

ECO-ETHOLOGY OF SHELL-DWELLING CICHLIDS IN LAKE TANGANYIKA

THESIS

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Requirements for the Degree of
MASTER OF SCIENCE
of Rhodes University

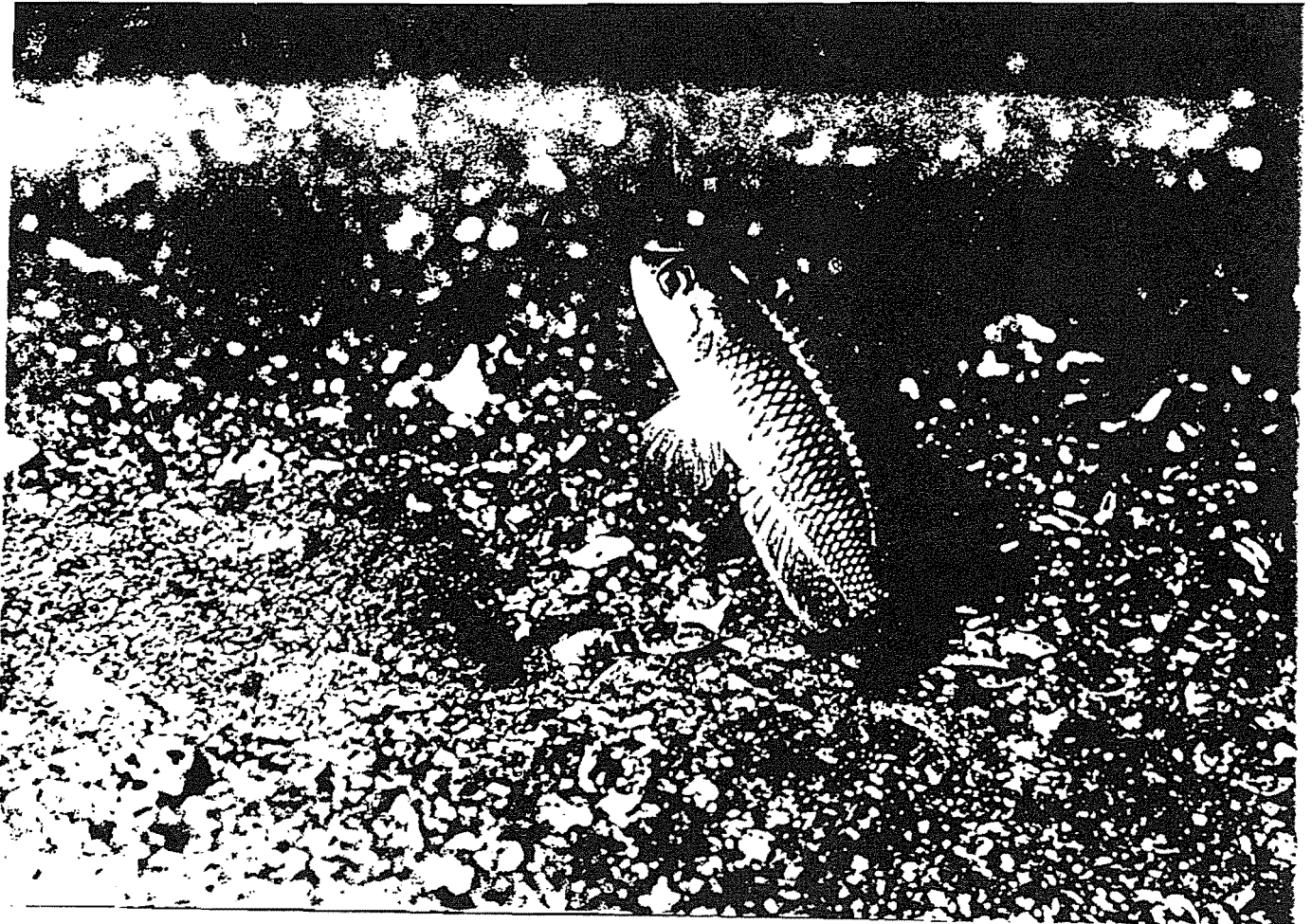
by

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'The more we get to know about the two greatest of the African Rift Valley Lakes, Tanganyika and Malawi, the more interesting and exciting they become.'

L.C. Beadle (1974).



A male *Lamprologus ocellatus* displaying at a heterospecific intruder.

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ABSTRACT

Observations of habitats are reported. A series of underwater experiments were conducted in natural habitats to answer questions concerning a) why *Lamprologus ocellatus* and *Lamprologus ornatipinnis* bury gastropod shells refuges into the substrate, and b) to examine interspecies differences in shell-using behaviours. Some behaviour patterns were analysed using phylogenetic methods.

Lamprologus ocellatus and *L. ornatipinnis* responded to new shells in a variety of ways, shells were moved, buried (and used) or hidden (buried and not used). How shells are utilised seems to be dependant on a complex of factors such as the size and quality of new the shell and the number already in the territory. Shell use may also be affected by neighbour species, sex, size and predation levels. There are interspecific differences in the size of shells used and the methods of shell use. The latter results in species-characteristic shell orientations, vertical burial in *L. ocellatus* and horizontal burial in *L. ornatipinnis*. Shell orientation does affect other species' use of shells. Shell movement and vertical orientation appear to be apomorphic while shell while shell hiding and burial are plesiomorphic within the genus *Lamprologus*.

Numerous cues are involved in stimulating shell burial. Most of these cues are actively sought by the fish by external and internal inspections. Shell burial therefore appears to be a method of reducing the information gathering ability of potential shell-dwelling competitors. Shell burial can therefore be regarded as an investment process which enhances the residents ability to defend its territory. Males can also control the distribution of open shells within territories and thus control mate access to shells. This behaviour could be a significant factor in the evolution of marked sexual dichromatism exhibited within the genus.

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CHAPTER 1

INTRODUCTION

Shell-dwelling fishes are uncommon and unusual components of marine and freshwater communities. The shell-dwelling cichlids of Lake Tanganyika represent the best known example of shell-dwelling fishes in the world. Over 25 species of fish use shells as refuges from predators and as breeding substrates. These species exhibit a considerable range of behaviours from those which use shells as occasional refuges to those which are found exclusively using shells as both breeding substrates and refuges for their entire lives. Shell-dwellers are unusual and therefore of particular interest because they manipulate shell resources and modify their environment. Shells may be excavated, moved and buried into the substrate. Many of the shell-dwelling fishes exhibit unique, species specific behaviour patterns relating to shell use (Paulo 1986).

Lakes Malawi and Tanganyika are famous for their diversity of rock-dwelling cichlid fish (Fryer & Iles 1972, Ribbink et al. 1983, Coulter 1991, and others). Estimates of species numbers vary but these fishes probably comprise over 300 hundred species in Lake Malawi and over 150 species in Lake Tanganyika. However, the extent of rocky habitats within both lakes is small (Ribbink et al. 1983, Coulter 1991). In Lake Tanganyika rocks are usually confined to a thin, fragmented strip extending from the lake shores to around 20-30m depth and often less than 100m offshore (Coenen et al. 1993). Rocky patches and strips do occur below 30m but most have become inundated by gravel, sand and mud. Thus the vast majority of oxygenated substrate in both lakes is comprised of soft substrates. Whilst some of the physical aspects of soft substrates in Lake Tanganyika have been described by Beadle (1981), Cohen and Thouin (1987), Tiercelin and Mondeguer (1991), and Coulter (1991), biological communities have received little attention.

Lake Tanganyika stands out from the other African lakes in several physical and biological respects.

- a) Estimated at 20 million years old it is the oldest African lake (Tiercelin & Mondeguer, 1991).
- b) Several non-cichlid species flocks occur: mastecembelid eels, centropomids, mochokid and

bagrid catfishes (Poll 1953); molluscs (Leloup, 1953); decapods (Calman 1928, Bott 1955); and ostracods (Martens 1984).

c) The water of Lake Tanganyika has a high conductivity (610 mohms) and pH (8.0-9.0) for a freshwater lake (Beadle 1981).

d) Many of the endemic molluscs are thick shelled (termed thalassoid). This is thought to be due to co-evolution with mollusc eating crabs (West et al. 1991).

