrognathous' form is good implicit evidence that it is a discrete species. Close inspection of other sibling species may also reveal consistent morphological differences which could be a useful aid in defining species.

Consistent ecological differences are also useful when attempting to resolve allopatric species affinities. For example, in some cases there are differences in depth distribution between allopatric species which are fairly similar in coloration. Nevertheless such differences should be viewed with caution, bearing in mind the marked differences in depth distribution that the same species can have at different localities (see Chapter 8).

From this study it appears as if there are at least 17 species of Petrotilapia in Lake Malawi and there are probably other species along the rocky shores and islands in Tanzanian and Mocambican waters.

KEY TO KNOWN SPECIES AND COLOUR FORMS OF PETROTILAPIA

1(a)	Dorsal fin of territorial male black or with black submarginal stripe	2
1(b)	Dorsal fin of territorial male not black, does not have black submarginal stripe	10
2(a)	Territorial male has predominantly black ground colour	3
2(b)	Territorial male has predominantly blue or brown ground colour	4
2(c)	Territorial male has extensive yellow on dorsal part of body	'MUMBO YELLOW' FORM
3(a)	Female ground colour bright gold	'GOLD' FORM
3(b)	Female ground colour brown, black blotches on the body	P. nigra
3(c)	Female ground colour pale grey or brown, narrow vertical and horizontal bars on the body, vertical bars may extend into the dorsal fin	'BLACK FLANK' FORM
4(a)	Territorial male has blue body, no yellow colour on the body	5
4(b)	Territorial male has yellow or ocher on the ventral area of the body or on the cheek area	6

5(a) Territorial male has blue pelvic fins .... 'MUMBO BLUE' FORM

5(b) Territorial male has bright orange pelvic fins'ORANGE PELVIC' FORM

6(a) Territorial male has a dark brown body with no barring, cheeks ocher coloured .... 'FUSCOUS' FORM

6(b) Territorial male blue or grey, body barred 7

7(a) Territorial male sky blue with yellow ventral surface on body .. 8

7(b) Territorial male does not have yellow ventral surface on the body 9

8(a) The yellow on the ventral surface of territorial males does not extend onto the cheeks or flanks. The leading edge of the pelvic fins is pale blue .... 'SMALL BLUE' FORM

8(b) Yellow on ventral surface of territorial males extends to cheeks and normally covers ventral third of flanks. Leading edge of pelvic fins grey .... 'CHITANDE' FORM

9(a) Cheek area rusty orange in territorial males ...... *P. genalutea*

9(b) Cheek area not orange in territorial males ... 'LIKOMA BARRED' FORM

10(a) Territorial males uniform sky blue 11

10(b) Territorial males have yellow or rust ventral surface to body .. 12

11(a) Female uniform brown colour, no markings on body .. *P. tridentiger*

11(b) Female variable ground colour, black markings on body .... 'LIKOMA VARIABLE' FORM

12(a) Mouth retrognathous .... 'RETROGNATHOUS' FORM

12(b) Mouth isognathous 13

13(a) Anal fin has black bar along distal edge in territorial males .... 'YELLOW VENTRAL' FORM

13(b) Territorial male does not have black bar in anal fin 14

14(a) Female uniform brown, no obvious markings on body 'YELLOW FIN' FORM

14(b) Female has obvious black or brown markings on body 15

15(a) Territorial male has bright yellow dorsal fin lappets, gular and belly bright yellow .... 'RUARWE' FORM

15(b) Dorsal fin lappets not bright yellow in territorial male, belly may be ocher coloured .... 'LIKOMA VARIABLE' FORM

CHAPTER 6

THE ABILITIES OF P. TRIDENTIGER, P. GENALUTEA AND P. NIGRA TO PENETRATE DEEP WATER

INTRODUCTION

One of the trends to emerge from Chapter 5 is that certain islands have different assemblages of Petrotilapia species compared with nearby mainland shores. For example, the three species from Chisumulu Island are different from those at Likoma Island which is approximately 9 km away. The species which occur both at Cinyankwasi and Cinyamwezi Islands are unique in the lake. Brooks (1950) was the first to suggest that local geographical isolation is probably an important factor contributing to the high rate of speciation in Lake Malawi cichlids, and the disjunct distribution of Petrotilapia species supports this theory. This aspect will be dealt with fully in the final section of this thesis, but one of the possible barriers to dispersal i.e. water depth, is considered here. Petrotilapia species are rarely seen more than 2 m above the substrate and it appears that they are always in visual contact with the bottom. Deep water can limit dispersal in two ways. Firstly water deeper than about 250 m is anoxic in Lake Malawi (Beauchamp, 1953) and secondly cichlid swimbladders are limited in terms of the pressure to which they can compensate. The maximum recorded depth for P. tridentiger (sensu Trewavas) is just over 60 m (Jackson, 1961). As it is doubtful that any species of Petrotilapia could penetrate to the limits of dissolved oxygen this chapter investigates limitations in swimbladder physiology of the three species of Petrotilapia at Monkey Bay.

MATERIAL AND METHODS

Territorial males were captured in water less than 3 m deep at Monkey Bay. They were housed in aquaria and maintained at 29 ± 1°C for a minimum of one week prior to experimentation. The ability of each species to compensate to pressure (= depth) changes was tested using an apparatus similar to that described by Hill & Caulton (1974). Four pressure chambers, which were interconnected and thus at equilibrium with one another at all times, were used. The pressure chambers were supplied with a constant flow of fresh lake water (6.6 ml - 10.5 ml H_2O g^{-1} live weight min^{-1}) pumped via a reservoir situated 100 m higher than the laboratory. The water was maintained at a temperature of 29 ± 1°C. The chambers were partitioned so that 10 fish could be tested simultaneously. Each species was tested separately.

The fishes were allowed to acclimate in the pressure chambers for 24 h in water 0.5 m deep. The pressure was then increased gradually to a simulated depth of 3 m over a period of 3 h. Thereafter the equilibration depth of each individual was determined every 12 h using the method described by Caulton & Hill (1973) whereby equilibration depths were measured by reducing the pressure until the fish just floated free of the bottom. After determining the equilibration depths the pressure was increased to give a simulated depth 5 m greater than the equilibration depth of the second 'deepest' fish. Using this method all fish were at all times exposed to a pressure greater than their equilibration pressure and were thus stimulated to further compensation. The fish were exposed to a regime of 10 h light and 14 h darkness. To facilitate accuracy, readings were taken in the dark, when fish were least active, using a small flashlight. The experiment was continued for a minimum of four days beyond the first indication that the maximum equilibration depth had been reached. The fish were initially decompressed by reducing the absolute pressure by 40% of the 'deepest' individual's equilibration depth. After this step, a reduction of 40% of the mean equilibration depth was used. The increase in bouyancy attending the sudden reduction in water pressure caused all fish to swim vigorously downwards. All individuals survived the decompression regime.

RESULTS

The depth equilibration curves for the three species of Petrotilapia are shown in Figure 50. All three species equilibrate at a fairly constant rate until they approach their maximum equilibration depths, when the rate of equilibration decreases. In all species there is considerable variation in maximum equilibration depth. Using all data from the plateau phase of the equilibration curve (Figure 50) it was established that mean maximum equilibration depths of the three species are significantly different from one another (t-test for two means, $p < 0.02$). Table 13 summarizes the data on maximum equilibration depths and rates of equilibration for the three species. Using a comparison of slopes test (Sokal & Rohlf, 1969) on all data until the plateau of the equilibration curve (Figure 50), it was established that P. tridentiger equilibrates at a significantly slower rate than the other two species ($p < 0.001$). There is no significant difference in the equilibration rates of P. nigra and P. genalutea (Table 13).

In each experiment some individuals (two P. tridentiger, one P. genalutea and one P. nigra) equilibrated very slowly and when there was more than a 40% discrepancy in equilibration pressure (expressed in absolute pressure)

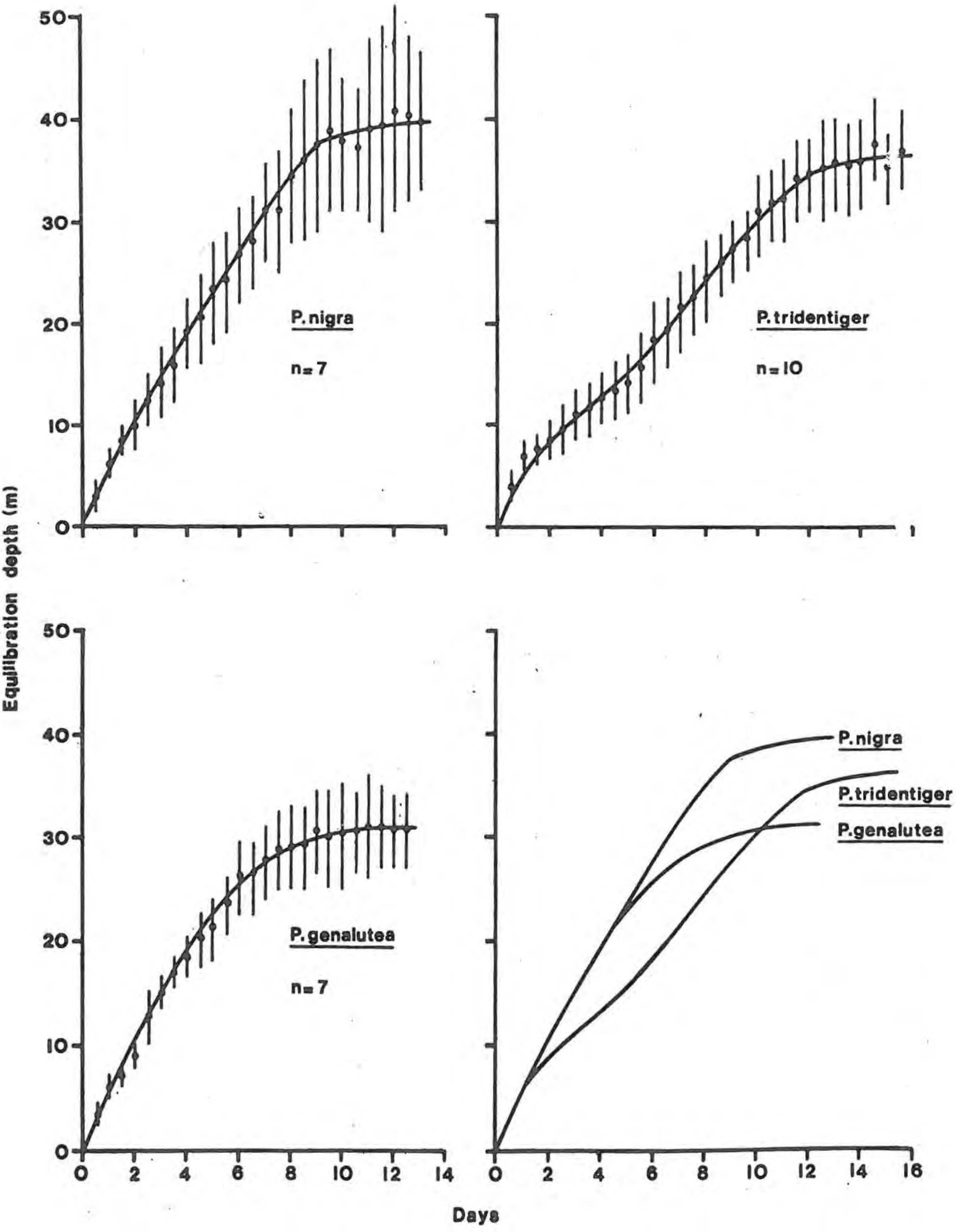

Figure 50. Depth equilibration curves of territorial male Petrotilapia species showing mean and two standard errors about the mean.

between any two individuals in the experiment it became necessary to discontinue readings on the less equilibrated fish. A 40% reduction in absolute pressure appears to be close to the safety limit of other Lake Malawi cichlids (Hill & Ribbink, 1978; Ribbink & Hill, 1979).

Table 13. Maximum equilibration depths and rates of equilibration for territorial males of the three species of Petrotilapia from Monkey Bay.

Species	Equilibration depth mean (m)	 range (m)	Rate of equilibration ($m\ day^{-1}$)	n
P. nigra	39.0	31.0 - 57.0	3.97	7
P. tridentiger	35.5	26.0 - 44.0	2.59	10
P. genalutea	30.4	23.0 - 34.0	3.98	7

Maximum equilibration pressure readings of these slow fish were determined during the period of decompression. The maximum equilibration depths achieved by the least able fish of each species are as follows: P. nigra 23 m, P. tridentiger 16 m and P. genalutea 15 m. These readings may reflect values from healthy individuals, in which case variation within species is considerably greater than mentioned, or these fish may have incurred some swimbladder damage during capture. The latter is probably more plausible but in the absence of any proof the former possibility cannot be discounted. These data are not incorporated into Figure 50.

DISCUSSION

The rates of depth equilibration are well within the limits found for other African cichlid fish (Caulton & Hill, 1973; Caulton, 1975;

Hill & Ribbink, 1978). Territorial males of all three species, but in particular P. tridentiger and P. genalutea, are regularly required to move through a depth range of approximately 3 m while patrolling their territories. The rate of compensation to changes in pressure is too slow to permit adjustments in swimbladder volume during these movements and the fish must, therefore, be capable of tolerating a certain amount of change in swimbladder volume. In water less than 10 m deep a 1 m change in depth is equivalent to a pressure change of approximately 5% and consequently a 5% change in swimbladder volume. The experiment showed that all three species can withstand a positive or negative change in absolute pressure of 40%. Thus these species of Petrotilapia should be capable of moving rapidly 8 m upwards or downwards from their equilibrium depth. It is unlikely that an individual would voluntarily subject itself to a change in absolute pressure as great as 40% as all fish exposed to this, during the experiments, showed signs of distress. Nevertheless the physiological tolerances of the three species considerably exceed their field requirements.

In other African cichlids the ability to penetrate deep water varies: some occur naturally down to depths approximating the physiological limits of their swimbladders (Caulton & Hill, 1973; Caulton, 1975) while others may use only a small part of their physiological range (Bruton & Boltt, 1975; Hill & Ribbink, 1978). Diving observations revealed that P. nigra occurs from 0 to 30 m whereas the other two species normally occur in water less than 8 m deep (Chapter 8). While P. nigra approaches the depth limits imposed by swimbladder physiology, the restriction of P. tridentiger and P. genalutea to shallow water at Monkey Bay cannot be explained on this basis. Some other factor(s), probably of an ecological nature, must be responsible for their distribution. Tolerances in field conditions are usually narrower than those observed under experimental conditions (Odum, 1971). For example, although Sarotherodon mossambicus can penetrate to 20 m in a simulated environment, in Lake Sibaya the maximum recorded depth for this species is 18 m and the majority of fishes occur in water less than 12 m deep (Bruton & Boltt, 1975).

Thus the maximum equilibration depths presented in Table 13 probably overestimate the depths to which the three species of Petrotilapia penetrate in their natural habitat.

Theoretically it would be possible for these species of Petrotilapia to cross a barrier of open water and colonize an island provided they did not need to exceed the limits imposed upon them by swimbladder physiology. The water depth between many of the islands exceeds 60 m and is often greater than 100 m and is therefore beyond the physiological tolerance of these species of Petrotilapia.

CHAPTER 7

BREEDING SEASONALITY OF PETROTILAPIA SPECIES AT MONKEY BAY

INTRODUCTION

In Lake Malawi numerous cichlids have definite breeding seasons. For example, many zooplankton-feeding Haplochromis species spawn between March and July (Iles, 1960, 1971), H. quadrimaculatus Regan only breeds in June (Jackson et al., 1963), Lethrinops longipinnis Eccles & Lewis spawns from May to October and L. parvidens Trewavas spawns from September to October (Tweddle & Turner, 1977). The two sibling species Sarotherodon saka (Lowe) and S. squamipinnis (Günther) have staggered breeding seasons: S. squamipinnis spawns during the rains (November to March) and S. saka spawns before the rains (September, October) (Lowe-McConnell, 1959).

In aquaria, with constant environmental conditions, rock-frequenting Mbuna from Lake Malawi breed throughout the year (Fryer & Iles, 1972) and Labeotropheus species can produce from five to seven broods per year under these conditions (Balon, 1977). It has been suggested that in the lake the rock-frequenting Mbuna breed continuously throughout the year and do not have breeding seasons (Fryer & Iles, 1972).

A recent study on the breeding biology of a community of rock-frequenting cichlids at Monkey Bay has revealed that there are fluctuations in breeding activity during the year (B.A. Marsh, in prep.). This study was based on monthly examinations of gonads but was initiated before it was appreciated that there is a complex of Petrotilapia species at Monkey Bay, and consequently the three species were treated together.