One of the characteristic features of Lake Tanganyika's southern basin benthic habitats is the presence of numerous dead mollusc shells (Coulter 1991, Sato 1989a). These shells, dominated by the gastropod *Neothauma tanganyicense*, litter the surface sediments (Figures 1.1 to 1.5). Partly due to mollusc shell thickness and partly to the high pH of the water, shells remain intact and as surface features for hundreds of years (Cohen 1989). The presence of gastropod shells has resulted in increased habitat complexity for fish and invertebrates by increasing surfaces and crevices. Shells have become colonized by a variety of animals particularly small substrate spawning cichlids of the tribe Lamprologini (Poll 1985, subsequently referred to as lamprologines). Whilst the majority of lamprologines are confined to rocky areas, a small group is adapted to using gastropod shells as refuges in soft substrate habitats. These fish live and breed around dead gastropod shells. Distinct communities of shell-dwellers are associated with rocky slopes with scattered shells (Figure 1.2); gravel-sand habitats with scattered shells (Figure 1.3); compacted gravel bottoms with complete shell cover (shell beds, Figure 1.4); and mud substrates with few shells (Figure 1.5).

SHELL-DWELLERS

In Lake Tanganyika

The shell-dwellers are dominated by *Lamprologus* (9) and *Neolamprologus* (9) species (Table 1.1). There are single species from the genera *Lepidolamprologus* and *Altolamprologus* and two species of *Telmatochromis*. Several bagrid catfishes e.g. *Phyllonemus typus*, *Chrysichthys* spp. use shells as juveniles. It is likely that, with further systematic research, the taxonomy of the lamprologine cichlids will change and some species will be ascribed to new and/or different genera. As could be expected

Family Cichlidae

Tribe Lamprologini

Genus *Altalamprologus* Poll 1985

Altalamprologus sp.

Genus *Lamprologus* Schilthuis 1891

L. lemairii Boulenger 1899 *L. callipterus* Boulenger 1906

L. ocellatus Steindachner 1909 *L. ornatipinnis* Poll 1949

L. signatus Poll 1952 *L. kungweensis* Poll 1956

L. meleagris Büscher 1991 *L. speciosus* Büscher 1991

Lamprologus n. sp.

Genus *Lepidolamprologus* Pellegrin 1903

L. attenuatus (Steindachner) 1909

Genus *Neolamprologus* Colombe & Allgayer 1985

N. hecqui (Boulenger) 1899 *N. brevis* (Boulenger) 1899

N. tetracanthus (Boulenger) 1899 *N. calliurus* (Boulenger) 1906

N. multifasciatus (Boulenger) 1906 *N. meeli* (Poll) 1948

N. boulengeri (Steindachner) 1909 *N. similis* Büscher 1992

N. pleuromaculatus (Trewavas & Poll) 1952

Genus *Telmatochromis* Boulenger 1898

T. vittatus Boulenger 1898

T. burgeoni Poll 1942

Family Bagridae

Genus *Phyllonemus* Boulenger 1906

P. typus Boulenger 1906

Genus *Chrysichthys* Bleeker 1858

Chrysichthys spp.



Figure 1.1 Shallow water shell deposits (less than 1m depth) on sand substrate in Chituta Bay, Zambia.

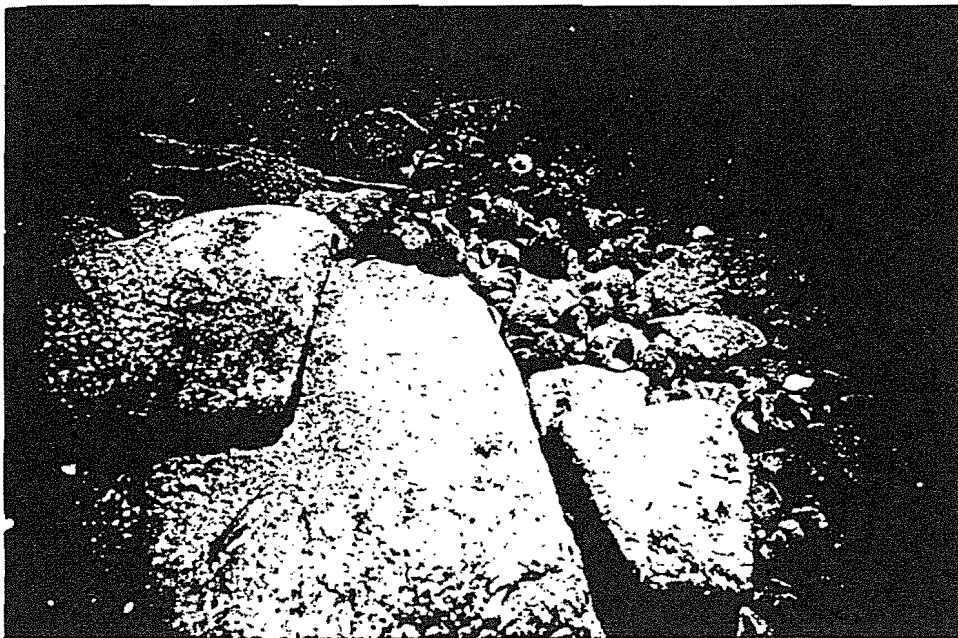


Figure 1.2 Shell deposits on rocky slopes of Mbita Island (20m depth), Zambia.

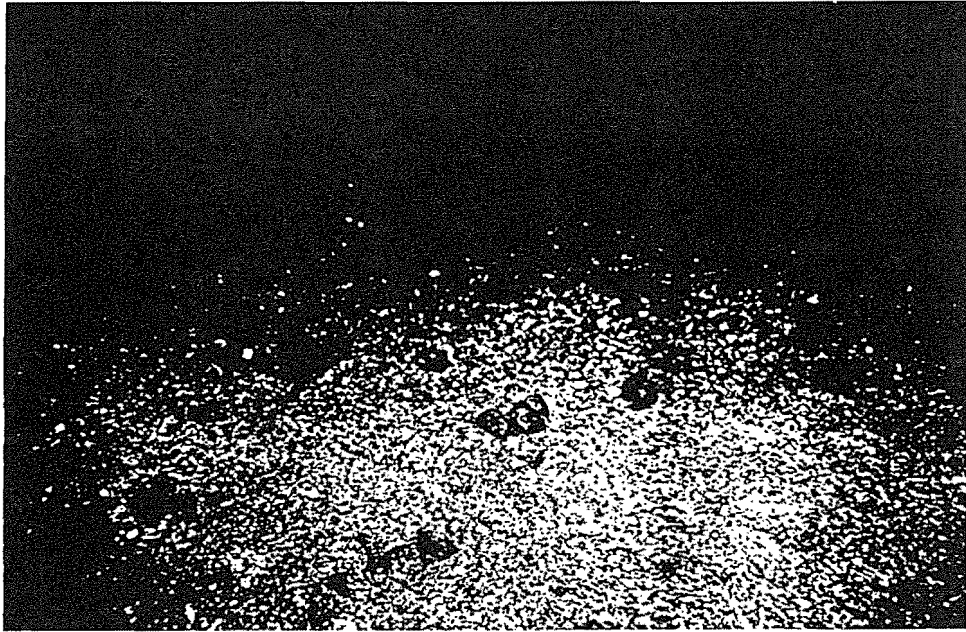


Figure 1.3 Scattered shell deposits on sublittoral gravel-sand slopes of Mbita Island (20m depth), Zambia.