Asynchronous breeding seasons in sibling species complexes could be an important mechanism for maximizing resource use (Lowe-McConnell, 1979) and may also facilitate sympatric speciation (McKaye, 1980). A study was therefore initiated to determine whether the three species of Petrotilapia at Monkey Bay breed asynchronously.

METHODS

Monthly observations were made on breeding behaviour as it was not practical to collect adequate regular samples for gonad analysis. P. tridentiger females, in particular, are difficult to capture and furthermore the removal of large numbers of Petrotilapia species females on a regular basis from Monkey Bay would have adversely affected ongoing research.

Every month eight territorial males of each species were observed for a period of 15 minutes per individual between 0800 and 1000 h. This study continued for the 12 months of 1980. All observations were made at site A (Figure 54) in 1-4 m of water, and courtship behaviour was recorded on a plastic slate. The number of courtships and intensity of each courtship that occurred during the observation period was recorded. Courtship intensity was divided into five categories:

1) The male slowly approaches the female, gives a brief 'side-shake' and 'follow-shake'. The female ignores the male's attempt at courtship.

2) The male approaches the female rapidly, gives a 'side-shake' and 'follow-shake' but the female ignores the male.

3) The male approaches the female rapidly and gives a vigorous 'side-shake', 'follow-shake' and a 'lead-swim'. The female briefly follows the male but does not reach the spawning site.

4) As for 3, but the female responds to the 'lead-swim' of the male and follows it to the spawning site.

5) As for 4 and spawning occurs.

A monthly search was made, on the east side of Thumbi East Island, for mouth-brooding females. These females are easily distinguished by their distended buccal cavities. A diver swam along the one metre contour for 400 m and counted all mouth-brooding females seen in 0-2 m of water. The diver then returned to the starting point, swimming at 5.5 m and counted all mouth-brooding females in 5-6 m of water. The same route was followed each month.

RESULTS

This is not a detailed study of breeding and has certain limitations. The techniques employed and the small sample size mean that at best the results will reflect obvious trends. Little reliance can be placed on any apparently subtle trends. A further limitation is that the study spans one year only and conditions during this year may have been atypical although there is no reason for suspecting this. Figure 51 represents the number of courtships witnessed for each species during the monthly observation periods of two hours. The number of mouth-brooding females seen on each monthly search is given above each histogram. In all three species there is an obvious mid-year and end of year depression in breeding activity. The mid-year depression is particularly marked. In between these two depressions, breeding activity rises to a peak. Breeding activity is, therefore, bimodal in these species. Taking into account both the number of courtships and the number of mouth-brooding females, the major peak in breeding activity occurs in the second half of the year between August and November. Table 14 shows the distribution of courtship intensity each month.

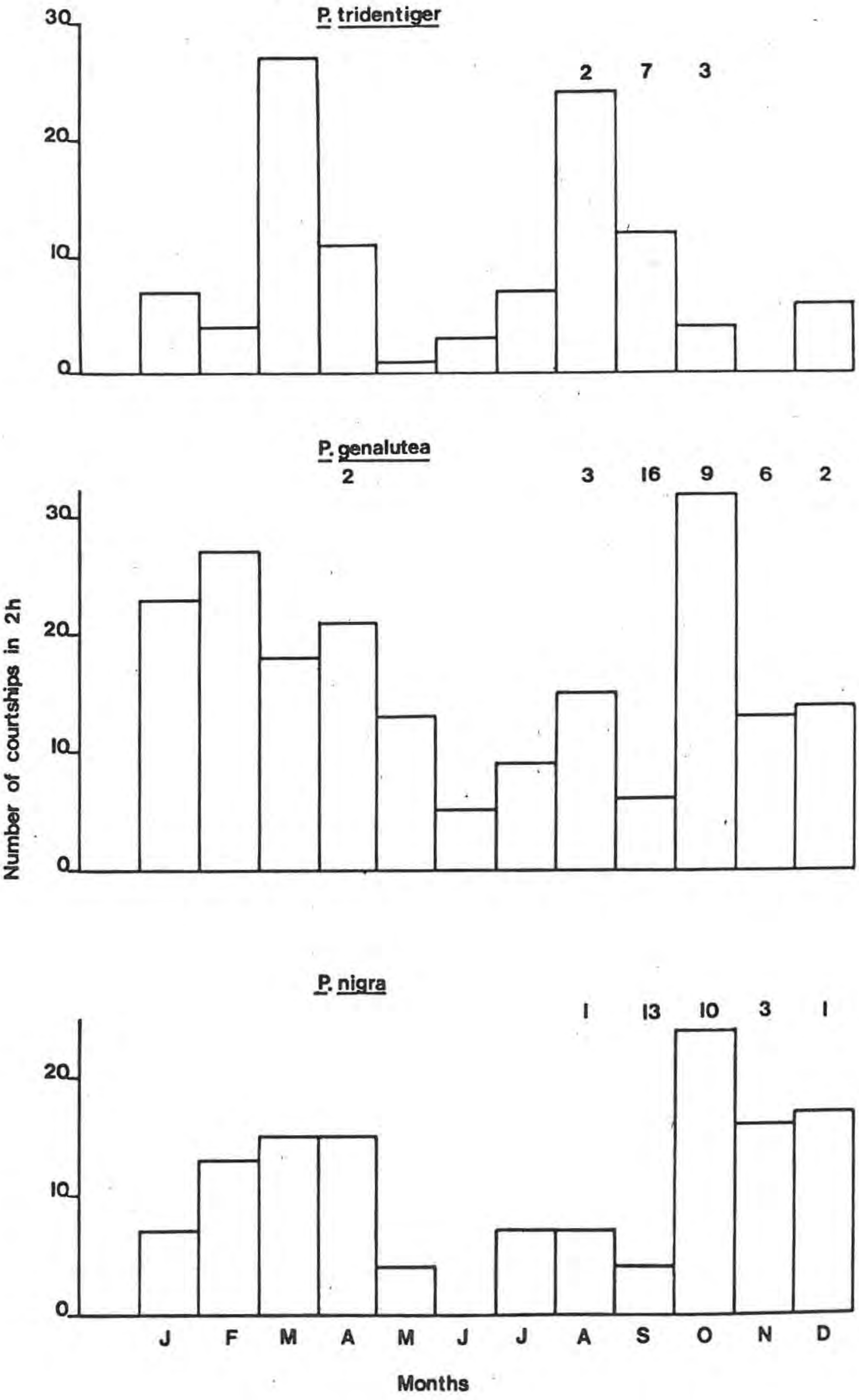

Figure 51. The number of courtships observed in a two hour period for the twelve months of 1980 for *P. tridentiger*, *P. genalutea* and *P. nigra*. The number of mouth-brooders observed each month is given above the histograms.

Table 14. Number of courtships and intensity of each courtship during a two hour period each month in three species of <u>Petrotilapia</u>. No spawnings were observed during this study.

	Intensity	J	F	M	A	M	J	J	A	S	O	N	D
<u>P. tridentiger</u>	1	3	3	13	6	1	3	7	12	5	2	5	5
	2	4	1	8	5			1	8	3	2		1
	3			6					4	4			
	4												
	Total	7	4	27	11	1	3	8	24	12	4	5	6

	Intensity	J	F	M	A	M	J	J	A	S	O	N	D
<u>P. genalutea</u>	1	12	18	10	10	8	2	6	12	2	8	6	9
	2	10	9	7	7	3	3	3	3	4	16	7	5
	3	1		1	4	2					4		
	4										4		
	Total	23	27	18	21	13	5	9	15	6	32	13	14

	Intensity	J	F	M	A	M	J	J	A	S	O	N	D
<u>P. nigra</u>	1	5	7	6	5	4		5	4	3	13	4	6
	2	2	6	8	9				3	1	8	12	7
	3			1	1			2					
	4										3		
	Total	7	13	15	15	4		7	7	4	24	16	13

There are no obvious interspecific differences in terms of the two periods of low breeding activity and the first breeding peak. *P. tridentiger* does, however, appear to peak earlier than the other two species in the second half of the year. *P. tridentiger* peaked in August and September whereas the other two species peaked in October and November. There is, therefore, some indication of asynchronous breeding although in general there is considerable overlap and no species has a discrete breeding season. Data spanning several years are required to confirm these results.

DISCUSSION

Fryer & Iles (1972a) suggest that the Mbuna probably breed throughout the year. The information on *Petrotilapia* species breeding activity confirms this suggestion. There are, however, marked fluctuations in breeding activity and the data agree closely with the results of a recent study of the breeding biology of some other rock-frequenting cichlids from Monkey Bay (B.A. Marsh, in prep.)

The fact that the three species have synchronous, or near synchronous breeding activity suggests that there are common environmental factors regulating the breeding cycles. The most likely cause of breeding fluctuations is the availability of food. In aquaria with a regular and ample supply of food, Mbuna breed throughout the year (Fryer & Iles, 1972) and individuals can spawn approximately once every two months (Balon, 1977). Energy demands of reproduction are high in female mouth-brooding cichlids as they require energy to produce eggs and to undergo a fast of approximately three weeks while mouth-brooding the developing fry. Therefore, the female needs to build up considerable energy reserves prior to breeding and scarcity of food could cause a decrease in breeding activity.

There is evidence that food availability fluctuates during the year. Sharp (in prep.) has demonstrated that, at Monkey Bay, the standing crop of epilithic algae varies seasonally, having its lowest abundance in May and its highest abundance in November. During the winter months of April to August, strong and persistent southerly winds can cause local upwelling of nutrient rich water in the south-eastern arm of Lake Malawi and this often results in phytoplankton blooms (Eccles, 1974). Furthermore, zooplankton is abundant at this time of the year (P. Degnbol, pers.comm.; K.R. McKaye, pers.comm.).

The rainy season occurs between mid-November and March (Eccles, 1974) and an additional input of nutrient salts from land runoff will probably stimulate primary productivity during this season. As Monkey Bay is in a rain shadow (Eccles, 1974) and there are no inflowing streams in this area, the input of nutrients from runoff is likely to be of secondary importance to upwelling. It appears, therefore, that there is a relationship between food availability and breeding activity in Petrotilapia species. This relationship is illustrated in Figure 52 which shows the breeding cycle of Petrotilapia species, the approximate fluctuations in epilithic algal standing crop and the postulated cycles of nutrients and plankton.

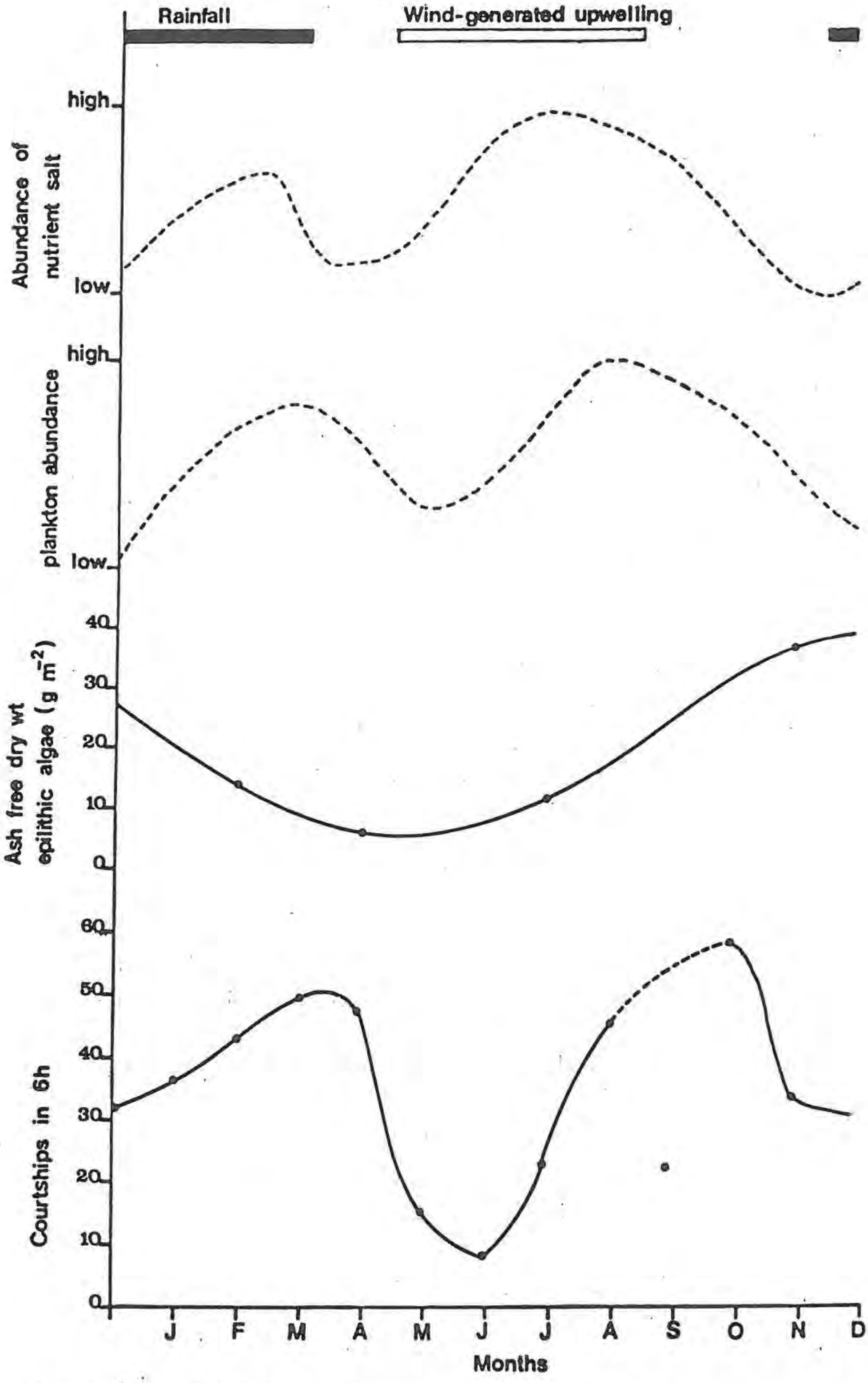

Figure 52. Postulated cycles of nutrient salt and plankton abundance (see page 125) and actual cycles of epilithic algal standing crop* and breeding activity of Petrotilapia species at Monkey Bay. Breeding activity cycle represents the pooled data for all three species depicted in Figure 51.

* Data from Sharp (in prep.).

CHAPTER 8

RESOURCE PARTITIONING AND COEXISTENCE OF THREE SPECIES OF *PETROTILAPIA* IN LAKE MALAWI

INTRODUCTION

Before the diversity of cichlid fishes in Lake Malawi can be understood, it is necessary to understand how cichlid communities are structured, in particular how the component species coexist. A great deal of research on vertebrates has indicated that competition plays an important part in shaping community structure. This research has embraced a broad spectrum of animals including birds (MacArthur, 1958; Orians & Horn, 1969; Cody, 1974; Diamond, 1975; Hespenheide, 1975), rodents (Brown, 1975; M'Closkey, 1976; Mares & Williams, 1977), lizards (Schoener, 1968; Schoener & Gorman, 1968; Pianka, 1973, 1975), salamanders (Krzysik, 1979) and fish (Zaret & Rand, 1971; Roughgarden, 1974; McKaye & Barlow, 1976; Werner & Hall, 1976; McKaye, 1977; Werner, 1977. These studies have all shown that resource partitioning can minimize actual or potential competition in vertebrate communities and thereby contribute towards stable coexistence.

Until recently, very little ecological research had been done on the cichlid fishes of Lake Malawi. Fryer (1959) showed that at Nkhata Bay the rocky shore community of fishes can be divided into the following trophic groups: algal feeders, invertebrate feeders, piscivores, plankton feeders and scale eaters. Competition between trophic groups is not apparent and within each trophic group competition may be avoided through resource partitioning. For example, some of the invertebrate feeders partition their food according to prey size and some species which belong to the same trophic group feed in different habitats. Within the algal feeding trophic group there are species which feed primarily on firmly attached algal strands and others which feed entirely on loose aufwuchs.+ Petrotilapia species and the Pseudotropheus zebra species complex are loose aufwuchs feeders. Fryer (1959) did not detect any differences in food or habitat between Petrotilapia tridentiger (sensu Trewavas) and the P. zebra species complex. Recently Holzberg (1978) showed that some resource partitioning does occur within the P. zebra species complex at Nkhata Bay. One of the species occurs predominantly in deep water and the other two occur sympatrically in shallow water, but differ from one another in terms of the feeding sites used and the frequency of plankton feeding.