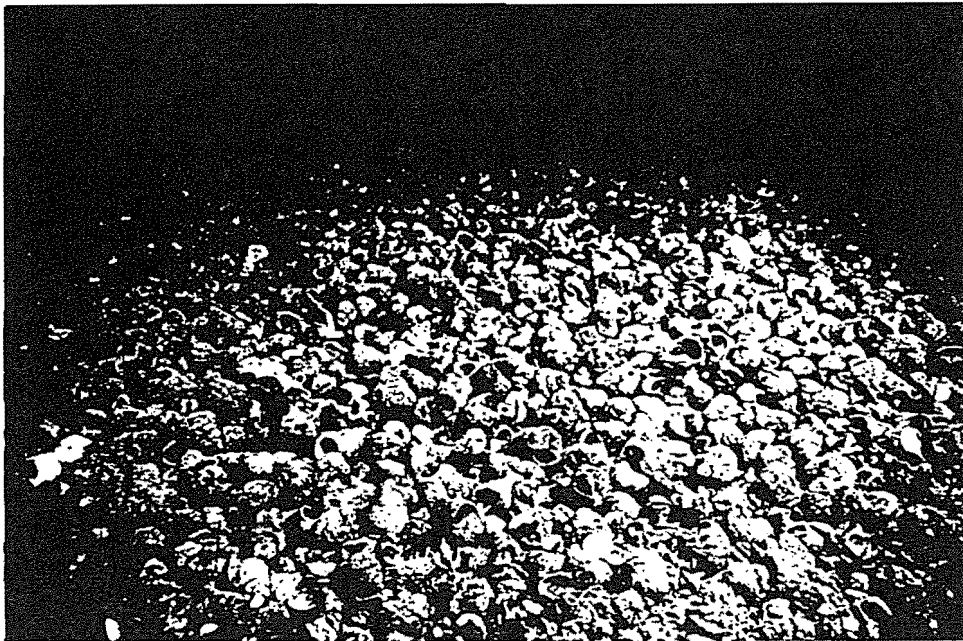


Figure 1.4 Shell beds near Onzye point (10m depth) near Mpulungu, Zambia.

behaviour. Certain species use shells as temporary refuges, e.g. juveniles of *Lamprologus lemairii* (Figure 1.6) and *Phyllonemus typus* (Figure 2.18). Others use shells only as breeding substrates e.g. *L. attenuatus* (Figure 1.7). The species with the most apomorphic shell using behaviour patterns are associated with shells for their entire life and use shells as refugia and as nest sites, such as *L. ocellatus* and *L. ornatipinnis* (Figures 1.8 & 1.9 respectively).

Some species will use other substrates or refugia if shells are not present, e.g. *N. multifasciatus*. Others are exclusively associated with shells for a portion of their lives, e.g. *L. ocellatus*. These species were termed facultative and obligate shell-dwellers respectively by Sato (1989a).

In Lake Malawi

The shell-dwellers of Lake Malawi are less common and less diverse than in Lake Tanganyika. This may be due to three factors:

- a) gastropod refuges are less abundant in Lake Malawi;
- b) the cichlid fauna is comprised entirely of mouth-brooding species; and
- c) the relative youth of Lake Malawi.

Presently two cichlids, *Pseudotropheus elegans* and *P. lanisticola*, are known to use gastropod shells (*Lanistes nyassanus*) as refuges (Burgess 1976, Konings 1988). There is also an undescribed amphiliid catfish (*Leptoglanis* sp.) which cohabits with the *P. lanisticola* (Burgess 1976, Eccles pers. comm.). Shells are used only as refuges by adults and juveniles (Konings 1988). As these species are mouth-brooders shells are not used as nest sites as in the Tanganyikan lamprologines. However, Konings (1988) speculates that the release of fry, five days earlier into shells by *P. lanisticola* may be an adaptation to shell use. Except for this and their small adult size, *Pseudotropheus* appear to exhibit few specialisations for using shells. Shell selection behaviour has not been investigated.

In marine habitats

In the marine environment dead gastropod shells accumulate in large numbers in intertidal habitats. This is quite different from the sublittoral regions of Lake Tanganyika. Intertidal zones are usually wave

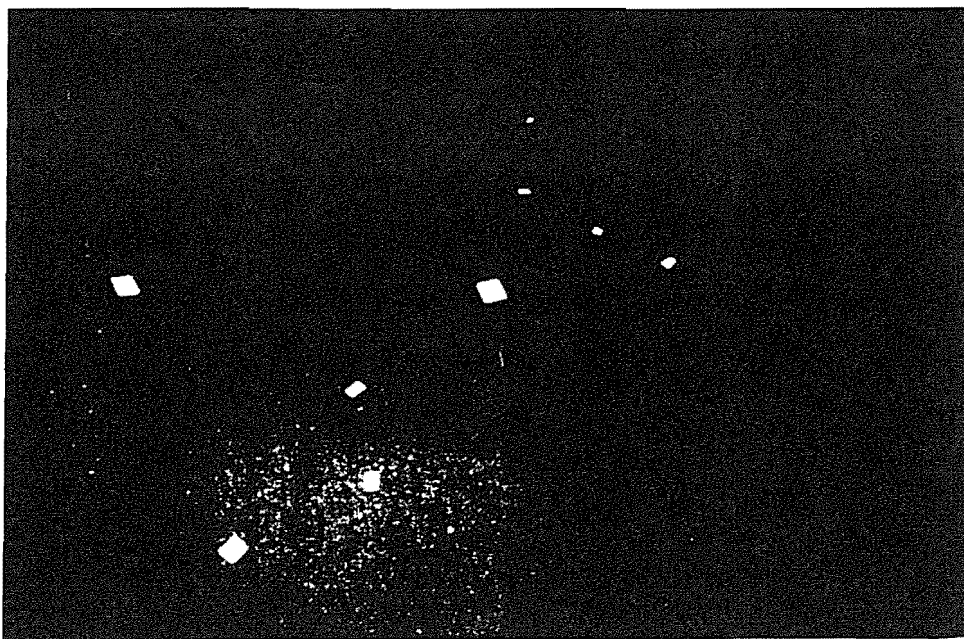


Figure 1.5 Mud substrate with low surface shell deposits (20m depth) at Mbita Island, Zambia. White markers indicate the location of holes excavated by *Lamprologus laparogramma*.



Figure 1.6 *Lamprologus lemairii* juveniles using a *Neothauma tanganyicense* shell for refuge.

boring or crushing methods. The result of these biological and physical activities is that intact dead gastropod shells are relatively short-lived and in limiting supply. Consequently, competition for them as refugia and breeding sites between shell-dwelling organisms is intense.

The marine shell-dwellers are dominated by hermit crabs (reviewed by Reese 1969) with hundreds of species occurring worldwide in tropical and temperate regions. Species of octopus (Hartwick et al. 1978, Mather 1982a & b) and fish (Breder 1950, McLean 1983) also exist but these are less common. A variety of gastropod species are used both as refuges from predators, and as nest sites.

Hermit crabs have attracted attention from scientists as they exhibit a variety of derived and complex behaviour patterns related to shell use. Due to their small size they are easily kept in captivity, which has facilitated investigations. Shell-using behaviour may be observed by providing crabs with new shells and fights may be staged to compare competitive abilities. What is particularly interesting about hermit crabs is that they assess shell size and quality prior to using shells. This process can be observed in the laboratory (Elwood & Neil 1992) and appears similar in many respects to the assessment process in some lamprologine cichlids (Konings 1988, Hausknecht & Kuenzer 1990).

SOFT SUBSTRATE SHELL-DWELLERS

In Lake Tanganyika the shell-dwelling community in soft substrate habitats is the most diverse. Up to seven species are present at some sites in Zambia. Several of these species, such as *L. ocellatus* and *L. ornatipinnis*, bury their shells in the substrate (Konings 1988). This behaviour comprises an assessment or inspection phase, a digging-in phase, and a final covering-over phase (Hausknecht & Kuenzer 1990). This behaviour pattern appears more complex than in hermit crabs. Fish, having determined the value of a shell, must then spend 1-2 hours burying the shell rather than simply occupying or rejecting it. In addition, there are interspecific differences in methods of shell burial (Paulo 1986).

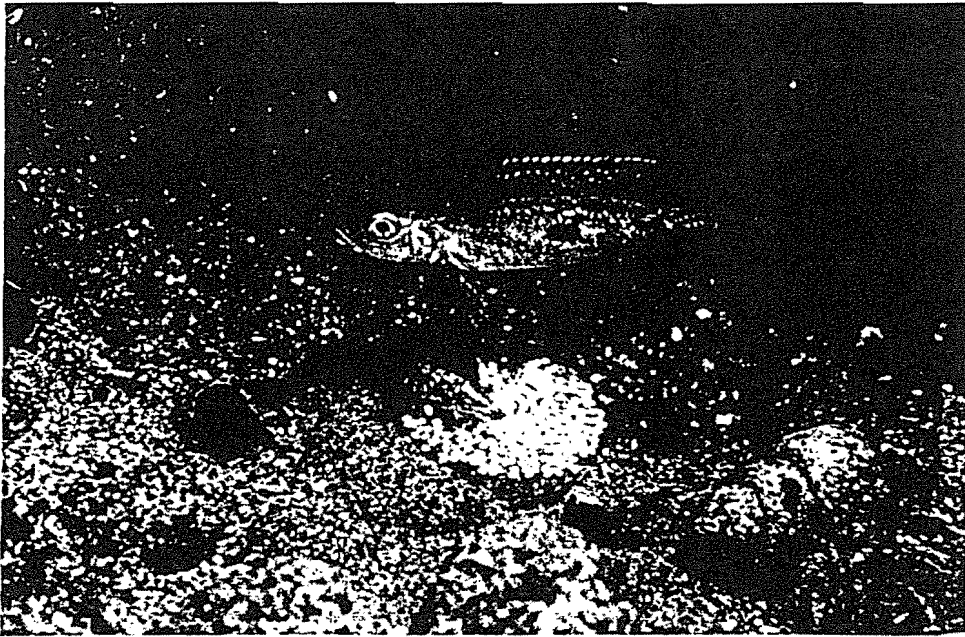


Figure 1.7 A female *Lepidolamprologus attenuatus* with eggs laid on the outside of a *Neothauma tanganyicense* shell. The juveniles will use the interior of the shell during the parental care period.

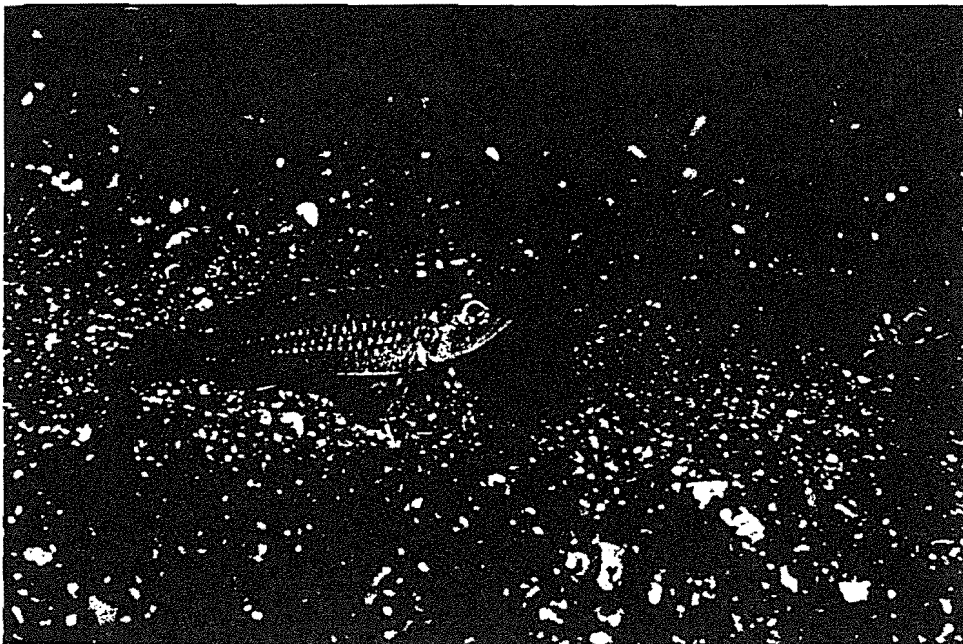


Figure 1.8 *Lamprologus ocellatus* male and female at the males' principal refuge shell.

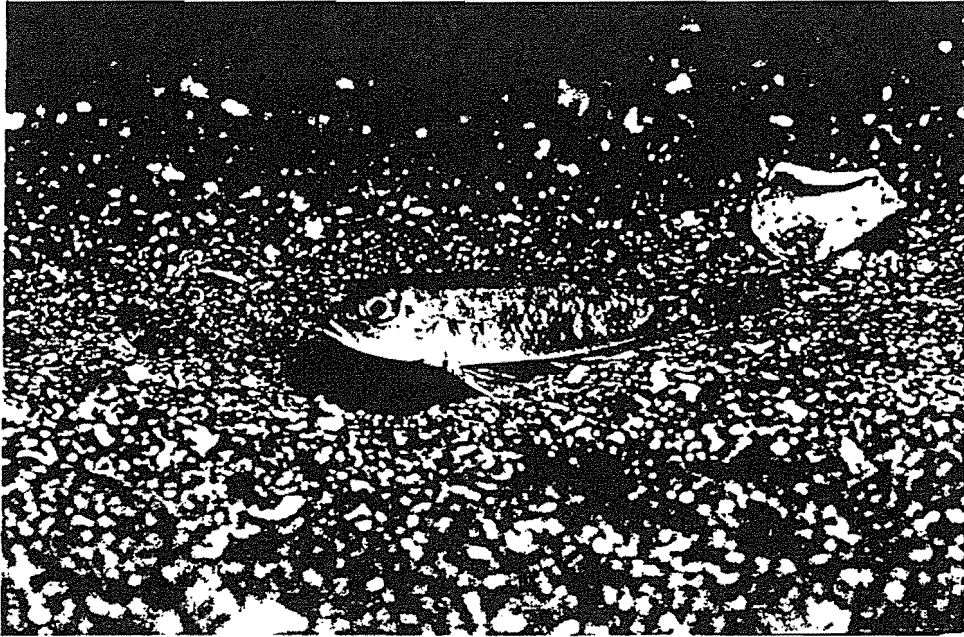


Figure 1.9 A male *Lamprologus ornatipinnis* at its principal refuge shell.



Figure 1.10 A male *Neolamprologus hecqui*.

DIAGNOSES OF THE SHELL DWELLERS STUDIED

Lamprologus ocellatus (voucher specimens: RUSI 38879). D XVI-XVIII, 6-8; A VII-VIII, 6-7.

Lateral line scales 25-30. Sexually dimorphic with male mean SL 38.8mm (n=30, SD=2.8) and female mean SL 24.9mm (n=30, SD=3.6). Slight sexual dichromatism, with females having more white pigmentation on the posterior sections of the dorsal and anal fins, otherwise females are similar to males. This species can be distinguished from the other shell-dwellers by a prominent opercular ocellus, rounded pelvic fins and purple iridescent sheen over the flank (Figure 1.8).

Lamprologus ornatipinnis (voucher specimens: RUSI 38822). D XV-XVIII, 7-9; A V-VIII, 6-8.

Lateral line scales 32-36. Sexually dimorphic with male mean SL 47.5mm (n=30, SD=2.0) and female mean SL 32.8mm (n=30, SD=1.7). Some sexual dichromatism with females having yellowish abdomens, darker flanks and a more pronounced iridescent sheen over the body. This species can be distinguished from the other species by the absence of opercular ocelli, rounded pelvic fins and a green-coloured interorbital region (Figure 1.9).

Lamprologus laparogramma (voucher specimens: RUSI 38780). D VIV-XV, 8-10; A V-VI, 6-7.

Lateral line scales 32-34. Sexually dimorphic with male mean SL 43.9mm (n=12, SD=2.8) and female mean SL 34.1mm (n=12, SD=1.2). Sexually dichromatic with males having up to eight vertical, braided bars on the posterior flank and females having a more brightly-coloured yellow belly. This species can be distinguished from the other three species by 6-8 vertical black lines on the belly, rounded pelvic fins, no opercular ocellus and a blue interorbital region (Figure 2.17).

Neolamprologus hecqui (voucher specimens: RUSI 38875-6). D XVIII-XIX, 8-10; A VI-VII, 6-8.

Lateral line scales 45-55. Sexually dimorphic with males larger than females. This species is sexually monochromatic, and so sexes were not separated during field experiments or during observations. This species can be distinguished from the other three species by its opercular spot, its pointed pelvic fins, and black dorsal fin lappets (Figure 2.9).

OBJECTIVES OF THIS STUDY

The two species of shell-dwelling cichlid which form the basis of this study are *L. ocellatus* and *L. ornatipinnis*. Both are associated with gastropod shells for their entire life histories and show highly derived behaviour patterns relating to the use of gastropod shells. They occur syntopically and there appears to be interspecific competition for shell resources and differences in certain behaviour patterns between the two species. Previous studies of shell-dwellers (Hausknecht & Kuenzer 1990, Walter & Trillmich 1994) have examined single species in aquaria and have not considered interspecies interactions. In this study I had the opportunity to examine the two species in their natural habitats and compare the behavioural differences, aspects of their ecology and natural habitats. As these species and their habitats are very poorly known a considerable amount of effort was involved in descriptive work. The specific aims were as follows.