Sharp (in prep.) investigated resource partitioning in some species in the Monkey Bay cichlid community, including a detailed study of three highly aggressive territorial species of Mbuna. These species are undescribed but all belong to the genus Pseudotropheus.* As a result of their aggressive attempts at excluding other fishes from their territories, the standing crop of aufwuchs is higher within their territories than elsewhere on the rocky shore. For a given depth, 'P. aggressive' territories support the highest biomass of aufwuchs. Sharp (in prep.) observed that male Petrotilapia species are the only fishes which

+ In this thesis 'loose aufwuchs' refers only to loosely attached epilithic algae. It does not include the aufwuchs infauna which is termed 'benthic invertebrates'.

* Specimens of these species are lodged at the J.L.B. Smith Institute of Ichthyology, Grahamstown as follows: 'Pseudotropheus aggressive', RUSI 13356; 'Pseudotropheus orange cheek', RUSI 13353; 'Pseudotropheus sky blue', RUSI 13357.

feed with impunity within the territories of the three aggressive *Pseudotropheus* species, but he did not distinguish between the three species of *Petrotilapia*.

In this chapter resource partitioning between the three species of *Petrotilapia* at Monkey Bay is investigated in order to show how they coexist.

STUDY AREA

All study areas are situated in the south-eastern arm of Lake Malawi (Figure 53), and the major study area was Monkey Bay (14°03' S; 34°55' E; Figure 54). Within the bay the rocky shore extends down to 6 to 10 m where it meets a sandy bottom overlain with sediment and patchily covered with beds of *Vallisneria aethiopica* Fenzl and *Ceratophyllum demersum* L.. On the east-facing side of the island of Thumbi East and on the mainland at site I (Figure 54) the rocky shore extends down to between 30 and 35 m before it strikes a sandy bottom. The nature of the habitats is variable but most sites are composed of a rubble of rock and boulders ranging in diameter from 0.3 to 2 m. At irregular intervals there are areas of very large, flat rock slabs, particularly between sites F and G and at site H.

Boadzulu Island (14°15' S; 35°08' E) has a rocky shore which extends down to at least 35 m. It is larger than Thumbi East Island and consists of a rubble of rock and boulders similar to the substrate at Monkey Bay. Mpandi Island (14°11' S; 35°05' E), Namaso Bay (14°10' S; 34°59' E) and Kanchedza Island (14°07' S; 34°56' E) are all very similar

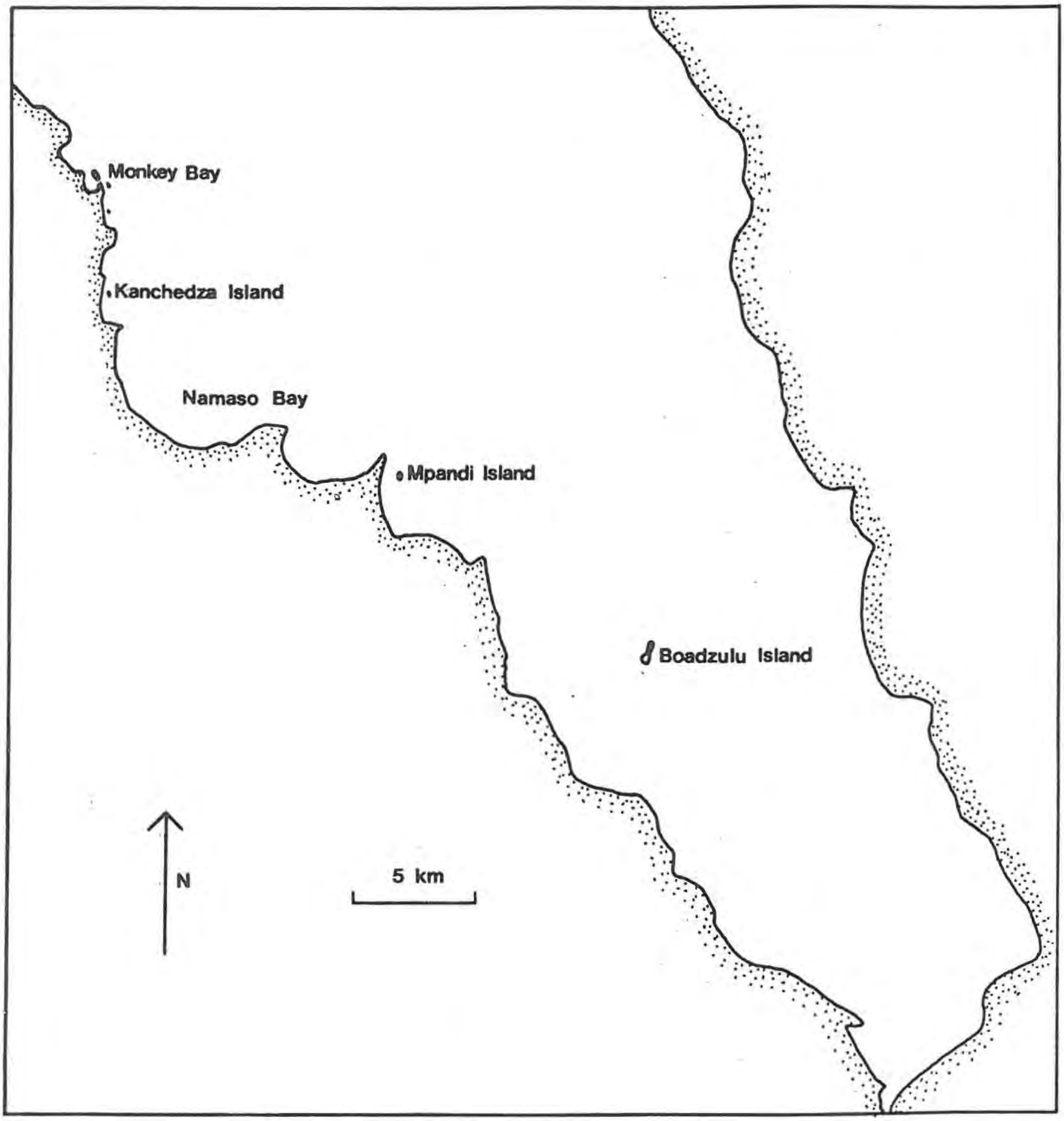

Figure 53. Map of the south-eastern arm of Lake Malawi showing location of study areas.

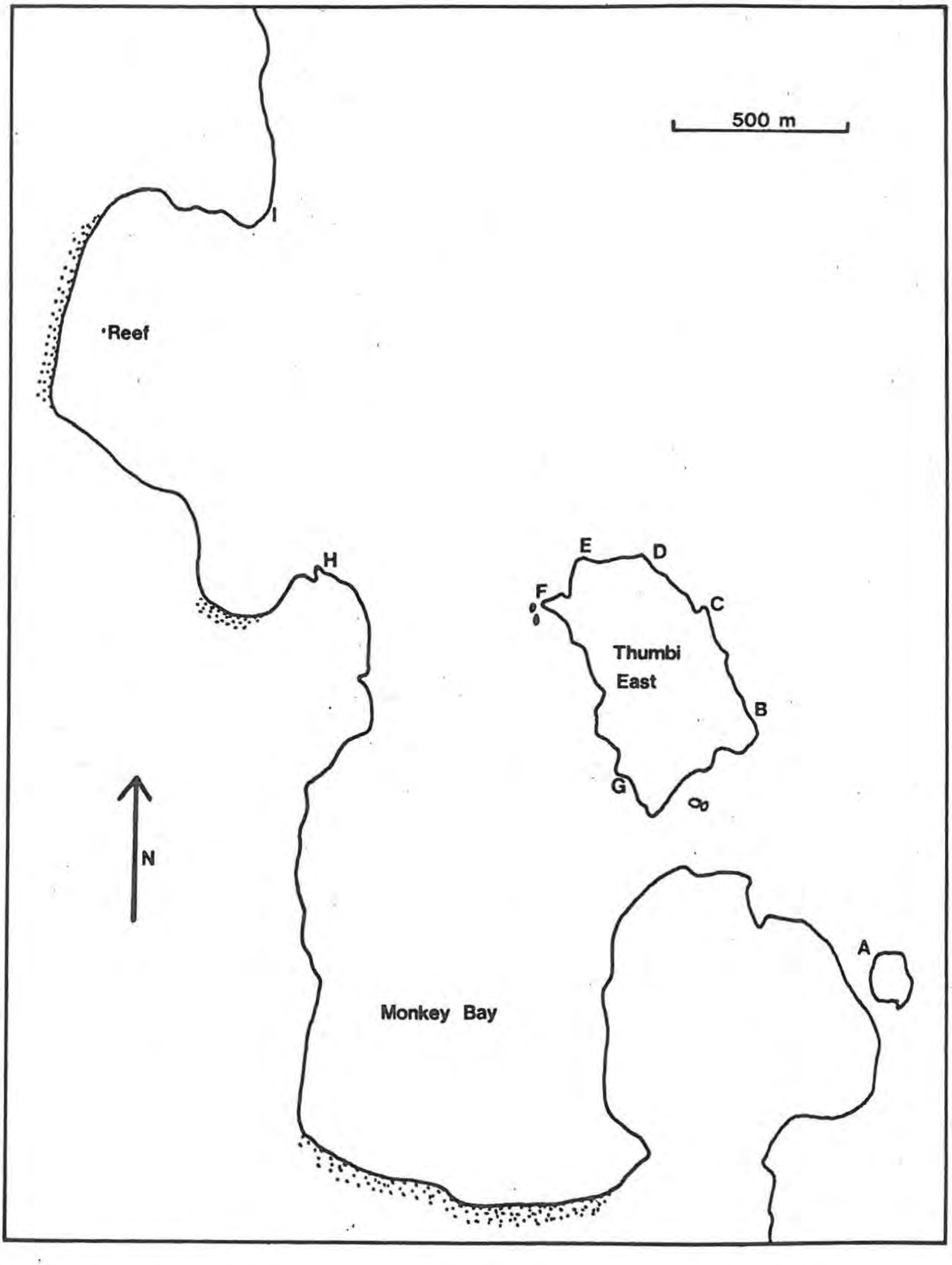

Figure 54. Map of Monkey Bay showing location of study sites and artificial reef. Stipled areas represent sandy beaches, the rest of the shore is rocky.

habitats. At these sites the rocky shore extends down from 4 to 5 m only, at which point there is sand. At the base of the rocky shore, and particularly where there are scattered rocks on the sand, beds of *Vallisneria aethiopica* occur. The most important difference between these sites is the length of rocky shore. At Namaso Bay there is at least 1 000 m of rocky shore, whereas Mpandi Island is approximately 200 m in circumference and Kanchedza Island is only about 100 m in circumference.

METHODS

The terms used in this chapter to denote different forms of *Petrotilapia* are defined below. *Territorial males* are adult males which hold territories and can readily be distinguished by their vivid coloration (see Chapter 3). Adult males which are not in possession of a territory are termed *non-territorial* males. This form is also distinguishable on the basis of distinctive coloration (see Chapter 3) and mature size. Immature males and females within a particular species have identical coloration (see Chapter 3). The term *female* is used, therefore, to denote all *Petrotilapia* greater than 100 mm TL which are neither territorial nor non-territorial males. This form inevitably includes subadult males as well as females. The term juvenile denotes *Petrotilapia* less than 100 mm TL.

Distribution

Quantitative data on depth distribution were collected from four sites at Monkey Bay (B, D, E & I; Figure 54), where all three species were well represented. To quantify depth distribution double line transects were used, comprising two 25 m lengths of rope held apart at each end by 3 m long piping. When laid over the rocky shore, with the ropes parallel to one another, an area of 75 m^2 was demarcated. Transects were laid along the 0.1 - 0.5, 1, 3, 5, 10, 15 and 20 m depth contours. After waiting for a period of five minutes, to allow the fish to recover from any diver disturbance, divers swam 1 - 2 m above the substrate recording all adult Petrotilapia species seen within the transect. Each count was repeated three times and the mean density of adult males and females of each species was calculated.

Although transects were not laid in water deeper than 20 m, divers swam to 35 m to determine which forms of Petrotilapia were present at these depths. Depth distribution data were also collected from Boadzulu Island, Mpandi Island, Namaso Bay and Kanchedza Island. Non-quantitative data on habitat preferences were made by exploring the littoral regions of the rocky shores of Monkey Bay down to a depth of 35 m.

Territory size and overlap

Initial observations indicated that considerable overlap of territories occurred among the three species of Petrotilapia. To obtain data on territory size and to determine the degree of overlap, a map of territory boundaries was plotted from sites E and D (Figure 54). The territorial behaviour of males was used as an aid in defining territory boundaries. Typically, territorial males when not feeding either hover motionless in the water column or patrol their territories. Intraspecific boundary disputes in established communities occur too infrequently to be used for mapping boundaries. On a number of occasions, however, patrolling males were observed to turn back towards the centre of their territory at approximately the same position at which previous boundary disputes had taken place. On the assumption that 'turnabout' points coincide with territory boundaries, individual males were observed until such time as a minimum of 10 metal markers had been evenly distributed on the territory boundary. Once all territorial boundaries of one species within the study area had been marked, the position of each marker in relation to all other markers was measured. To do this a perspex disc, graduated at intervals of 5° was placed in a fixed central position in the survey area and the distance from the centre of the disc to each marker as well as the angle between the zero line and a straight line linking the marker and disc centre were noted (Figure 55). These data were then transcribed onto paper, in a scaled down form, thus producing a two dimensional map of territory boundaries for each species. Interspecific overlap of territories was assessed by superimposing the three maps. Territory areas were measured from the maps and scaled up to life size.

Individual feeding site preferences

A 12 m x 10 m grid comprising nylon lines, arranged in such a way that they subdivided the area into 1 m x 1 m squares, was laid in the shallows (1 - 4 m) at site E (Figure 54). At 0.5 m intervals the lines were labelled with plastic tags and consequently the grid could be accurately subdivided into 0.5 x 0.5 m segments. Usually the position of a fish could be assigned to a 0.25 x 0.25 m segment. The territorial boundaries and feeding sites of territorial male Petrotilapia that occurred in the grid were plotted on an underwater slate. This was achieved by observing each individual for a total of six hours over a period of seven consecutive days. The number of feeding movements executed at each feeding site was recorded for each observation period. A feeding movement commenced when

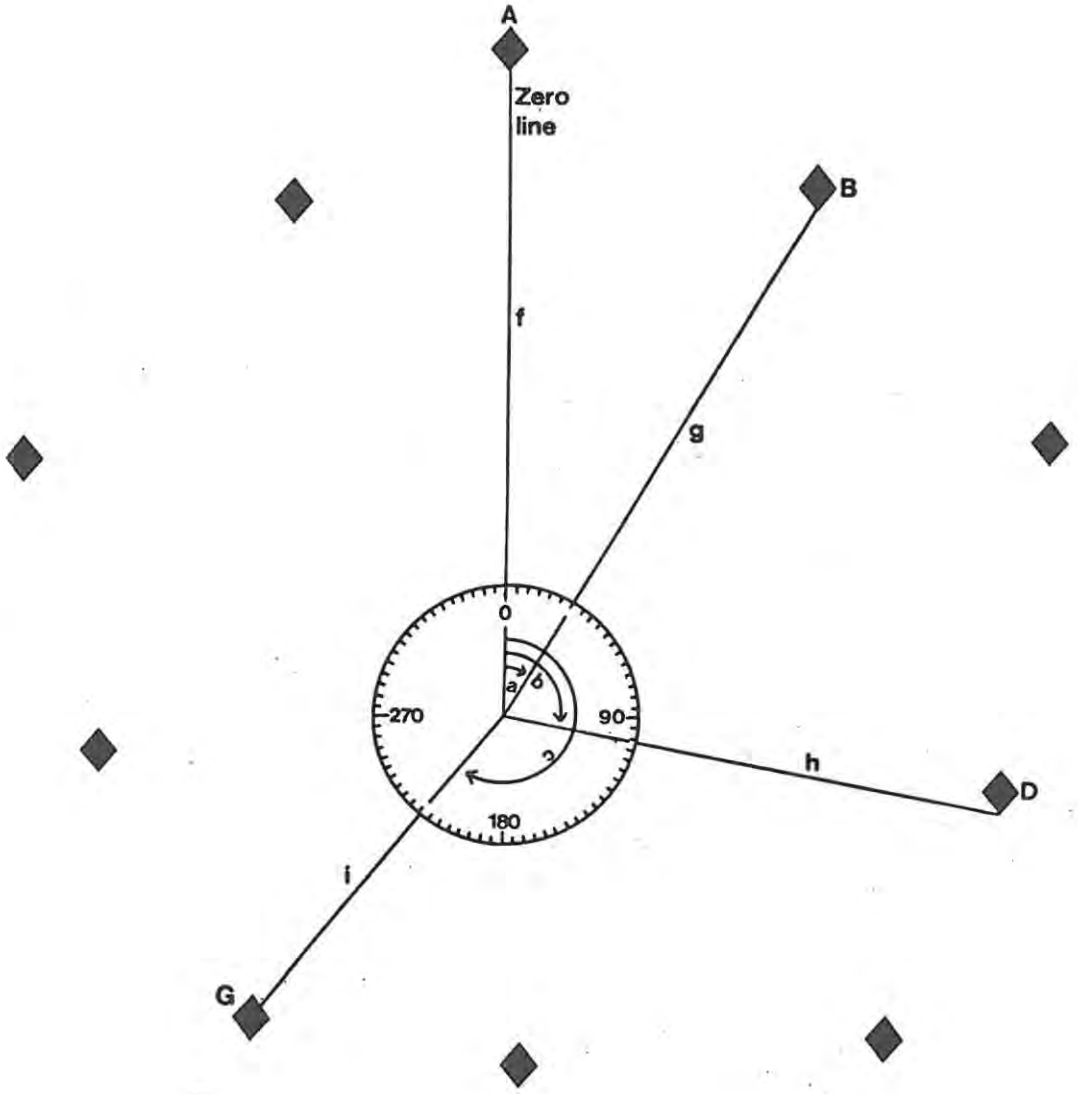

Figure 55. Apparatus used to obtain information necessary to construct scaled down maps of territories. Metal markers (e.g. A, B, D, G) demarcate the territory boundary. A graduated perspex disc is held in a fixed position by one diver with the zero line pointing towards a marker (A). A thin nylon line, which pivots from the disc centre, is then taken from one marker to the next by a second diver. The angle subtended by the line at each marker and the zero line as well as the distance from the disc centre to each marker is recorded. This information can then be used to draw a map. For example the relative positions of 'A', 'B', 'D' and 'G' can be plotted with accuracy using the angles 'a', 'b' and 'c' and the distances 'f', 'g', 'h' and 'i'. The disc was 200 mm in diameter whereas the distance between markers ranged between one and two meters.

a fish applied its jaws to a rock and ended when, after a series of rapid brushing movements, the fish broke contact with the rock. At the end of the seven day period a composite map representing the space utilization for each species was drawn on transparent paper. The three maps were then superimposed and overlap of feeding sites was assessed.

Species feeding site preferences

Observations were made on the utilization of different types of feeding site by the three species of Petrotilapia between sites C and F (Figure 54) in 1 - 5 m and 6 - 10 m deep water. Whenever a Petrotilapia was seen feeding the feeding site was categorized according to each of the three criteria listed in Table 15. Observations were made over a 14 day period in May 1979 and again over a 14 day period in November 1979.

The feeding behaviour of all species of Petrotilapia during a dense phytoplankton bloom which occurred on the afternoon of 7 May 1979 was also noted. During a swim along a 2 - 3 m contour between sites D and E (Figure 54) a record was made as to whether each Petrotilapia encountered fed on the phytoplankton in the water column or on loose aufwuchs.

Juvenile feeding behaviour was studied between sites F and C (Figure 54) in June, July and August 1980. Whenever a juvenile was seen a note was made as to whether it fed on plankton or on loose aufwuchs.

Aggression

(a) Field observations

Information on aggression was collected during the monthly observations of breeding behaviour (see Chapter 7). Every month eight territorial

Table 15 Categories used to describe the feeding sites of adult *Petrotilapia*. A crack is defined as a steep sided gap of 10-40 cm width formed by a minimum of two rocks.

Category	Description				
Rock slope	<80°	>80°			
Crack proximity	<400 mm from crack	>400 mm from crack			
Territory type	*Pseudotropheus* "aggressive" territory, occupant >100 mm TL	*Pseudotropheus* "aggressive" territory, occupant < 100 mm TL	*Pseudotropheus* "sky blue" territory	*Pseudotropheus* "orange cheek" territory	undefended site

males of each species were observed continuously for 15 minutes each between 0800 h and 1000 h. A record was made of all aggressive encounters that occurred between the territorial males and other Petrotilapia during each observation period. A note was made as to which fish in each encounter was dominant.

(b) Aquarium observations

Field observations indicated that there may be a social dominance hierarchy in the fish community at Monkey Bay. The following experiments were performed to supplement the field observations. Territorial male Petrotilapia were captured in Monkey Bay and housed in aquaria which ranged in size from 130 cm x 50 cm x 42 cm to 120 cm x 60 cm x 40 cm. Each aquarium was partitioned down the centre with an opaque plastic sheet and one male Petrotilapia was placed in each half of the aquarium. All aquaria were screened from one another and thus the Petrotilapia males were visually isolated from one another and had no prior experience of an encounter with other Petrotilapia males in an aquarium situation. A few Pseudotropheus zebra males and females were housed with each Petrotilapia male. These fishes are easily dominated by males of all species of Petrotilapia. Once the Petrotilapia males had established dominance over the Pseudotropheus zebra and developed the intense coloration associated with territoriality in the natural habitat, the partition was removed and the responses of the two Petrotilapia males were monitored. The males were then released into the lake and new individuals were placed in the aquaria.

Field observations indicated that the three species of Petrotilapia fed within the territories of 'Pseudotropheus aggressive' and

'Pseudotropheus orange cheek' to different extents. A possible explanation for this is that the two aggressive Pseudotropheus species dominate certain species of Petrotilapia more than others. Therefore dominance experiments, similar to those reported above, were performed using Petrotilapia territorial males and the two species of Pseudotropheus as the protagonists.

Stomach content analysis

Fish were collected in 1 - 5 m depth of water at quarterly intervals in the last week of each of the following months: October 1979, January 1980, April 1980 and July 1980. A 40% solution of formaldehyde was injected into the abdominal cavity of each fish immediately after capture. The stomachs were removed at a later stage and the contents spread on a cover-slip on a glass slide and examined with a compound microscope. The stomach contents were divided into five food categories: firmly attached epilithic algal strands, zooplankton, phytoplankton, benthic invertebrates (infauna of aufwuchs mat) and loose aufwuchs. In order to distinguish between zooplankton and benthic invertebrates, and between loose aufwuchs and phytoplankton, rock scrapings and plankton samples were collected periodically and semi-permanent mounts were prepared to act as references. Each slide was thoroughly scanned at a magnification of 40x to obtain an overall impression of the composition of the stomach contents. Five positions on the slide were then chosen randomly and an estimate of the percentage cover of each food category relative to the other categories was made at a magnification of 100x. The results from the five positions were then pooled together.

Reassessment of semi-permanent preparations six months after the initial assessment indicated that the technique gave fairly consistent results.

The maximum deviation obtained was 10% and most estimates were within 5% of the original.

RESULTS

Distribution

(a) Monkey Bay

There was little variation in the pattern of Petrotilapia depth distribution at each of the four sites (B, D, E & I) and consequently the data for the same species from different sites were pooled together to produce Figure 56. Males of all three species were present from 0.1 to 8 m although P. tridentiger and P. genalutea were rare beyond 5 m. Only P. nigra occurs deeper than 8 m and males of this species penetrate to a maximum of 27 m. Although there is a broad zone of overlap the males of each species have peak densities at different depths. P. nigra males are most common between 5 and 10 m where P. tridentiger and P. genalutea are rare. P. tridentiger males are most abundant between 1 and 3 m and P. genalutea are most abundant at 3 m and relatively rare at 1 m.

Females of all three species, by contrast, are most common at 1 m and their numbers decline markedly with increasing depth. P. tridentiger females occur down to 4 m only, whereas P. genalutea and P. nigra females penetrate to 8 m and 30 m respectively. The absolute abundance of the three species of Petrotilapia varies from site to site. This is particularly so for females and is reflected in the relatively large standard deviations obtained (Figure 56).

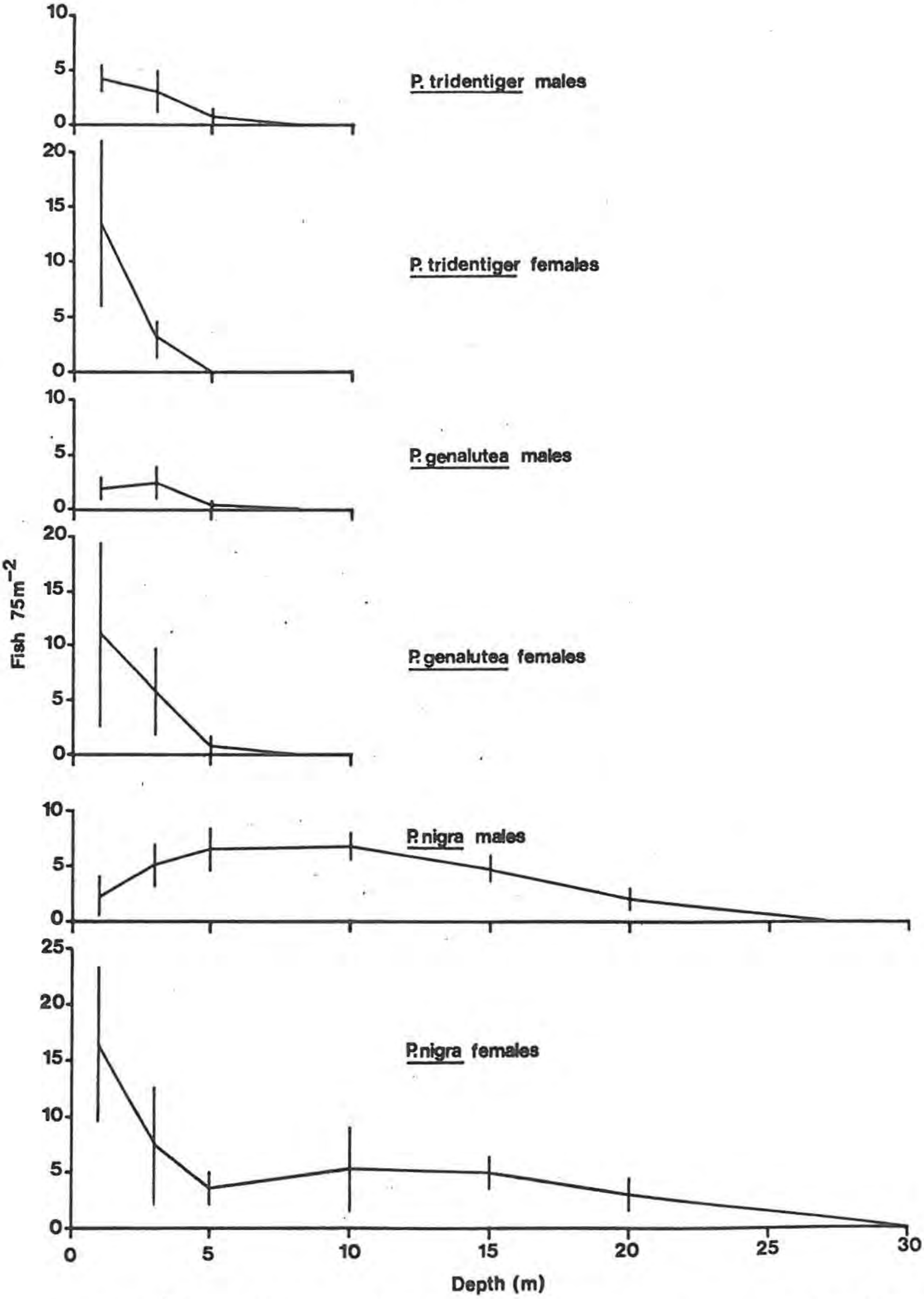

Figure 56. Bathymetric distribution of the three species of Petrotilapia at Monkey Bay. Vertical lines represent standard deviation about the mean.

Pianka's (1973) measure for resource overlap was used to quantify overlap in depth distribution between males and females of the three Petrotilapia species :

$$\alpha_{ij} = \sum_{a}^{n} p_{ia}\, p_{ja} \Bigg/ \sqrt{\sum_{a}^{n} p_{ia}^{2} \quad \sum_{a}^{n} p_{ja}^{2}}$$

where p_{ia} and p_{ja} are the proportions of the a^{th} resource used by the i^{th} and j^{th} Petrotilapia forms respectively. Resource overlap, α, ranges in value from zero to one, where a value of zero implies no overlap in resource use and a value of one implies total overlap in resource use (i.e. the two forms have identical requirements). In this case depth is the resource and the depth contours where fish abundances were measured are the 'a' resource divisions. The overlap figures are presented as a symmetrical matrix in Table 16. Overlap values are high with the notable exception of P. nigra males which have relatively low overlaps with all forms of P. tridentiger and P. genalutea.

Table 17 gives the densities (fish 75 m^{-2}) of Petrotilapia species in 1 to 5 m deep water from four different sites in Monkey Bay. These results show that site G, which is composed of large rock slabs, is not occupied by any territorial male Petrotilapia species and P. tridentiger females. P. genalutea and P. nigra females do occur at site G but are not common there. It appears therefore that the preferred habitat for all three species of Petrotilapia comprises a rubble of broken rock and boulder. Non-quantified observations from elsewhere in Monkey Bay confirm that this is true.

The distribution of juveniles of all three species of Petrotilapia is very discontinuous. Juvenile P. tridentiger are restricted to shallow

Table 16. Depth distribution overlap figures for the three species of *Petrotilapia* at Monkey Bay. The method used in calculating the overlap is explained in the text (page 142).

	P. tridentiger males	*P. genalutea* males	*P. nigra* males	*P. tridentiger* females	*P. genalutea* females	*P. nigra* females
P. tridentiger males	1.00	0.98	0.48	0.91	0.97	0.94
P. genalutea males		1.00	0.55	0.76	0.89	0.84
P. nigra males			1.00	0.28	0.42	0.73
P. tridentiger females				1.00	0.98	0.90
P. genalutea females					1.00	0.92
P. nigra females						1.00

Table 17. Numerical density (fish 75 m^{-2}) of adult Petrotilapia at various depths from four sites at Monkey Bay. Site G is composed of large rock slabs whereas all the other sites consist of a rubble of broken rocks. Females were not counted at site H.

Species and category	SITES											
	G			H			E			D		
	1m	3m	5m	1m	3m	5m	1m	3m	5m	1m	3m	5m
P. tridentiger males	0	0	0	5	4	2	4	3	0	4	6	2
P. tridentiger females	0	0	0	-	-	-	4	1	0	24	2	0
P. genalutea males	0	0	0	1	1	0	1	2	0	3	6	1
P. genalutea females	4	1	0	-	-	-	3	0	0	21	7	0
P. nigra males	0	0	0	1	2	3	6	8	10	7	7	10
P. nigra females	7	3	3	-	-	-	14	6	1	30	14	4

water, the deepest recorded sighting being 1.5 m. They only occur in regions dominated by broken rock where they are generally found well within narrow cracks. P. genalutea juveniles occur between 0.1 and 3 m and P. nigra juveniles from 0.1 to 10 m. P. nigra and P. genalutea juveniles are less secretive in their habits than P. tridentiger juveniles. They occur frequently in shallow water over broken rock, large rock slabs or among twigs of submerged branches. In these circumstances the juveniles of each species tend to aggregate together, and groups of up to 50 juveniles have been seen at a submerged branch.

P. genalutea and P. nigra juveniles also occur over submerged macrophyte beds. P. genalutea, as small as 30 mm TL, have been seen in the Vallisneria aethiopica beds at site F (Figure 54) and P. nigra juveniles have been seen above the Ceratophyllum demersum bed at site G (Figure 54). In both instances the fishes were on the periphery of the plant beds in close proximity to the rocky shore.

Juvenile P. nigra and P. genalutea regularly shoal with Pseudotropheus zebra in the water column between 0.1 and 5 m. P. nigra juveniles also congregate over patches of small stones (less than 120 mm diameter), and individuals as small as 25 mm TL have been found in these habitats.

(b) Other sites

P. tridentiger and P. genalutea have a broad distribution in the south-east arm of Lake Malawi whereas the distribution of P. nigra is very restricted (Figure 21). The southern limit for P. nigra is Monkey Bay.

The depth distribution of territorial male *Petrotilapia* species at the south-eastern corner of Boadzulu Island is shown in Table 18. A comparison of Table 18 and Figure 56 reveals that at Boadzulu Island, where *P. nigra* does not occur, *P. tridentiger* and *P. genalutea* penetrate considerably deeper and are more abundant at each depth contour than at Monkey Bay. The maximum recorded depth for territorial males of both species at Boadzulu Island is 16 m compared to 8 m at Monkey Bay. At Boadzulu Island *P. tridentiger* females occur between 0.1 to 20 m and *P. genalutea* females occur from 0.1 to 18 m.