1. To describe habitats where *L. ocellatus* and *L. ornatipinnis* occur and where experiments were conducted (Chapter 2).
2. To investigate the purpose of shell-burying and associated behaviours using field experiments (Chapter 3).
3. To investigate differences in shell-burial behaviour between *L. ocellatus* and *L. ornatipinnis* (Chapter 4).
4. To study the development of these shell-using behaviour patterns within the genus *Lamprologus* by phylogenetic methods (Chapter 5).
5. Where relevant and feasible, species which occurred syntopically with *L. ocellatus* and *L. ornatipinnis* were also studied.
6. During this study one species was recognised as undescribed and two other species (*Lamprologus signatus* and *L. kungweensis*) as inadequately described. These were described and this work is placed in Appendix 1.

CHAPTER 2

FIELD OBSERVATIONS IN SOFT SUBSTRATE HABITATS OF LAKE TANGANYIKA.

INTRODUCTION

The objectives of this chapter are to describe the physical and biological aspects of the habitats in which field experiments were conducted.

The benthos of the Zambian sector of Lake Tanganyika is characterised by high numbers of shells of dead molluscs (Sato 1989a, Coulter 1990). Coulter (1990) described the 20-60m depth range as a 'shell zone'. The high pH of the lake waters (8.0-9.0, Beadle 1981) results in shells remaining on the substrate surface for hundreds of years before dissolving (Cohen 1989). These shells increase the structural and biological complexity of habitats by adding hard substrate surfaces which become colonised by various animals, plants and gastropods, and provide refuges for animals. A small group of substrate-spawning cichlid fish (lamprologines) use dead gastropod shells as refuges and or nesting sites.

Of the few studies concerning Tanganyikan shell-dwelling cichlids, most have been conducted in laboratories (Hausknecht & Kuenzer 1990, Paulo 1986, Walter & Trillmich 1994). This is partly because these fish are easily kept in aquaria and partly due to the inaccessible nature of Lake Tanganyika. However, Sato (1989a, b, c & 1994) does provide details of habitats and behaviour of *L. callipterus* and its associated nest 'parasites' in the lake. These species occur on rocks and at the rock boundary. Details of habitats of soft-substrate-dwelling species such as *L. ocellatus*, *L. ornatipinnis* and others have not been reported.

The soft substrate-dwelling species attracted my attention because they appeared to exhibit more complex behaviour patterns compared to species occurring in shell bed and rocky habitats. Shells were being buried, moved and hidden and there appeared to be inter-specific differences in behaviour patterns.

Field observations are of significance in ethology for two reasons.

1. Preliminary field observations identified behaviour patterns and enabled the posing of several questions. These questions formed the basis for a series of experiments which are tested in Chapters 3 and 4.

2. Knowledge of the physical and biological environments in which species live is essential for understanding their behaviour.

The interpretation of experimental results is therefore affected by one's understanding of natural habitats and the animals' behaviour patterns within these habitats (discussed in Chapters 3, 4, and 6). Two examples which illustrate this point are discussed by Haussknecht and Kuenzer (1990) and Walter and Trillmich (1994).

In Haussknecht and Kuenzer's (1990) study of shell-burying (they refer to this as shell-building) they consider that shell burial is related to the avoidance of predators. They support this assumption by the laboratory observation that even juveniles bury shells. However, in natural habitats juvenile *L. ocellatus* rarely bury shells. This also does not account for the several species of shell-dwellers which do not bury shells but which occur syntopically with *L. ocellatus*. They later state: 'in its natural environment minor repairs will often be required, whereas the complete building procedure is seldom necessary.' This is not correct as shells are regularly exhumed, new shells are deposited into territories and individuals acquire new territories. There appears to be a considerable flux of shells and territories.

In Walter and Trillmich's (1994) study of female-female aggression in *L. ocellatus* no natural observations were made. They considered this species a planktivore (Brichard 1989) and suggested that food resources are not defensible. They concluded that food resource depression is unlikely to be a factor in female-female aggression. However, Brichard (1989) states: 'It is a microfeeder on invertebrates like so many *Lamprologus* species.' My own observations indicate it feeds predominantly from benthic invertebrates and defends feeding territories.

Biological observations of the main species studied, such as social organisation, feeding behaviour and use of shells, are reported. Where feasible, data were collected for all the species which occurred in the different habitats. However, in many cases limited diving time restricted work to *L. ocellatus* and *L. ornatipinnis*.

OBSERVATIONS, DESCRIPTIONS OF STUDY SITES AND METHODS

Fish were observed and collected using SCUBA. Specimens were fixed in 10% formalin and preserved in 70% alcohol and deposited at the JLB Smith Institute of Ichthyology. Most of the invertebrates have been deposited at the Albany Museum, in the Central African Waters collection (CAW). Where relevant RUSI and CAW voucher numbers are given.

The fish community, at the main study site, during the day and night was recorded. Shell-dwelling fish abundance was measured with one meter wide transects which were set on the substrate using nylon ropes and metal pegs. Various transect lengths were used during the course of the study and fish and shell numbers were converted to fish and shells/m² values. Estimates of species abundance were made by swimming along the outside of the transects and recording (on plastic slates) fish and molluscs present within the transect lines.

Observations of the social structure, i.e. shell distributions within territories and male-female behaviour, of shell-dwellers were made and noted underwater.

Total numbers of shells and 'open' shells in *L. ocellatus* and *L. ornatipinnis* territories were recorded. No distinction was made between buried and unburied shells. Approximately 50 males and females of each species were observed from the Musende Rocks area (Figure 2.1). 'Open' shells are defined as being clear of sand and useable. 'Hidden' or 'closed' shells are those which have been filled in with sand and are, in this state, not usable.

The distances between open shells within territories were measured with a plastic tape. The reference point for all measures was the male's principal shell which was the shell at which the resident male was observed to spend most time. The following abbreviations are used:

the male's principal shell = ms1

the male's secondary shells = ms2, ms3, ms4

the principal shell of the closest female = f1s1

the principal shell of the second female = f2s1

any female principal shell to its secondary shell = fs1-fs2

the distance between the first and second female = f1-f2

The 'principal' and 'secondary' female titles are simply given to denote proximity to the male and do not imply status.

During the day-time, shell-dwelling fish were approached and their shell-using behaviour observed. Categories recorded were: 'enter principal shell', 'move to and enter secondary shell' and 'move away over substrate'. A few night dives were made.

Oviposition sites were determined by making collections of twenty five males and females of *L. ocellatus* and *L. ornatipinnis* together with their shells. Fish were bagged individually with their shells in plastic bags. At the surface shells were cracked open to determine the presence of eggs.

Limited feeding observations were conducted. Five individuals of *L. ocellatus*, *L. ornatipinnis*, *L. laparogramma* and *N. hecqui* were observed for periods of 5-10 minutes. The methods of feeding were noted.

Live molluscs and empty shells were collected for identification. Observations of shells used by shell-dwelling fish were made at all the sites. These collections were sent to the University of Arizona (Tucson), The British Natural History Museum (London) and The Albany Museum (Grahamstown).

Shell occupancy levels were investigated. Shells with and without fish occupants were collected and individually bagged underwater at the site of collection. At the surface, shells and their occupants were either preserved in 10% formalin or the shells were immediately broken open and the occupants preserved. The size of shells (height and width), fish (TL, SL and body depth), crabs (carapace width and length) and shrimps (TL) were measured to 0.1mm using Camlab plastic vernier callipers.

Notes on study and collection sites were made underwater using SCUBA and plastic slates. Samples of sediments from different substrates were collected by hand and were placed into plastic bags underwater. These were dried at the surface. Size sorting analysis was carried out (Klute 1986) at the Geography Department, Rhodes University.

RESULTS

THE FISH COMMUNITY

Forty-five species were observed in the experimental area at Musende Rocks (Figure 2.1, Table 2.1). The only territorial species were shell-dwelling lamprologines, *Limnochromis auritus* and *Triglachromis otostigma*. The latter two species were rare and only found over mud substrates.

Daytime. After the shell-dwellers *Xenotilapia bathyphila*, *X. sima*, *Grammatotria lemairii* and *Enantiopus melanogenys* (sand-sifting invertebrate feeders) were the most common fish. They occur in large, mixed-species shoals (up to 100 individuals) and cause a considerable disturbance of the substrate whilst feeding. This is exploited by two predators, *Lamprologus callipterus* (non-territorial individuals) and *Lepidolamprologus cunningtoni*, which prey on both invertebrates and fish disturbed by the other foragers. Numerous attacks by these two species upon shell-dwellers were observed and *L. cunningtoni* often probes into shell mouths for prey. They appear to be the main daytime predators upon shell-dwellers.