Niche breadths, using depth distribution data, were calculated for territorial males of *P. tridentiger* and *P. genalutea* at both Boadzulu Island and Monkey Bay using the formula of Petraitis (1979)

$$\text{where} \quad W = r^{E};$$

and r is the number of resource classes;

$$E = p_{ij} \log_{r} q_{j} - \sum_{j=1}^{r} p_{ij} \log_{r} p_{ij} ,$$

p_{ij} is the frequency of utilization of resource j by species i, and q_j is the frequency of occurrence of resource j in the environment. In this instance each resource is a particular depth zone. p_{ij} is therefore the relative abundance of territorial males of a particular species (i) at a particular depth (j). q_j is the frequency of occurrence of a particular depth zone. In this example all depth zones are considered to be equally abundant. W ranges from zero for a narrow niche to one for a broad niche.

Table 18. Depth distribution (fish 75 m^{-2}) of *Petrotilapia* territorial males at the south-east corner of Boadzulu Island.

Species	Depth categories					
	1 m	3 m	5 m	10 m	15 m	20 m
P. tridentiger	13	8	8	6	3	0
P. genalutea	16	10	8	6	2	0

Table 19. Niche breadths, from depth distribution data, for *P. tridentiger* and *P. genalutea* territorial males at Monkey Bay and Boadzulu Island. The method used in calculating niche breadth figures is explained in the text (page 146).

Species	Locality	
	Monkey Bay	Boadzulu Island
P. tridentiger	0.494	0.912
P. genalutea	0.494	0.853

The niche breadth values generated by this formula are given in Table 19. It can be seen that the bathymetric niche breadths for both species at Boadzulu Island are considerably greater than at Monkey Bay.

Territory size and overlap

The territory boundaries of conspecifics abut or overlap slightly whereas interspecifically there is complete overlap of territories. Thus where the habitat is suitable the entire area, in shallow water, is partitioned by males of all three species of Petrotilapia and the density of territorial males of each species is, therefore, independent of the presence of territorial male congeners.

As there were no significant intraspecific differences in territory size between the two study sites, these data are considered together (Table 20).

Table 20. Mean territory area of the three species of Petrotilapia at Monkey Bay.

Species	Mean area (m^2)	S.D.	n
P. tridentiger	22.16	11.06	20
P. genalutea	19.88	7.90	20
P. nigra	6.79	3.58	20

P. nigra has significantly smaller territories than both *P. tridentiger* and *P. genalutea* ($p < 0.001$; t-test for two means), whereas there is no significant difference in territory size between *P. tridentiger* and *P. genalutea*. There is considerable intraspecific variation in territory size related to differences in topography and probably to the size of the tenant (data were not collected on tenant size as it would have disrupted continuing ecological research). Furthermore, the largest territories of *P. tridentiger* and *P. genalutea* were always found at the limits of their distribution where intraspecific competition for space is presumably less intense than in the centres of their preferred habitats.

Feeding behaviour

Although the three species of *Petrotilapia* are generally solitary when feeding, groups of feeding fishes were occasionally seen. These groups were of two kinds: relatively stationary aggregations in the water column, and tightly packed groups feeding from the rocks. The latter group moved as a school between feeding sites.

(a) Schools

Schooling *Petrotilapia* species were relatively common in May and June of 1978 and 1979 and were present until October in both years. All the schools were seen in 1 to 5 m of water. The number of individuals in the schools ranged from 30 to 300. Schools were composed largely of *P. genalutea* females and non-territorial males. Occasionally a few *P. nigra* females and non-territorial males and at most one *P. tridentiger* female were seen in the schools. Non-territorial male *Labeotropheus fuelleborni* Ahl and '*Pseudotropheus* orange cheek' (*sensu* Sharp) females were also present in small numbers. The *Petrotilapia* schools moved up to 10 m between feeding sites. When moving between feeding sites the fishes formed long (3 to 8 m) and narrow (± 30 cm) columns. When feeding the schools were very compact with individuals often making body contact (Figure 57). At all times when schools of *P. genalutea* were present many *P. genalutea* females remained solitary and therefore schooling behaviour does not appear to be obligatory in this species. School membership is flexible. Occasionally fishes were recruited to a school as it passed by and likewise individuals frequently remained behind at feeding sites when the school moved away.

Table 21 shows that 94% of the sites in which the schools fed were within the territories of '*Pseudotropheus* aggressive' and '*Pseudotropheus* orange cheek'. The preferred feeding sites tended to be in areas where a number of '*Pseudotropheus* aggressive' and '*Pseudotropheus* orange cheek' held abutting territories. Part of the school could therefore utilize '*Pseudotropheus* aggressive' territories while simultaneously other school members foraged in '*Pseudotropheus* orange cheek' territories.

The first members to arrive at a potential feeding site were normally prevented from settling by the vigorous attacks of the territorial occupants. With large numbers of *Petrotilapia* individuals attempting to settle simultaneously these attacks were futile. '*Pseudotropheus* aggressive' individuals normally withdrew into the centre of their territories where they continued to defend a small area. '*Pseudotropheus* orange cheek' usually became passive after a while and fed alongside the intruders. Occasionally schools utilized '*Pseudotropheus* sky blue' territories but these occurrences have been omitted from the analysis in Table 21 as this species is rare at Monkey Bay.

Figure 57. A group of Petrotilapia genalutea females. Part of the group is feeding in a dense cluster while the remainder is moving away as a school.

Table 21a. The utilization of defended territories and undefended sites as feeding areas by adult *Petrotilapia* forms in May and November 1979. Data are expressed as a percentage of n, where n represents the total number of feeding observations for a particular *Petrotilapia* form. For example, in May 1979, of the 122 feeding observations recorded for *P. tridentiger* territorial males 69% occurred within the territories of large '*Pseudotropheus* aggressive' individuals. Unless indicated to the contrary data were collected in 1-4 m deep water.

	'*Pseudotropheus* aggressive' > 100 mm TL	'*Pseudotropheus* aggressive' < 100 mm TL	'*Pseudotropheus*' orange cheek	Undefended	n
		MAY			
P. tridentiger territorial males	69	20	7	4	122
P. genalutea territorial males	4	28	36	32	128
P. nigra territorial males	4	26	51	19	146
P. tridentiger females	3	22	20	55	126
P. genalutea and *P. nigra* females	0	3	12	85	147
P. genalutea schools	41	15	38	6	130
P. nigra territorial males (6-10 m)	4	24	46	26	136
		NOVEMBER			
P. tridentiger territorial males	58	27	5	10	59
P. genalutea territorial males	4	29	22	45	55
P. nigra territorial males	3	16	39	42	74
P. tridentiger females	5	24	20	51	66
P. genalutea females	0	1	10	89	70
P. nigra females	0	5	15	80	65

Table 21 b. The relative abundance of the various categories of feeding site utilized by adult Petrotilapia forms at Monkey Bay. The data are expressed as a percentage of the total surface area of rocky shore at two depths. All the information is from Sharp (in prep.).

Depth	'Pseudotropheus aggressive' >100 mm TL	'Pseudotropheus aggressive' <100 mm TL	'Pseudotropheus orange cheek'	Undefended
1 - 4 m	11.9	6.1	8.6	69.7
6 -10 m	14.6	7.5	21.8	56.1

(b) Aggregations in the water column

On certain days, particularly in May, June and July, P. genalutea females and occasionally P. nigra females congregate near large boulders which project from the rocky floor. These fish hover in the water column making frequent, rapid snapping movements with their jaws. Analysis of stomach contents of such individuals showed that they had been feeding on zooplankton, in particular Diaptomus kraepelini Poppe & Mrāzek. On other occasions the same Petrotilapia forms group together in the water column and make frequent gulping movements while slowly swimming forwards. Stomach content analysis of these individuals revealed that they had been feeding on phytoplankton, especially Anabaena species. Both of these events, and in particular the latter, are rare at Monkey Bay.

Individual feeding site preferences

Figure 58 shows a map of the space utilization of one P. genalutea territorial male, two P. tridentiger territorial males and six P. nigra territorial males at site E (Figure 54). Although there is considerable interspecific overlap of territories there is little overlap of feeding sites between individuals. Only 3% of the total feeding space used by these nine fish was shared.

The individuals observed did not feed at random within their territories, and although some utilized up to 13 feeding sites, each individual fed predominantly in one to four sites only. The fish are, therefore, selective as to where they feed. In this particular example most of the feeding sites of the P. genalutea male were on exposed boulder faces whereas most feeding sites of P. tridentiger and P. nigra males were in

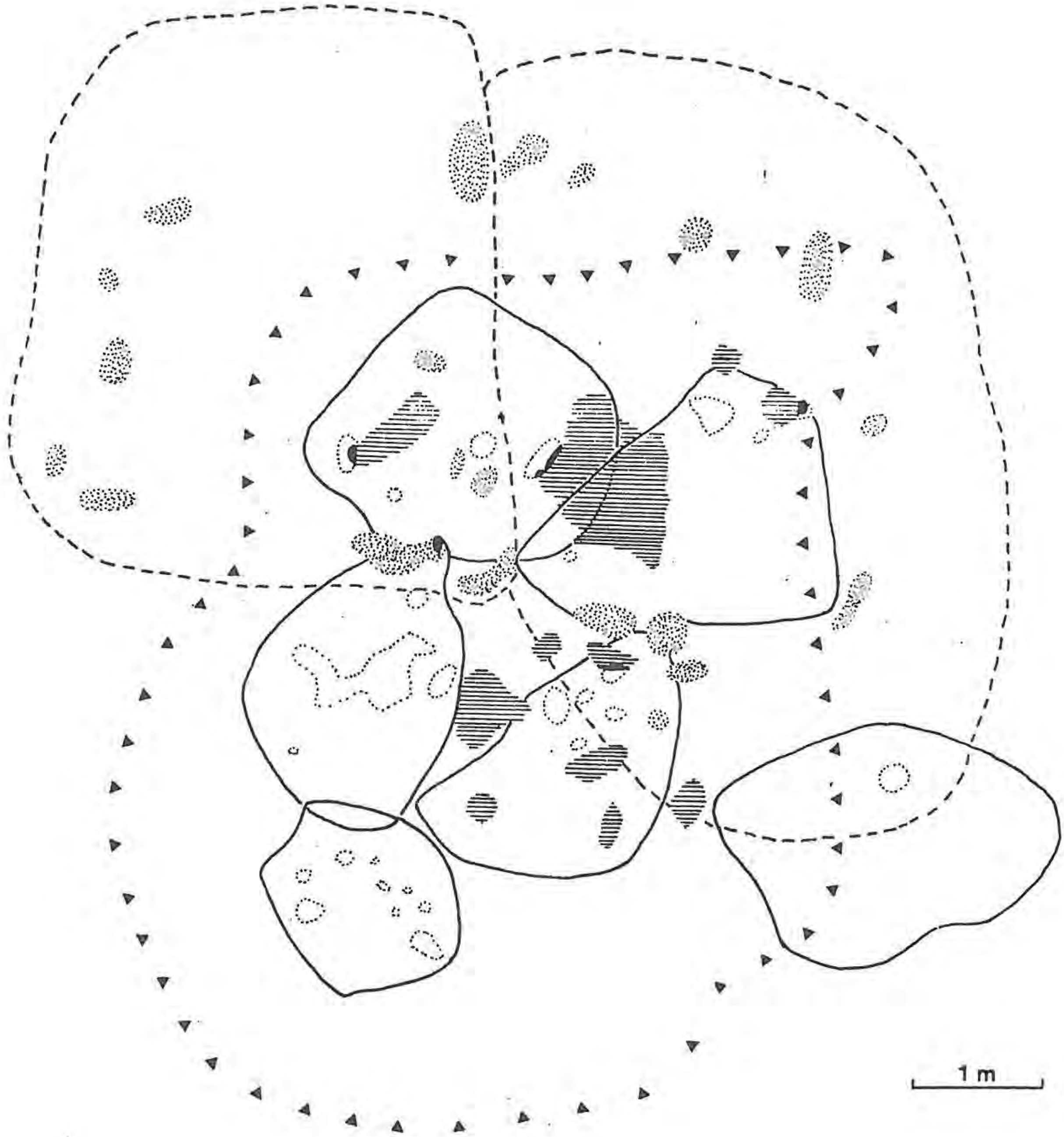

Figure 58. Map showing territories and feeding sites of territorial male *Petrotilapia* species. *P. tridentiger* territory boundaries------, feeding sites ⠿; *P. genalutea* territory boundaries▲▲▲, feeding sites ▤ ; *P. nigra* territory boundaries——, feeding sites ⬭. Areas shaded black represent regions of feeding site overlap between individuals. Each individual was observed for a total of six hours.

steep sided cracks, where 'Pseudotropheus aggressive' and 'Pseudotropheus orange cheek' individuals held territories, and on the undersurface of over-hanging rocks.

Species feeding site preferences

It is apparent from Table 21 that none of the Petrotilapia forms feed at random on the rocky shores. Territorial male Petrotilapia of all three species, P. tridentiger females and P. genalutea schools select sites defended by 'Pseudotropheus aggressive' and 'Pseudotropheus orange cheek' individuals. By contrast solitary P. genalutea females and P. nigra females rarely use defended sites. P. tridentiger males feed almost exclusively in 'Pseudotropheus aggressive' territories, favouring territories occupied by large individuals. Territorial males of the other two species, however, feed mainly in 'Pseudotropheus orange cheek' territories and rarely within territories held by large 'Pseudotropheus aggressive' individuals. Petrotilapia females of all three species, but in particular P. genalutea and P. nigra, utilize undefended sites to a far greater extent than do territorial male Petrotilapia. In May, due to identification difficulties, P. genalutea and P. nigra females were treated together. In November, when the identity of the two forms had been resolved and they were treated separately, they had almost identical patterns of feeding site utilization.

Although the patterns of feeding space utilization are similar for each Petrotilapia form in May and November, there are certain differences. These differences become more meaningful when niche breadth and overlap figures for the two months are compared. Table 22 presents the niche breadth figures calculated using the formula of Petraitis (1979) as

Table 22. Niche breadth (W) for various forms of *Petrotilapia* based on their use of defended and undefended sites during May and November. Unless otherwise stated all observations were made in 1-4 m deep water. The method used in calculating the niche breadth figures is explained in the text (page 146).

Species and category	May (W)	November (W)
P. tridentiger territorial males	.265	.332
P. genalutea territorial males	.519	.654
P. nigra territorial males	.367	.604
P. tridentiger females	.750	.734
P. genalutea and *P. nigra* females	.818	.828
P. genalutea schools	.344	-
P. nigra females	-	.797
P. nigra territorial males (6-10 m)	.697	-

presented on page 146. In this case, p_{ij} is the frequency with which a particular form of Petrotilapia was seen feeding in one of the following four site categories : territories of small 'Pseudotropheus aggressive' individuals, territories of large 'Pseudotropheus aggressive' individuals, territories of 'Pseudotropheus orange cheek' individuals and undefended areas. q_j is the frequency of occurrence of a particular feeding site category in the environment. The niche breadths for territorial males of each species increases substantially in November whereas female niche breadths for all species of Petrotilapia remain more or less constant. The increase in niche breadth of territorial males is largely due to the increased utilization of undefended space that occurred in November (Table 21). Disregarding the special case of feeding schools, the territorial males of all three species have narrower niches than the females. The narrowest niche of all is held by P. tridentiger males whereas the broadest niche is occupied by female P. genalutea and P. nigra. In 1 to 4 m, where all three species occur, P. nigra males have a narrower niche than at 6 to 10 m where other Petrotilapia species are absent or very rare. Solitary P. genalutea females have a broader niche than schooling P. genalutea females.

Niche overlap figures for all adult Petrotilapia forms were calculated from the data in Table 21 using the formula of Pianka (1973) as discussed on page 142 of this chapter. In this case the resource is feeding space and each of the three categories of defended sites and undefended sites are the 'a' resource divisions. Feeding site niche overlap figures for adult Petrotilapia are presented in Table 23. In May the feeding site niche of P. genalutea males overlaps considerably with P. nigra males and P. tridentiger females. Females of all three species of Petrotilapia overlap considerably with one another, and

Table 23. Niche overlap values for all forms of *Petrotilapia* in May and November based on the utilization of defended or undefended sites for feeding. The method used in calculating the niche overlap values is explained in the text (page 142).

MAY

	P. tridentiger males	*P. genalutea* males	*P. nigra* males	*P. tridentiger* females	*P. genalutea* & *P. nigra* females	*P. genalutea* schools
P. tridentiger males	1.00	0.32	0.30	0.21	0.13	0.82
P. genalutea males		1.00	0.91	0.88	0.67	0.69
P. nigra males			1.00	0.73	0.44	0.74
P. tridentiger females				1.00	0.73	0.44
P. genalutea and *P. nigra* females					1.00	0.21
P. genalutea schools						1.00

NOVEMBER

	P. tridentiger males	*P. genalutea* males	*P. nigra* males	*P. tridentiger* females	*P. genalutea* & *P. nigra* females	*P. genalutea* schools
P. tridentiger males	1.00	0.43	0.31	0.38	0.18	
P. genalutea males		1.00	0.97	0.98	0.84	
P. nigra males			1.00	0.95	0.81	
P. tridentiger females				1.00	0.95	
P. genalutea and *P. nigra* females					1.00	

P. tridentiger males overlap substantially with P. genalutea schools. Other than the above cases overlap figures in May are fairly low. In November, however, there is an overall tendency for overlap to increase.

The utilization of different rock slopes and cracks as feeding sites by the Petrotilapia forms is shown in Table 24. The degree of selectivity by each form cannot be assessed in the absence of data on resource availability. There are, however, apparent differences in the utilization of rock slope and cracks by the different forms. P. tridentiger males and females and P. nigra males utilize steep rock faces more than gently sloping or horizontal ones whereas P. genalutea males and females and P. nigra females show no preference for either steep or horizontal rock faces. Similarly P. tridentiger and P. nigra males utilize cracks to a greater extent than exposed surfaces whereas P. genalutea males and all Petrotilapia females utilize exposed surfaces more than cracks.

Adult response to phytoplankton bloom

Thirty individuals of each species were observed during the dense phytoplankton bloom of 7 May 1979. No specific or sexual differences in behaviour were evident and consequently the data were pooled. Of the fish observed, 67% fed on phytoplankton in the water column while the remainder fed on loose aufwuchs.

Juvenile feeding habits

Table 25 summarizes the results of observations on juvenile feeding behaviour. P. tridentiger juveniles feed exclusively on aufwuchs by

Table 24. The percentage utilization of different rock slopes and cracks as feeding sites by adult Petrotilapia in May

Species	n	Rock slope		Proximity to crack	
		>80°	<80°	>400 mm	<400 mm
P. tridentiger territorial males	122	21	79	27	73
P. genalutea territorial males	128	59	41	67	33
P. nigra territorial males	146	37	63	45	55
P. tridentiger females	126	41	59	60	40
P. genalutea and P. nigra females	143	60	40	84	16

Table 25. Summary of the food preferences of *Petrotilapia* juveniles. Data are derived from observations on feeding behaviour and are expressed as a percentage of n.

Species	Feeding site (and associated food)		
	Rock (loose aufwuchs and benthic invertebrates)	Water column (zooplankton and phytoplankton)	n
P. nigra	21	79	189
P. *genalutea*	17	83	153
P. *tridentiger*	100	-	110

rock scraping whereas P. nigra juveniles and P. genalutea juveniles feed mainly on plankton in the water column. There was no obvious preference for either zoo- or phytoplankton, the fishes apparently fed opportunistically on the most abundant planktonic organism. Thus on certain days most P. genalutea and P. nigra juveniles fed predominantly on zooplankton and on other days phytoplankton was favoured. Plankton feeding was observed in all of the habitats occupied by these fish. Juvenile P. nigra and P. genalutea were also observed feeding on loose aufwuchs by scraping the surfaces of rocks, submerged branches and twigs. P. genalutea juveniles also scrape Vallisneria aethiopica fronds.

Stomach content analyses

Due to considerable individual variation, it was not possible to detect any seasonal shifts in diet or any interspecific differences in diet of adult Petrotilapia species. Consequently the data from the three species were pooled together (Table 26). From Table 26 it is apparent that the most prominent food items in the stomach contents of adult Petrotilapia species were loose aufwuchs and benthic invertebrates. Although the mean percentage of plankton in stomachs was only 8%, some individuals had as much as 100% of this item in their stomachs. The results in Table 26 may therefore obscure the importance of plankton as a secondary food source. By contrast firmly attached strands of epilithic algae do not appear to be important dietary components for these species. No individual had more than 10% of this item in its stomach.

Aggression

(a) Field observations

There were relatively few overt interactions between territorial males

Table 26. Percentage composition of stomach contents of *Petrotilapia* adults. Data were pooled for the three species. 'n' represents the number of stomachs analysed: 60 *P. tridentiger*, 60 *P. genalutea* and 60 *P. nigra*.

Loose aufwuchs	Benthic invertebrates	Zooplankton	Phytoplankton	Firmly attached epilithic algae	n
58	32	5	3	2	180

of the three species of Petrotilapia. In all of the observed aggressive encounters P. tridentiger territorial males were dominant over P. genalutea and P. nigra territorial males. P. genalutea territorial males dominated P. nigra territorial males on eight out of nine occasions (Table 27). A Chi square test indicates that these results are statistically significant ($p < 0.001$). It is evident from this data that a dominance hierarchy exists amongst territorial male Petrotilapia species, with P. tridentiger being the most dominant species and P. nigra the least dominant.

On numerous occasions male P. genalutea and P. nigra were seen to move out of the way of an approaching P. tridentiger male without any sign of aggression from the P. tridentiger. It therefore appears as if avoidance behaviour plays a role in the social dominance hierarchy. Territorial males of the three species of Petrotilapia dominated all other non-territorial Petrotilapia forms, irrespective of species, in every observed interaction.

(b) Aquarium observations

The results of the aquarium dominance experiments are given in Table 28. It is apparent that territorial male P. tridentiger dominated P. genalutea and P. nigra territorial males in every encounter, whereas, P. genalutea dominated P. nigra males in 16 out of 20 encounters. These results are significant (Chi square test, $p < 0.001$) and support the field observations.

Territorial males of all three species of Petrotilapia were dominant over 'Pseudotropheus aggressive' and 'Pseudotropheus orange cheek' territorial males in all encounters ($n = 10$ for each series of interactions ($p < 0.001$, Chi square test)).

Table 27. Aggressive interactions between territorial male *Petrotilapia* species at Monkey Bay. The data represent the total number of encounters observed during 60 hours of observation. The results are significantly different for the three species ($p < 0.001$; Chi square test)

	Territorial males submissive to focal territorial males		
Focal territorial males	*P. tridentiger*	*P. genalutea*	*P. nigra*
P. tridentiger	16	19	15
P. genalutea	0	26	8
P. nigra	0	1	15

Table 28. Results of interactions between *Petrotilapia* territorial males in aquaria. A dash indicates that this combination of categories was not used in the experiments.

		Submissive		
		P. tridentiger	*P. genalutea*	*P. nigra*
Dominant	*P. tridentiger*	-	10	10
	P. genalutea	0	-	16
	P. nigra	0	4	-

DISCUSSION

It is difficult to provide conclusive proof of competition in natural communities. Sale (1974) noted that the preferred method for assessing competition is the measurement of changes in population size following experimental changes in the amount of resources, or in the numbers of presumed competitors. In practice, however, this is often not possible and less direct techniques have to be employed. Colwell & Futuyma (1971) proposed that the detection of niche shifts could provide evidence of competitive interactions. They suggested looking for niche shifts after resource availability or numbers of presumed competitors had been experimentally manipulated, and by comparing natural situations where primary competitors are absent to situations where they are present. Another possibility is to look for evidence of niche shifts where resource availability undergoes seasonal changes. For example, Zaret & Rand (1971) demonstrated that certain tropical stream fishes undergo niche shifts which coincide with seasonal changes in food abundance. They found that niche overlap was highest during times of relative food abundance and lowest when food was scarce. From this evidence they concluded that the 10 species studied were competing with one another for food.

At Monkey Bay there is a seasonal cycle of aufwuchs abundance (Sharp, in prep.; see Chapter 7). Loose aufwuchs and its attendant invertebrate fauna is the primary food source of adults of the three species of Petrotilapia. If these species compete for food the intensity of competition should be higher in May, when aufwuchs standing crop is low, than in November, a time of relative abundance. The data in this chapter confirm this trend and show that there is greater niche overlap between the various Petrotilapia forms in November than in May. Furthermore, with the exception of P. tridentiger females, niche breadths are also greater in November. These niche shifts strongly suggest that competition between the three species does occur.

Further evidence that competition occurs can be found through analysis of situations in which competitors are absent. The feeding site niche of territorial male P. nigra at Monkey Bay shows a marked expansion in 6 to 10 m deep water, where P. tridentiger and P. genalutea are rare or absent, relative to shallower water where all three species are common. Similarly P. tridentiger and P. genalutea territorial males have broader depth distribution niches at Boadzulu Island, in the absence of P. nigra, than at Monkey Bay where all three species occur. Although it is not possible, from the available data, to calculate niche breadths for female P. tridentiger and P. genalutea at Boadzulu Island, they do have considerably wider depth distributions than at Monkey Bay. As Werner & Hall (1976) observe, one of the limitations of comparative studies is the difficulty of separating the effects of competition from the effects of the relative availability of habitats and food. Despite this limitation the above mentioned data supplement the data on changes in feeding site utilization. There is, therefore, substantial evidence that the three species of Petrotilapia compete with one another. Competition is particularly directed towards feeding space.

The coexistence of the three species of Petrotilapia at Monkey Bay appears to be facilitated by partitioning feeding space. The observations on individual territorial males suggest that interspecific overlap of feeding sites may be considerably less than Tables 21 and 23 suggest. For example, within each territory of a *Petrotilapia* male there are normally numerous '*Pseudotropheus* aggressive' and '*Pseudotropheus* orange cheek' territories some, but not all, of which are utilized by the territorial *Petrotilapia* species. Furthermore, only a few of these territories are extensively utilized. When a territorial male *Petrotilapia* of any species forages within the territory of any other *Petrotilapia* species, the two do not normally utilize the same feeding sites.

The intensity of competition is also reduced by differences in the range of habitat occupied by the three species of *Petrotilapia*. For example *P. nigra* has a much broader depth distribution at Monkey Bay than the other two species. *P. nigra* therefore has a deep water refuge where it does not come into direct competition with the other species of *Petrotilapia*. Female and juvenile *P. genalutea* and *P. nigra*, in addition to occurring in habitats suitable for territorial males of all three species and *P. tridentiger* females, occur over large rock slabs. Juveniles forage within narrow cracks which are inaccessible to adults. Furthermore, juvenile *P. genalutea* and *P. nigra* forage in submerged macrophyte beds, around submerged branches and in stony patches, all of which are not utilized by adult *Petrotilapia* species.

In a review of resource partitioning, Schoener (1974) concluded that, as a general rule, habitat dimensions are more important in facilitating coexistence than food-type dimensions. Food-type dimensions, in turn, are generally more important than temporal dimensions. He found that habitat dimensions are of particular importance for animals that feed on relatively small food items. Various studies of fish communities support these conclusions. Ecological segregation amongst the fish species of two temperate lakes in southern Michigan is primarily by habitat (Werner et al., 1977). Similarly Smith & Tyler (1973), in discussing coral reef fish communities, consider how and where the various species feed to be of much more importance than the type of food consumed. The results on Petrotilapia resource utilization show that habitat partitioning is particularly prevalent whereas partitioning of food types is not, as a rule, important.

Owing to great individual variation, no specific differences in the stomach contents of adult Petrotilapia species were found. In contrast to Fryer's (1959) suggestion that P. tridentiger (sensu Trewavas) is a highly stenotypic feeder, it appears that the three species studied here are opportunistic feeders. The different conclusions reached by Fryer (1959) and the present work, including that of McKaye & Marsh (in prep.), are probably attributable to the different approaches adopted. Fryer's conclusions are based on an analysis of 48 stomach contents and are supplemented with an unspecified but probably limited amount of underwater observations. The conclusions in this thesis are mainly based on over 600 hours of underwater observations and are supplemented with an analysis of the contents of 180 stomachs. As a rule, adult Petrotilapia feed on loose aufwuchs but will utilize an alternative food supply such as plankton, when it is abundant. The occurrence of plankton in abundant supply is, however, infrequent. It is therefore possible that even if Fryer had captured each of the 48 specimens on separate days that no plankton would have been detected in the stomachs of these fishes.

The flexibility of Petrotilapia feeding behaviour and the versatility of the feeding apparatus have been demonstrated by Liem (1980) and

McKaye & Marsh (in prep.). The ability of the three species of Petrotilapia to utilize transient sources of food in addition to loose aufwuchs is one of the mechanisms which can reduce the intensity of interspecific competition and thereby facilitate coexistence. In this respect it is significant that the abundance of plankton in Lake Malawi is particularly high in winter when the aufwuchs standing crop is low (see Chapter 7). Therefore when interspecific competition for loose aufwuchs is most intense an alternative food source is available.

The most consistent dietary differences are between adults and juveniles. Adult Petrotilapia of all three species feed primarily on loose aufwuchs and its associated invertebrate fauna, whereas P. genalutea and P. nigra juveniles feed primarily on plankton and secondarily on loose aufwuchs. The juveniles are, therefore, not in direct competition with adults for food.

The high proportion of benthic invertebrates in the diet of adult Petrotilapia is of interest. Fryer (1959) found that there were as many as 30 invertebrates cm^{-2} on the upper surfaces of rocks (i.e. within the aufwuchs mat) at Nkhata Bay. Despite this high numerical density he apparently found no invertebrates in the stomachs of P. tridentiger (sensu Trewavas). This is a surprising result in view of the feeding method and structure of dentition of Petrotilapia species which is well adapted for collecting any loose matter between the firmly attached strands of epilithic algae. The present study shows that benthic invertebrates are a prominent item of diet in the three species of Petrotilapia from Monkey Bay.

Morse (1974) has documented numerous examples of interspecific social dominance hierarchies in vertebrate communities. In these communities the position of individuals and species in the hierarchy determines their access to resources such that the most dominant have priority access. Social dominance hierarchies, therefore, represent an example of interference competition. In these hierarchies subordinate species characteristically have broader niches than the dominant species, i.e. dominants are 'specialists' and subordinates are 'generalists'. There is also frequently a positive correlation between size and dominance. Generally there are relatively few overtly aggressive interactions and avoidance of dominants by subordinates is a characteristic of these communities.

Within the Petrotilapia community there are both interspecific and intraspecific social dominance hierarchies. P. tridentiger territorial males are the most dominant form of Petrotilapia and they utilize the prime feeding sites i.e. territories of large 'Pseudotropheus aggressive' individuals. The most subordinate adult forms, P. genalutea and P. nigra females, utilize sites with the lowest aufwuchs standing crop i.e. undefended areas. It appears as if interactions with 'Pseudotropheus aggressive' and 'Pseudotropheus orange cheek' force these subordinate fishes to utilize undefended sites. This implies that to understand the resource allocation of the various Petrotilapia forms, interactions with non-congeners need to be taken into account as well. The work of Sharp (in prep.) and personal observations in the field suggest that the most important species affecting the resource utilization of the Petrotilapia species at Monkey Bay are the highly aggressive 'Pseudotropheus aggressive', 'Pseudotropheus orange cheek' and 'Pseudotropheus sky blue' forms. In general, the Petrotilapia species dominate all other Mbuna in the study area although it is likely that territorial male Pseudotropheus zebra and Labeotropheus fuelleborni are dominant over female P. genalutea and female P. nigra. Unfortunately there is no data available on the influence of these species on Petrotilapia resource utilization.

In general there is a negative correlation between niche breadth and dominance in the Petrotilapia community. An exception concerns territorial males of P. genalutea and P. nigra. Despite its lower rank, P. nigra territorial males utilize defended sites to a greater extent than P. genalutea territorial males and consequently P. nigra territorial males have a narrower niche as well. The explanation probably involves interactions with 'Pseudotropheus orange cheek'. Sharp (in prep.) has shown that the abundance of 'Pseudotropheus orange cheek' reaches a peak at about 10 m and Figure 56 indicatesthat P. nigra territorial males are also most abundant at approximately the same depth. Furthermore, 'Pseudotropheus orange cheek' is relatively rare in water less than 4 m deep where P. genalutea are common. It is possible, therefore, that P. nigra territorial males, by virtue of their similar distribution pattern to that of 'Pseudotropheus orange cheek', are better adapted to utilizing these defended sites than P. genalutea territorial males.