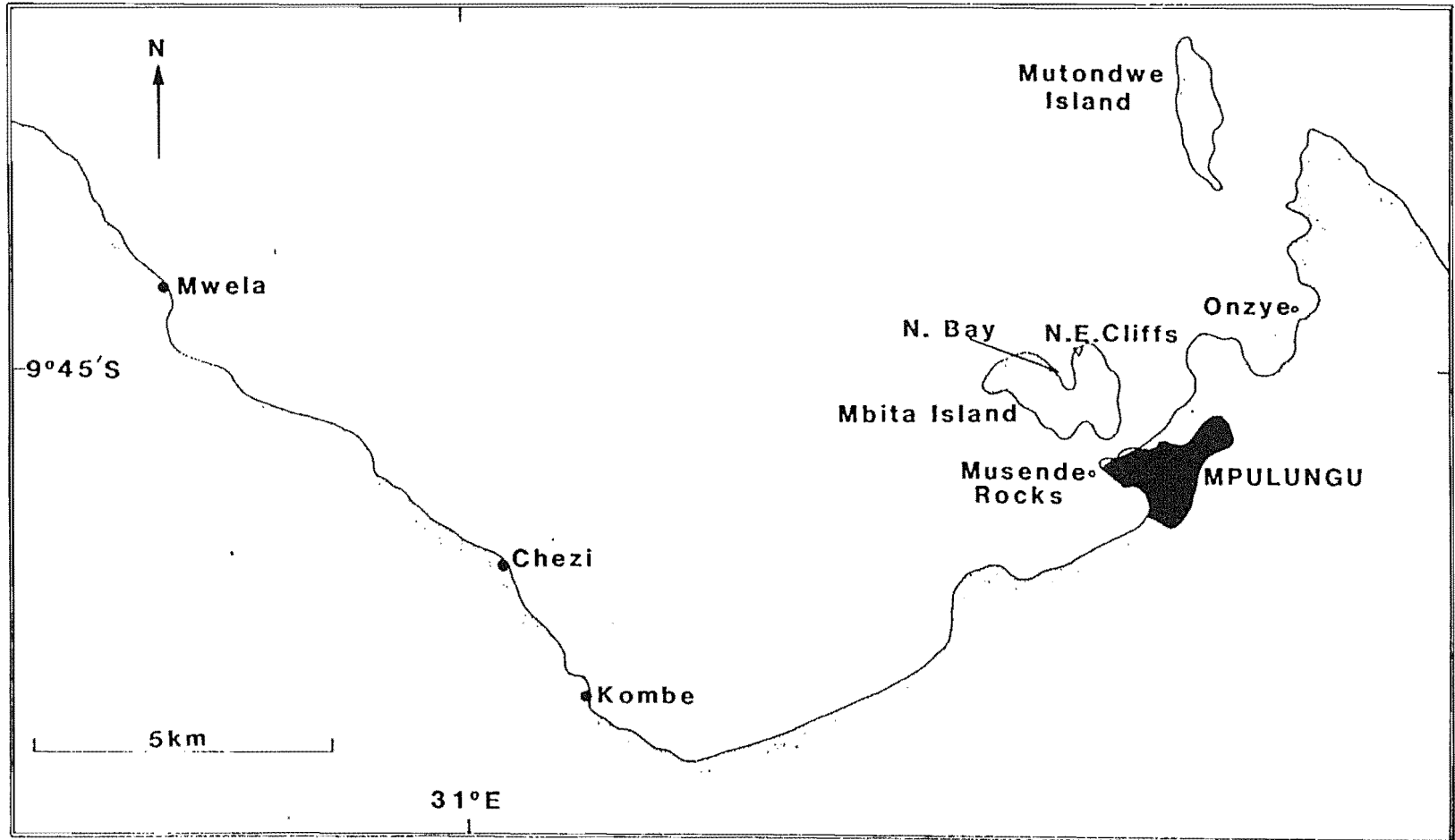
Night time. During the night, shell-dwellers were rarely observed outside of their shells. Those that were observed, typically rested in the mouths of their shells but entered the shells immediately if disturbed. Many species more typical of rocky shores, such as *Cyathopharynx furcifer*, *Aulonocranus dewindti* and *Haplotaxodon microlepis*, were observed resting on or over soft substrates. The actively foraging fishes were dominated by bagrid catfishes and mastecembelid eels. The latter were observed probing into shells.

OBSERVATIONS OF SHELL-DWELLING FISHES

Abundance. Shell-dwelling fish populations varied considerably from site to site and in some areas over time. The lowest shell and fish numbers were found along the Chezi-Mwella coast. In some transects (26m²), no surface or buried shells were located. At Mwella the only shell-dwellers present were *L. ocellatus* and *L. laparogramma*. The latter were using holes, 2cm in diameter and up to 15cm deep

Table 2.1 Checklist of fishes found in soft substrate habitats at Musende Bay.

Species	Day	Night
<i>Auchenoglanis occidentalis</i>	+	+
<i>Aulonocranus dewindti</i>	-	+
<i>Boulengerochromis microlepis</i>	+	+
<i>Crysiichthys platycephalus</i>	-	+
<i>C. sianenna</i>	-	+
<i>Crysiichthys</i> sp.	-	+
<i>Cyathopharynx furcifer</i>	-	+
<i>Enantiopus melanogenys</i>	+	+
<i>Grammatotria lemairii</i>	+	-
<i>Haplotaxodon microlepis</i>	-	+
<i>Hemibates stenosoma</i>	-	+
<i>Lamprologus callipterus</i>	+	+
<i>L. laparogramma</i>	+	+
<i>L. ocellatus</i>	+	+
<i>L. ornatipinnis</i>	+	+
<i>Lepidolamprologus attenuatus</i>	+	+
<i>L. cunningtoni</i>	+	+
<i>L. elongatus</i>	+	+
<i>Limnochromis auritus</i>	+	-
<i>Limnothrissa miodon</i>	+	+
<i>Lobochilotes labiatus</i>	+	+
<i>Malapterus electricus</i>	-	+
<i>Mastecembelus cunningtoni</i>	-	+
<i>M. ellipsifer</i>	-	+
<i>M. moorei</i>	-	+
<i>M. ophidium</i>	-	+
<i>M. plagiostomus</i>	-	+
<i>Neolamprologus hecqui</i>	+	+
<i>N. multifasciatus</i>	+	+
<i>N. tetracanthus</i>	+	+
<i>Phyllonemus typus</i>	-	+
<i>Perissodus microlepis</i>	+	+
<i>P. paradoxus</i>	+	+
<i>Synodontis dhonti</i>	-	+
<i>S. polli</i>	-	+
<i>S. multipunctatus</i>	-	+
<i>S. petricola</i>	-	+
<i>Trematocara stigmaticum</i>	-	+
<i>Triglachromis otostigma</i>	+	+
<i>Tylochromis polylepis</i>	+	+
<i>Xenotilapia bathyphila</i>	+	+
<i>X. caudofasciata</i>	+	+
<i>X. flavipinnis</i>	+	+
<i>X. sima</i>	+	+
<i>Xenotilapia</i> sp.	+	+



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Figure 2.1 A map showing study sites in the Zambian portion of Lake Tanganyika.

(Figure 21, Appendix 1), excavated in the mud substrate. Total numbers varied from 0.04-0.1 fish/m².

The highest numbers of fish were found at Mbita Island. Total numbers ranged from 0.7-2.0 fish/m² of which *L. laparogramma* comprised 72-97% of the community. *L. ocellatus* and *L. ornatipinnis* were also present. However, fish numbers were observed to be variable (Table 2.2).

Table 2.2 Increasing numbers of *L. laparogramma* over a six month period in a fixed transect set at Mbita Island (20m depth).