An understanding of the importance of interference competition to resource allocation in the Petrotilapia community may be used to interpret the observed niche shifts and distribution patterns. Morse (1974) suggests that the niche dimensions of dominant species are unlikely to be affected by subordinate species. A comparison of the depth distribution patterns of Petrotilapia species at Monkey Bay and Boadzulu Island show that the two dominant species, P. tridentiger and P. genalutea, have a broader depth niche at Boadzulu Island in the absence of P. nigra than at Monkey Bay, where all three species occur. These results could imply that P. nigra, despite its low rank in the community, restricts the habitat utilization of the dominant species at Monkey Bay. It seems more likely, however, that P. tridentiger and P. genalutea penetrate deeper water at Boadzulu Island because the habitat is suitable there whereas at Monkey Bay they confine themselves to the shallows because of the unsuitability of deeper water habitats. The absence of P. nigra from Boadzulu Island is possibly a result of it having been excluded from this area by the more dominant species. A major difference between Monkey Bay and Boadzulu Island is the presence of a large cormorant colony at Boadzulu Island. There is almost certainly an additional and localized input of nutrients, in the form of guano, at Boadzulu Island and this may result in higher primary productivity at this site. It is therefore possible that at Boadzulu Island deeper waters are more productive and consequently more suitable habitats for P. tridentiger and P. genalutea than at Monkey Bay.

Similarly the absence of P. nigra at Namaso Bay, Mpandi Island and Kanchedza Island is probably due to P. nigra being excluded from these sites by the more dominant species of Petrotilapia. It appears that in order for P. nigra to coexist with the other two species of Petrotilapia it must have a deep water refuge in which the other two species are rare or absent. The absence of P. genalutea as well as P. nigra from Kanchedza Island is probably also a result of interference competition from P. tridentiger.

Caution is, however, required when analyzing these distribution patterns as factors other than competition may be operative. For example, the absence of P. nigra and P. genalutea from certain sites may be due to the absence of certain other species (e.g. 'Pseudotropheus aggressive' and 'P. orange cheek') which are important for their existence. Alternatively, it is possible that the absent Petrotilapia species have not attempted to colonize these sites.

The tendency for territorial males of all three species of Petrotilapia to decrease their utilization of prime feeding sites when loose aufwuchs is abundant does not fit in with the predictions of Morse (1974) concerning the niche of dominant species or forms. The explanation for these niche shifts probably is related to interactions with 'Pseudotropheus aggressive' and 'Pseudotropheus orange cheek'. Despite the fact that territorial males of Petrotilapia species dominate these two Pseudotropheus species, gaining access to their territories requires an expenditure of energy. The optimal feeding strategy for these Petrotilapia forms would be to utilize defended sites only to the extent that the net energy gained exceeded the energy that could be derived from feeding in the less productive but undefended areas.

Recent work on coral reef fishes has shown that certain pomacentrid and acanthurid fishes school in order to swamp the aggressive actions of highly territorial species and thereby gain access to food sources which are otherwise unavailable to solitary individuals (Barlow, 1974; Vine, 1974; Belk, 1975; Brawley & Adey, 1977). Similarly it appears that Petrotilapia schools are formed principally to gain access to the rich food supplies within the territories of 'Pseudotropheus aggressive' 'Pseudotropheus orange cheek' and 'Pseudotropheus sky blue'. Schools are formed principally in the winter months when the aufwuchs standing crop is relatively low. The schooling fishes exploit a completely different niche from that utilized when they are solitary. Schools therefore reduce feeding pressure on the relatively unproductive feeding sites. Although schooling *Petrotilapia* apparently overlap with territorial male *Petrotilapia* in terms of feeding space requirements, there is probably considerably less overlap than the data in Table 21 imply. The reason for this is that schools primarily feed at sites where a number of '*Pseudotropheus* aggressive' and '*Pseudotropheus* orange cheek' territories abut whereas territorial male *Petrotilapia* utilize only one defended site at a time and these sites are not normally in areas where defended sites are concentrated.

The role of interference competition in the community structure of fishes is controversial. In freshwater environments competition appears to be important in determining the structure of fish communities. For example, the experimental work of Werner & Hall (1976) on communities of sunfishes, which occur in small lakes in central North America, shows that interspecific competition for food is an important determinant of community structure. Similarly McKaye (1977) has demonstrated the occurrence of interspecific competition for breeding space amongst the cichlid communities in Lake Jiloa, Nicaragua. His results suggest that community structure may be influenced by competition. Studies on coral reef fish communities suggest however that competition may not be an important determinant of community structure in this instance. The coral reef habitat is continuously changing, while, on one hand, wave action can destroy parts of the reefs, other parts can grow. Sale (1977) has proposed that the structure of complex coral reef fish communities is largely a result of chance recruitment of pelagic young to vacant sites. In this situation interspecific competition is largely ineffective because the unpredictability of vacant sites prevents any one species from evolving strategies which would effectively exclude other species from colonizing any new space.

By contrast, habitat structure in Lake Malawi is relatively stable. Furthermore, the Mbuna are sedentary at all stages of their life histories (Fryer, 1959). The cichlid communities of Lake Malawi can therefore be expected to be stable. In a stable and predictable environment interspecific competition could play an important role in determining community structure. The data presented in this chapter indicate that interference competition is a prominent feature in the Mbuna communities of the south-east arm of Lake Malawi. Furthermore, competition appears to be an important mechanism which regulates resource partitioning in these communities and consequently facilitates species coexistence.

CHAPTER 9

DISCUSSION ON SPECIATION, WITH SPECIAL REFERENCE TO THE GENUS PETROTILAPIA

INTRODUCTION

Speciation is a controversial topic and this is probably attributable to the fact that it can only be studied by inference (Mayr, 1969). There is a wealth of literature on the subject and only those aspects which are of direct relevance to this thesis are discussed. Previous ideas on speciation in the cichlids of the Great Lakes of Africa and in Lake Malawi in particular are reviewed. Finally, speciation in the genus *Petrotilapia* is discussed.

GENERAL COMMENTS ON SPECIATION

A confusing number of models have been proposed for the process of speciation (Bush, 1975). According to Paterson (1978), however, only two models of speciation have widespread support amongst evolutionists. These are speciation in allopatry (Mayr, 1942) and speciation by reinforcement (Dobzhansky, 1951).

Speciation in allopatry

According to this model a small sub-population becomes isolated from the mother population and by the process of natural selection adapts to its new environment. If, during the process of adaptation, the specific mate recognition system (SMRS) of this sub-population becomes modified to the extent that it is incompatible with that of the mother population, then speciation has occurred. It should be noted that natural selection acts to increase an organism's 'fitness' and not to modify the SMRS of the organism. Any modification of the SMRS that occurs during the process of adaptation to the environment is fortuitous (Paterson, 1978). Speciation is therefore an incidental consequence of isolation. If the two sister species later become sympatric they will either be sufficiently ecologically distinct to permit co-existence or one of the species will be forced into extinction through competition with the other.

Speciation by reinforcement

According to this model, a sub-population diverges to some extent while it is geographically isolated, but then becomes sympatric with the mother population. During the period of sympatry natural selection acts to increase positive assortative mating to the extent that interbreeding between the two populations no longer occurs. Thus modifications of the SMRS which may have occurred during the period of allopatry are reinforced in sympatry. Furthermore when the two populations become sympatric, ecological differences may evolve which minimize competition between the incipient species and thereby facilitate co-existence.

Although speciation by reinforcement is popular amongst evolutionists, good *prima facie* evidence exists only for the speciation in allopatry model (Paterson, 1978). Paterson believes the reason the reinforcement model is invoked so often is that it justifies preconceived ideas concerning the nature of species. In particular, species are regarded as adaptive devices that evolve for the purposes of mastering a greater range of environments and ways of living (Dobzhansky, 1951). Thus species are considered to be the direct products of natural selection and not merely an incidental consequence of it.

Most of the early literature does not distinguish between the above mentioned models of speciation. Where no distinction has been made the process is herein referred to as allopatric speciation sensu lato. Where a distinction has been made the two models are referred to as speciation in allopatry and speciation by reinforcement.

SPECIATION IN THE GREAT LAKES OF AFRICA

One of the most outstanding characteristics of the Great Lakes of Africa is the large numbers of endemic cichlid fishes which occur in them. Much of the literature on African Great Lake cichlid fish deals with the diversity of species and in particular with the mode or modes of speciation involved (Worthington, 1937, 1954; Trewavas, 1949; Fryer, 1959, 1960, 1969; Greenwood, 1964, 1965, 1974; Hubbs, 1961; Lowe-McConnell, 1969; Fryer & Iles, 1972; McKaye, 1980).

The basin of Lake Malawi was formed approximately two million years ago (Beadle, 1974) and at this time was probably invaded by a few fluviatile cichlid species (Regan, 1922; Worthington, 1954). Such rapid speciation has occurred that today there are approximately 500 endemic species of cichlid in the lake (see Chapter 1). Lake Malawi is particularly interesting in that most of the endemic species probably arose as a result of intralacustrine speciation (Fryer & Iles, 1972). The suggestion of Mayr (1942) that multiple colonization by riverine species may have been important in Great Lake cichlid speciation, has been rejected by researchers more familiar with the lakes and their faunae (Fryer, 1959; Fryer & Iles, 1972; Greenwood, 1974).

Many of the early workers on cichlid speciation considered that because speciation was intralacustrine in Lakes Malawi and Tanganyika, it had to be sympatric in nature (Plate, 1913; Rensch, 1933). Brooks (1950) was the first to point out that geographical isolation could occur within one body of water and that allopatric speciation sensu lato was therefore a possibility in these lakes. Since then numerous authors have stressed the importance of allopatric speciation sensu lato through microgeographical isolation in Lake Malawi (Fryer, 1959, 1969; Mayr, 1963; Fryer & Iles, 1972; Greenwood, 1974). Fryer (1959) suggested that speciation in the Mbuna could be facilitated by fluctuations in lake level and siltation from inflowing rivers. These two events could expose and disrupt corridors of rock interlinking two major rocky shores. As Mbuna are strongly lithophilous and sedentary these environmental changes could facilitate speciation by isolating sub-populations from the mother population.

Greenwood (1974) has, however, pointed out that Fryer's theory is only feasible if the fish are lithophilous and sedentary, but it fails to explain how the very generalized fluviatile ancestors became habitat specific in the early phase of the lake's history. Greenwood (1974) suggests that the topography of Lake Malawi, during its early genesis, may have been considerably different from what it is today. In particular, there may have been more than one basin and fluctuating lake levels could therefore have produced the isolation necessary for the development of habitat specific species. The early evolution of the cichlid species flocks in Lake Malawi may therefore have been similar to that in Lake Victoria which was fragmented into numerous bodies of water during its genesis (Greenwood, 1974). In later stages of the development of Lake Malawi, speciation would almost certainly have been intralacustrine and provided that habitat specific species existed at this stage, Fryer's (1959) theory of microgeographical speciation would be feasible. Unfortunately there is at present no geological evidence to support or reject Greenwood's (1974) idea.

Recently McKaye (1980) has suggested that the two colour morphs of the South American cichlid, *Cichlasoma citrinellum*, may be incipient species in the process of sympatric speciation. In the light of the implicit evidence presented, McKaye (1980) suggests that the role of sympatric speciation in the Great Lakes of Africa should be reconsidered. He postulates that both allopatric speciation *sensu lato* and sympatric speciation have occurred in Lake Malawi. Similarly the occurrence of eleven endemic cichlid species in the crater lake of Barombi Mbo, West Cameroon, appears to be a result of sympatric speciation (Trewavas *et al.*, 1972).

As speciation cannot be observed directly and has to be inferred, it is not possible to prove or disprove the various theories of speciation. Nevertheless, according to Paterson (1978), good *prima facie* evidence exists for one mode of speciation only i.e. the speciation in allopatry model of Mayr (1942). Present knowledge concerning the genus *Petrotilapia* is considered below in the light of Mayr's theory.

SPECIATION IN THE GENUS *PETROTILAPIA*

A number of sympatric species of *Petrotilapia* occur on most rocky shores in Lake Malawi. Many of these species have extremely limited distributions, for example, the three species that occur at Chisumulu Island are not found anywhere else in the lake and the two species which occur nine kilometers away at Likoma Island are endemic to that island.

If the present species of *Petrotilapia* are the result of speciation in allopatry, a number of conditions must be satisfied: During the history of

Lake Malawi geographical barriers to gene flow must have arisen so that populations of Petrotilapia species became divided. The sub-populations of Petrotilapia must have been isolated in environments sufficiently distinct from that of the mother population for divergence of the specific mate recognition system (SMRS) to have occurred. The sub-populations of Petrotilapia must have been genetically isolated from one another for a sufficiently long period for speciation to have taken place. The geographical barriers would have had to disappear after speciation in order for sympatry to occur. To persist in sympatry the species would have to be ecologically compatible. Finally, to arrive at the extant distribution and abundance of Petrotilapia species, the above events would have had to occur a number of times.

Evidence that the above mentioned events are likely to have occurred is reviewed below.

Geographical barriers

Water depth and a non-rocky substrate are two geographical features which could act as barriers to gene flow between populations of Petrotilapia. The deepest observation of a Petrotilapia species in the lake is 42 m for the 'Small Blue' form at Nkhata Bay. Although observations were not made below this depth, the density of this species was low at 42 m and indications were that it was approaching its maximum depth. Jackson (1961) reports that P. tridentiger sensu Trewavas have been caught in gill nets set at just over 60 m near Nkhata Bay. In view of the steep bottom profile in this part of the lake, however, it is possible that these fish were captured in shallower water as the net descended or ascended. Physiologically, certain species of Petrotilapia are capable of penetrating deeper than 42 m (e.g. *P. tridentiger* and *P. nigra*, see Chapter 6) but in the field neither of these species occurs below 30 m.

It appears, therefore, that depths greater than or equal to 40 m could act as effective barriers to population dispersal and gene flow in *Petrotilapia* species. At present most large islands are separated from the mainland and from each other by depths in excess of 30 m and many are separated by depths of more than 60 m. For example, Figure 59 represents the bottom profile between Katari Island and Mpanga Rocks, Chilumba. This profile shows that Katari Island is separated from Mpanga Rocks by an 80 m trough. At the present lake level, no genetic exchange could take place between populations of *Petrotilapia* that occur at these two sites. If the lake level were to drop by 40 m, or more, there would no longer be a barrier to dispersal between these two sites. Thus the topography of Lake Malawi is such that populations of *Petrotilapia* species can be isolated and rejoined quite simply by fluctuations in lake level.

Fryer (1959) states that Mbuna are very sedentary fish which are restricted to a particular habitat by their stenotypic habits, and considers that a 20 m stretch of sand will inhibit movement of Mbuna across it. The work of Liem (1980), McKaye & Marsh (in prep.) and in this thesis indicates that trophically the genus *Petrotilapia* is not as stenotypic as their highly adapted oral dentition suggests. It is possible that *Petrotilapia* species could obtain food in various habitats, as they are not entirely restricted to a diet of loose aufwuchs, and, as a result, migrations over sand are possible.

There is evidence from artificial reef studies that *Petrotilapia* species

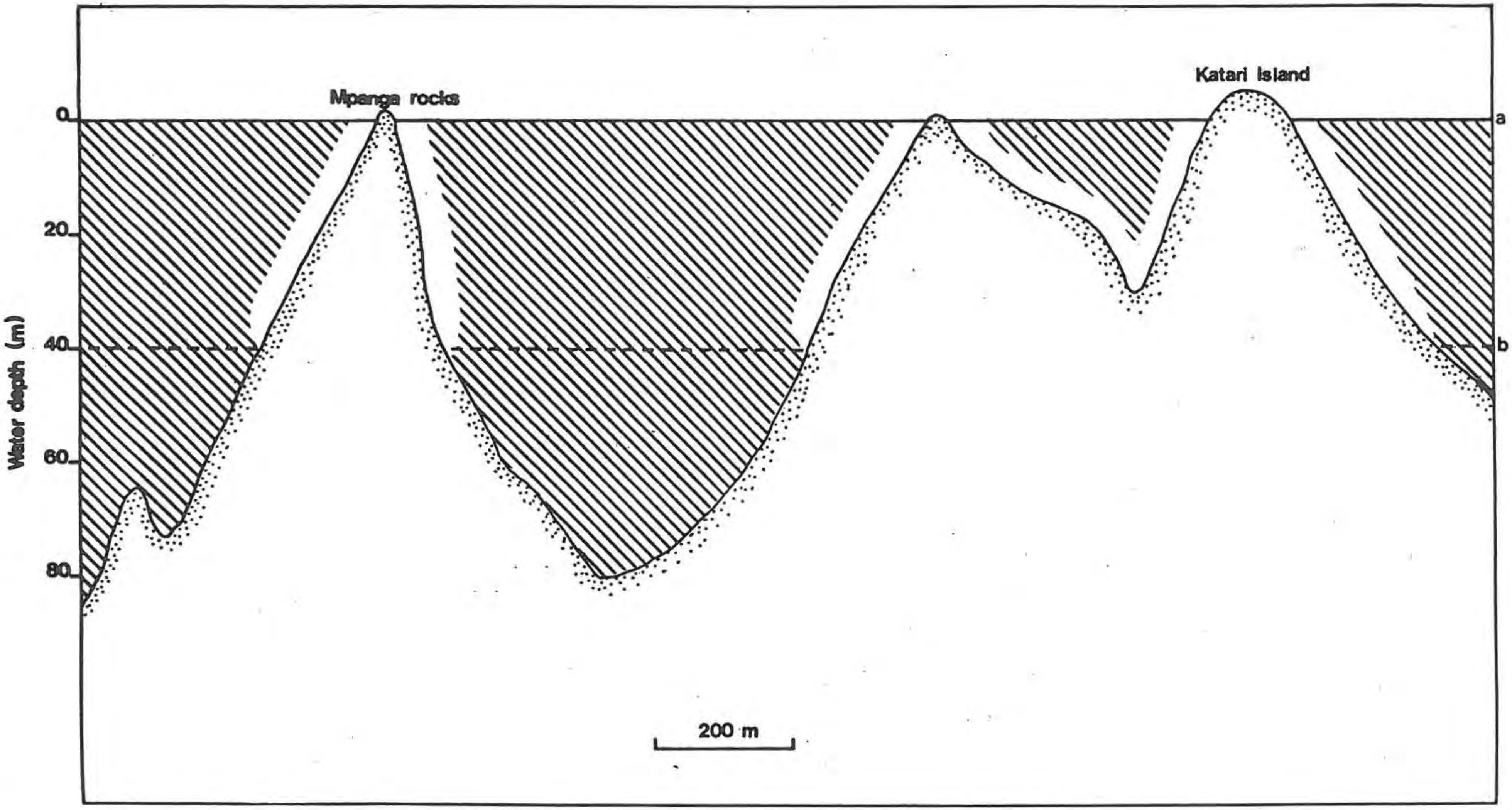

Figure 59. Bottom profile of a section of Lake Malawi near Chilumba. Unhatched areas represent zone to which *Petrotilapia* species are restricted at the present lake level (a). The theoretical lake level which would permit free movement of *Petrotilapia* species between Katari Island and Mpanga Rocks is indicated (b).

do occasionally migrate over sand. In July 1978 an artificial reef comprising small boulders and bricks was laid in four meters of water on a sandy substrate at Zambo near Monkey Bay (Figure 54). The reef is situated approximately 350 m from the nearest rocky shore. During the first year the reef was censused on a monthly basis and thereafter once every three to four months until October 1980. After eleven months a sub-adult male *P. tridentiger* colonized the reef followed three months later by a sub-adult male *P. genalutea*. These fish became territorial at a relatively small size (approximately 100 mm SL) and were still on the reef at the last census in October 1980. In September 1980 another *P. tridentiger* individual, a juvenile of approximately 60 mm TL, also settled on the reef. No other rock-frequenting Mbuna had colonized the reef by October 1980.

In July 1978, K.R. McKaye built a number of concrete block reefs at depths of 5 m and 10 m on a sandy bottom near Otter Point (Figure 21b). These reefs are at least one kilometer from the nearest rocky shore. In July 1979, one non-territorial male *P. nigra* and three juvenile *P. nigra* were seen on a reef in 10 m of water. *Petrotilapia* species have also been seen over sand between these reefs and Otter Point (K.R. McKaye, pers. comm.). Thus *Petrotilapia* species do migrate over sand and gene flow between populations is not necessarily prevented by sandy stretches. Nevertheless gene flow is probably retarded in proportion to the length of sandy shore separating two populations of *Petrotilapia* species.

From the foregoing it appears as if depth of water is a more effective barrier to gene flow than a sandy substrate. If the present distribution and abundance of Petrotilapia species is the result of speciation in allopatry then it is necessary that the two geographical barriers (depth and sand) can form, disappear and re-form. This could be achieved through fluctuations in lake level. There is evidence that the depth of Lake Malawi has fluctuated considerably during the past two million years. There are, for example, raised beaches more than 100 m above the present lake level (Crowley *et al.*, 1964). Fryer (1959) reports that there is evidence that at some stage the sandy beaches in the Nkhotakota district were under approximately 50 m of water and that the region was probably more rocky than it is at present. Although no quantitative evidence is provided, Beadle (1974) suggests that considerable fluctuations in lake level could have occurred during the pluvial and interpluvial periods.

Environmental differences

One of the requirements of the theory of speciation in allopatry is that a sub-population must be isolated in an environment which differs from that of the mother population. Most rocky shores in Lake Malawi differ from one another in terms of rock size, depth of rocky shore, exposure to currents and degree of sedimentation. The biotic environment also varies considerably with locality. For example, the Ornamental Fish Project survey has shown that the species composition of rocky shore fish communities differs from site to site. Thus there are likely to be biotic and abiotic differences between most rocky shore sites in Lake Malawi.

Time for speciation

To explain the extant species of Petrotilapia on the basis of speciation in allopatry, populations must have been isolated from one another for a sufficient period for speciation to have occurred. Greenwood (1965) has shown that as little as 3 500 years is required for cichlid speciation to occur in allopatry. Unfortunately very little is known about how long the water has remained at different levels in Lake Malawi, but it is conceivable that in two million years there may have been numerous occasions when the lake level remained fairly constant for periods in excess of 4 000 years.

Ecological compatibility

It has been suggested for tropical animals in general (Mayr 1963) and for African lake cichlids in particular (Lowe-McConnell, 1969) that one of the reasons for high species diversity in these situations is the year round availability of food. Such conditions permit extreme morphological specializations and therefore fine subdivisions of resources resulting in small feeding niches. This theory is relevant to Lake Malawi where the cichlid fish have undergone adaptive radiation to the extent that virtually every niche is occupied by at least one species (Fryer & Iles, 1972).

Speciation is not always accompanied by adaptive radiation and Greenwood (1965, 1974) mentions several examples in Lakes Victoria and Nabugabo where species multiplication has occurred within trophic groups without any noticeable adaptive changes in feeding structure or habits. Similarly, within the genus Petrotilapia, speciation has not been accompanied by marked morphological adaptive radiation. Of the seventeen species of Petrotilapia, only one, the 'Retrognathous' form, has any obvious morphological feature which distinguishes it from other species of Petrotilapia. Even this difference, a slightly protruding upper jaw, is fairly subtle and does not appear to have any adaptive function. The persistence of so many sibling species of Petrotilapia in Lake Malawi is not therefore related to any adaptive differences in trophic apparatus.

The results in Chapter 8 indicate that the coexistence of Petrotilapia sibling species is related to differences in behaviour. Coexistence is partially facilitated by partitioning feeding space. Feeding space partitioning is probably determined in part by species preferences but is also influenced by the social dominance hierarchies which exist in Mbuna communities. The elaborate social behaviour of cichlids is therefore an important factor, not only assisting the process of species formation as Fryer & Iles (1972) stress, but also permitting species coexistence.

In addition to fine resource segregation,one of the keys to species diversity is the ability of many Mbuna, including Petrotilapia species, to switch from their staple food to abundant but transient foods despite their elaborate trophic specializations (McKaye & Marsh, in prep.). Similarly Greenwood (1974) has shown that many species of Haplochromis in Lake Victoria are facultative and opportunistic feeders. Greenwood (1974) believes that this flexibility in feeding could have had important survival value in isolated populations during the lake's genesis.

Nature of species

Dobzhansky (1951) considers a species to be an adaptive device which is a direct consequence of natural selection, whereas Mayr (1942) and Paterson (1978, 1980) consider the species to be an incidental consequence of natural selection. The evolution of colour differences in cichlid species favours Mayr's idea of the nature of species. Greenwood (1965, 1974) has stressed the ease with which colour can apparently diverge in isolated populations of cichlids. For example, in Lake Nabugabo, which was isolated from Lake Victoria approximately 3 500 years ago, five of the six Haplochromis species are endemic and although they differ strikingly from their sister species in Lake Victoria in terms of male breeding livery, they show only slight anatomical differences (Greenwood, 1965). Greenwood (1974) suggests that colour divergence is likely to accompany any reorganization of the genotype. Change in colour is therefore not necessarily adaptive and may be due to pleiotropy i.e. a gene having multiple phenotypic expressions. If Greenwood (1974) is correct, then colour divergence is an incidental consequence of isolation. Earlier (in Chapters 3, 4 & 5) it has been argued that colour is the most important component of the specific mate recognition system (SMRS) in the genus Petrotilapia. As it is differences in the SMRS which distinguish one species from another, it can be argued that if colour changes and therefore SMRS changes are incidental consequences of isolation, then so too is species formation an incidental consequence of isolation.

Conclusion

Although there is inferential evidence supporting speciation in allopatry in the genus Petrotilapia it would be naive to be too dogmatic about the mode of speciation. The possibility that sympatric speciation and speciation by reinforcement have occurred within Lake Malawi and within the genus Petrotilapia does exist and in the absence of explicit evidence these two theories cannot be rejected. However it is not necessary to invoke sympatric speciation or speciation by reinforcement as a less controversial mode of speciation, namely speciation in allopatry, can adequately account for the extant species of *Petrotilapia*.

CHAPTER 10

CONCLUDING REMARKS AND RECOMMENDATIONS FOR FURTHER RESEARCH

In view of the phenomenal diversity within the Cichlidae of the Great Lakes of Africa, it is not surprising that most of the work that has been published on these fishes has either been of a taxonomic nature or speculation as to why there are so many species in these lakes (Greenwood, 1974). With the growing need to find sufficient protein to sustain the human population in East and Central Africa and the development of an ornamental fish trade in this area, interest in the cichlid species is no longer of academic interest only. A deeper understanding of the biology of these fishes is essential to ensure that there is a balance between their conservation and exploitation.

In this section the contribution that this study makes towards a better understanding of cichlid biology is briefly reviewed, limitations of the work are stressed and suggestions for future research are made. The major difference between this study on the genus Petrotilapia, and almost all previous published studies dealing with the diversity of Great Lake cichlids, is that the present research consists mainly of a field study with observations being made in situ in Lake Malawi as opposed to laboratory orientated studies on preserved specimens.* For example the work of Greenwood, who is responsible for most of the systematic work on Lake Victoria cichlids, has been largely confined to laboratory work.

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* A notable exception is the field study of Holzberg (1978) on the Pseudotropheus zebra species complex.

Similarly the work of Fryer (1959), which was the first and until recently the only study of cichlid community ecology, was predominantly based on preserved specimens. It should be noted that Fryer was the first research worker to use an underwater mask for making field observations in Lake Malawi but he was restricted to making observations from the surface of the water.

The use of SCUBA and diving suits in the present work has meant that extensive observations were made to a depth of 35 m on the fishes in their natural habitat. Consequently the cichlids were seen with a new perspective, and biological and ecological information were obtained directly rather than inferentially. For example, the importance of plankton feeding to certain *Petrotilapia* forms was established through field observations on feeding behaviour, whereas the inferential method of stomach content analysis did not give such conclusive results. Detailed field observations have also resulted in an accurate description of each species' niche. These observations have permitted the detection of resource partitioning, particularly in the space dimension. Thus one of the enigmatic aspects of Mbuna ecology, namely the coexistence of sympatric loose afuwuchs feeders *sensu* Fryer (1959), can now be attributed to a partitioning of feeding space as well as to food switching behaviour.

The use of SCUBA has also facilitated an analysis and documentation of some of the complex interspecific interactions which occur within Mbuna communities. For example, the territorial behaviour of certain *Pseudotropheus* species creates feeding niches for certain forms of *Petrotilapia*. Such complex interactions need to be taken into account when formulating strategies for the conservation and exploitation of the

Mbuna. Cognisance needs to be taken that every species of Mbuna is a member of a complex community in which many species are interdependent. Thus heavy exploitation of '<u>Pseudotropheus</u> aggressive' at Monkey Bay could effectively reduce the availability of the main feeding niche of <u>P. tridentiger</u> territorial males. These males, by virtue of their position in the social dominance hierarchy of the community, would probably adjust to this change by displacing some other species from its feeding niche. This sort of reaction could continue down through the hierarchy with as yet unknown effects on community structure.

It is important at this stage to emphasize a limitation of the present ecological study. On the rocky shores at Monkey Bay there are over twenty species of cichlid forming a comparatively simple community (by Lake Malawi standards). In this study only five of these species have been investigated. Therefore, although the results on the importance of competition and resource partitioning to species coexistence are valid, and interspecific relationships are probably considerably more complex than indicated.

The zoogeographical information in this thesis emphasizes an aspect of Mbuna biology which is relevant to conservation and exploitation. Many of the Mbuna have very limited distributions and these species are particularly vulnerable to overexploitation. In formulating management strategies it is important to differentiate between species with extremely limited distributions and consequently small population sizes, and those with wider distributions. For example <u>P. tridentiger</u>, a species with a lakewide distribution, could withstand considerably higher commercial exploitation than the 'Gold' form <u>Petrotilapia</u> which is restricted to the small islands of Cinyankwasi and Cinyamwezi.

In this thesis the traditional taxonomic approach to species definition is shown to be inadequate when dealing with the Petrotilapia species complex. Results obtained during the lakewide Ornamental Fish Project survey indicate that the taxonomic complexity of the genus Petrotilapia is not exceptional. It appears that many nominal Mbuna species comprise numerous distinct colour forms. For example, there are five distinct male and female colour forms of Pseudotropheus tropheops sensu Regan at the island of Thumbi West, and at Nkhata Bay there are six distinct male and female colour forms of P. tropheops sensu Regan. Similarly there are four distinct male and female colour forms of Pseudotropheus zebra at the Marelli Islands. From these few examples it is apparent that the phenomenon of sibling species complexes may be widespread amongst the Mbuna. Furthermore, sibling species are known to occur within the genus Sarotherodon (Lowe, 1952) and within the genus Lethrinops (Eccles & Lewis, 1977). Similarly Greenwood (1974) reports the occurrence of several species clusters in Lake Victoria. The members of each group differ mainly from one another in terms of male breeding livery. There is no doubt that the resolution of the taxonomic problems that these colour forms and sibling species complexes pose requires an integrative approach, in which biological information is of considerable importance. The present work represents such an integrative approach to the systematics of the genus Petrotilapia. Behavioural, ecological, physiological and morphological data have been used to determine the taxonomic status of the Petrotilapia forms.

This type of integrative approach is limited mainly to the resolution of sympatric species-complex problems. The recognition of species in allopatric populations is less conclusive and relies on inferential evidence. Further research on the specific mate recognition system (SMRS) of the Mbuna in general and Petrotilapia species in particular would constitute an important sequel to the work presented here. In Chapter 3 it was argued that a knowledge of the important components of a species' SMRS would enable allopatric affinities to be determined. SMRS studies, therefore, offer a solution to one of the major systematic problems in the Mbuna. The following lines of research would be useful:

i) Determination of the relative importance of colour and movement to mate recognition. All Mbuna have the same basic courtship repertoires but differences in the frequency of execution of certain displays may be important in mate recognition. Information could be obtained, relatively easily, in the field or laboratory, by filming the courtship procedure.

ii) Determination of the relative importance of coloration of different parts of the body in the SMRS. For example P. tridentiger is very similar to the 'Mumbo Blue' form. The major difference concerns dorsal fin markings. Comparisons of the response of P. tridentiger males to P. tridentiger females and 'Mumbo Blue' females could give an indication of the importance of dorsal fin markings to the SMRS. Choice chambers could be used for these experiments.

iii) Cichlids are capable of sound production (Myrberg et al., 1965; Rodman, 1966) and differences in sound could be important in mate recognition. Hydrophones placed in an aquarium or field situation could be used to obtain comparative data on sound production.

iv) Numerous experiments have indicated that cichlids can communicate their species identity chemically (Noble & Curtis, 1939; Myrberg, 1975; Barnett, 1977). There may therefore be a chemical component to the SMRS and this aspect should be investigated.

An extensive, rather than intensive, approach has been adopted in the present work, partly because relatively little is known about the cichlids of Lake Malawi and partly because the phenomenon of species diversity is multi-faceted. Although a broad perspective of species diversity in Petrotilapia has been gained by this study, much remains to be learned about species definition, speciation, and community structure and function within the genus. The present study does, however, identify specific problems and provides a framework upon which further research may be profitably structured.

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