Date	<i>L. laparogramma</i>	<i>L. ornatipinnis</i>	Fish /m ²
18/8/1990	16	0	0.8
9/11/1990	38	2	2.0
5/2/1991	12	1	0.7

The highest numbers of obligate shell-dwellers were found along shell bed boundaries at various sites around Mpulungu. At Musende Rocks, shell numbers were more than 40 shells/m² and fish, dominated by *N. hecqui* (71%), were 2.4 fish/m². At the south end of Musende Bay (13m depth), *N. hecqui* dominated (83%) the community and total numbers were 1.1 fish/m². At the north of Mbita Island, where mud substrates bordered shell beds, *L. ocellatus* (76%) dominated and total numbers were 1.2 fish/m².

Social structure of shell-dwellers (territories and breeding systems).

Individuals of *L. ocellatus* and *L. ornatipinnis* are either monogamous or polygamous but more frequently the latter. Males' territories are about 1-3m² (depending on habitats), usually consisting of one to five (Table 2.3), dispersed shells which are buried into the substrate by the male. Females' territories are smaller and are within males' territories and generally contain fewer shells. When two females occur in the same male territory, their territories' boundaries do not usually overlap (Figure 2.2).

L. laparogramma is monogamous and has territories which are more circular (Figure 2.3) than those of *L. ocellatus* or *L. ornatipinnis*. Territories are approximately 2m in diameter. These are centred

around males' and females' holes. Where shells are abundant in muddy habitats, often only one partner uses a shell and the other uses a hole close by. Shells are buried into the substrate, usually by the male.

N. hecqui is monogamous. A male starts a territory by occupying a single shell, around which it digs a circular depression. Excavations continue resulting in up to 100 shells being uncovered. A female will later pair with the male and use one of these shells. Later other shells are used by the juveniles (Figure 2.4). Territory size is difficult to determine as, unlike the other three species, *N. hecqui* wanders and forages outside the borders of the defended territories. The size of the depression varies between 20-50cm in diameter. Of the many shells within nests, usually only those in use are 'open'.

Numbers of shells in territories.

Males' territories contained higher numbers of shells than those of females (Table 2.3). *L. ornatipinnis* generally held territories containing greater shell resources than *L. ocellatus*. Males of both species most frequently maintain two open shells within territories which are spaced apart by up to 1.5m (see below). Females most frequently maintain a single open shell. However, whilst juveniles are present in territories numerous shells may be opened to varying extent and juveniles spread out amongst these.

Table 2.3 The number of good quality shells in *L. ocellatus* and *L. ornatipinnis* territories at the Musende Rocks site.

Species / sex	Sample number	Number of good shells in a territory					mean	SD
		1	2	3	4	5+		
<i>L. ornatipinnis</i>								
male	50	12	15	8	2	13	2.96	1.84
female	49	18	23	3	2	3	2.06	1.41
<i>L. ocellatus</i>								
male	54	21	17	10	2	4	2.15	1.33
female	50	30	11	6	3	0	1.64	0.91

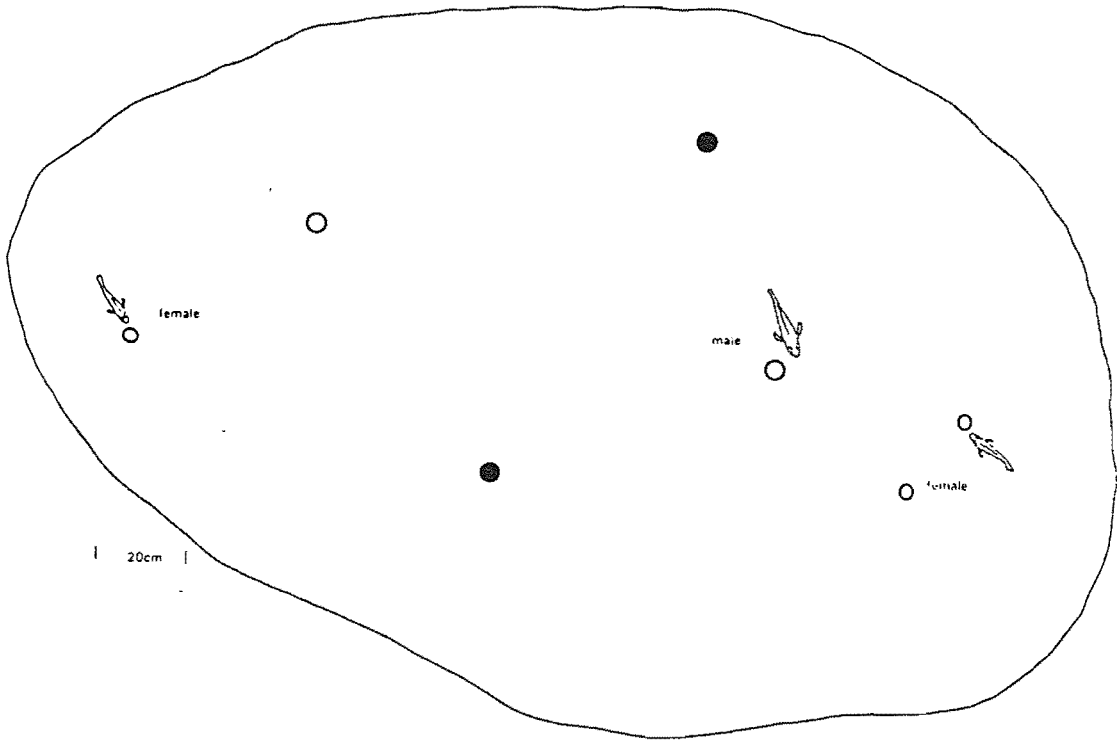


Figure 2.2 A diagram of a territory of *L. ornatipinnis* and *L. ocellatus*. Open shells are open circles, hidden shells are closed circles and the territory boundary the solid line.

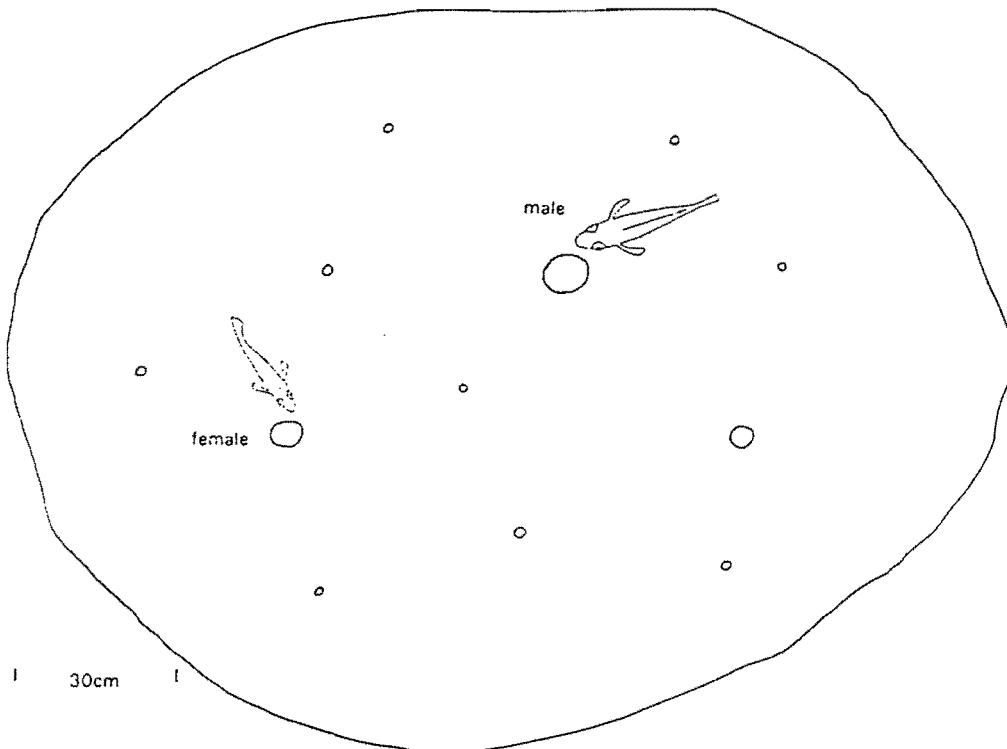


Figure 2.3 A diagram of an *L. laparogramma* territory. The male and female each use a single refuge hole and juveniles use numerous smaller holes.

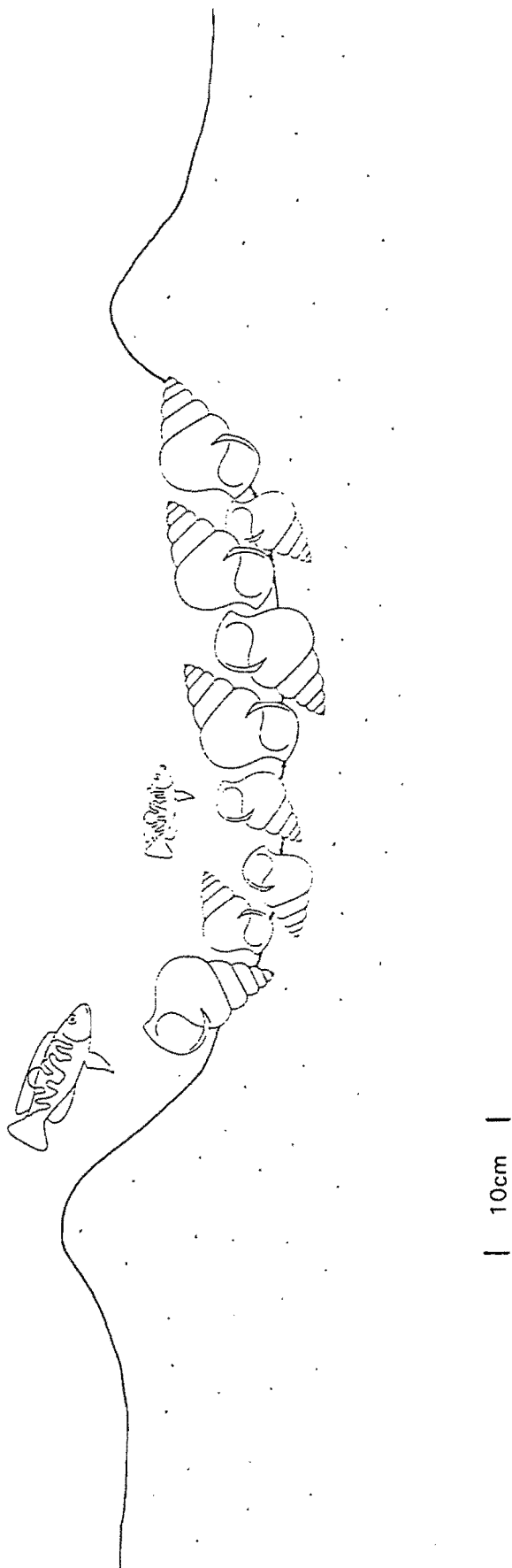


Figure 2.4 A diagram of a *N. hecquii* territory.

Most of these 'juveniles' shells' are only partially opened, which might indicate that juveniles are opening these shells themselves.

Inter-shell distances and shell distributions (Table 2.4).

Distances between shells within territories seemed to vary between sites. The greatest distances occurred along the Chezi-Mwella coast where shells were rare (0.01 to 0.1 shells/m²). However, due to the time-consuming nature of the work, measurements were only made at Musende Rocks in sand-mud habitats.

In most cases, male *L. ocellatus* and *L. ornatipinnis* held territories with more than one open shell and with at least one mate. Females of both species rarely defended two open shells, but where they did so these were about 20cm-30cm. The greatest distances between shells within a territory was that between two females' shells (usually more than 80cm).

Table 2.4 Distances between 'open' shells in shell-dwelling fish territories.

Species	Distances between shells						f1-f2
	ms1- ms2	ms1- ms3	ms1- ms4	mS1- f1s1	mS1- f2s1	fs1-fs2	
<i>L. ornatipinnis</i>							
no.	27	7	2	34	15	5	9
mean	47.1	65.0	76.0	65.1	90.9	21.4	108.6
SD	20.4	10.7	29.0	26.7	25.5	6.1	35.3
<i>L. ocellatus</i>							
no.	12	3	1	19	8	6	5
mean	58.3	48.0	55.0	59.1	77.0	31.8	106.6
SD	41.8	21.8	-	36.1	52.8	8.1	41.3
		h1-h2	h1-h3	h1-h4	h1-s1	s1-s2	
<i>L. laparogramma</i>							
no.		9	2	2	6	1	
mean		36.3	28.0	29.5	54.2	67.0	
SD		17.2	0	0.5	29.2	0	

In *L. laparogramma* territories there are usually two large holes (one male's and one female's) close together. Additional holes may or may not be present but these are always of much smaller size.

In all three species, the use of greater numbers of shells and holes is associated with the presence of juveniles. In territories of *L. laparogramma* juveniles dig and occupy single holes (Figure 1.5). In *L. ocellatus* adults or juveniles may open hidden shells (Figure 2.5) and juveniles may also use a variety of small surface shells such as those of *T. rufofilosa* (Figure 2.6). Often the larger *L. ocellatus* juveniles will individually occupy single shells within the territory. These larger juveniles defend their shells and space against siblings. Remaining siblings will occupy one or both of the parent's shells.

Refuge use and fleeing behaviour - day-time.

One of the main functions of shells is as refuges from predators (Konings 1988, Hausknecht & Kuenzer 1990). However, some fish were observed to flee across the substrate, and not into shells, when approached by predators. Fish responded to approaching divers in several ways: enter principal shell, move to and enter secondary shell and escape across substrate (Table 2.5).

There were inter-specific differences in the frequency of these responses (Table 2.5). The percentage of the individuals for each species which retreated into principal shells were: 85% of *L. ocellatus*; 69% of *L. ornatipinnis*; 47% of *N. hecqui*; 31% of *L. laparogramma* which used shells; and 7% of *L. laparogramma* which used holes. The opposite order was found for adults fleeing over the substrate.

These differences are significant: *L. ocellatus*-*L. ornatipinnis* ($\chi^2=8$, $df=2$, $p<0.05$); *L. ornatipinnis*-*N. hecqui* ($\chi^2=9.5$, $df=2$, $p<0.01$); *N. hecqui*-*L. laparogramma* ($\chi^2=75.8$, $df=2$, $p<0.001$); *L. laparogramma* using shells-*L. laparogramma* using holes ($\chi^2=18.2$, $df=2$, $p<0.001$). There were no sexual differences within species. The only adult-juvenile differences were shown by *L. ornatipinnis* ($\chi^2=18.0$, $df=2$, $p<0.001$) where juveniles dispersed over the substrate more frequently than adults.

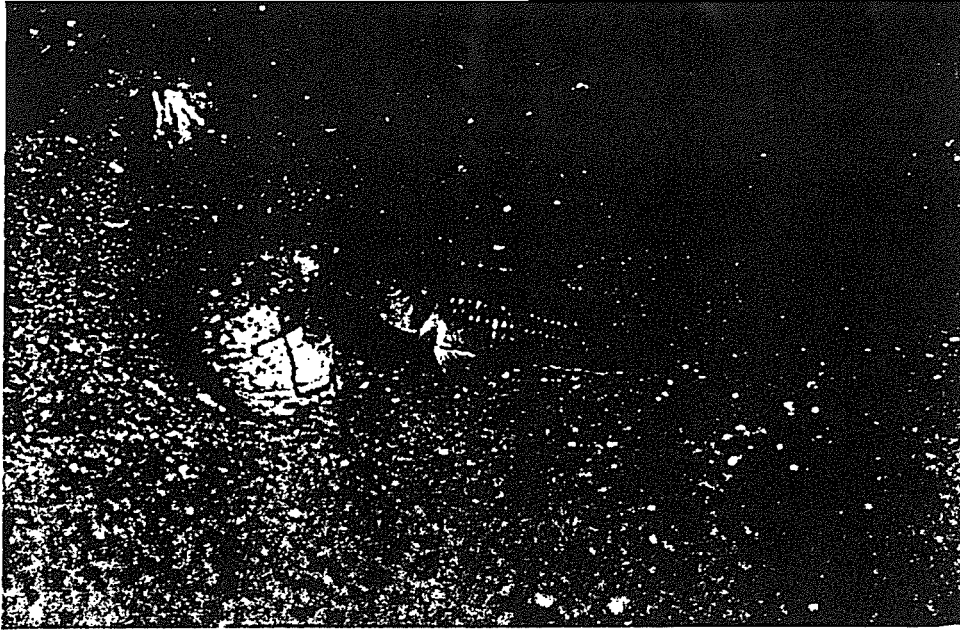


Figure 2.5 A male *L. ocellatus* at its principal shell. The shell in the background has been partially opened to allow juveniles access.

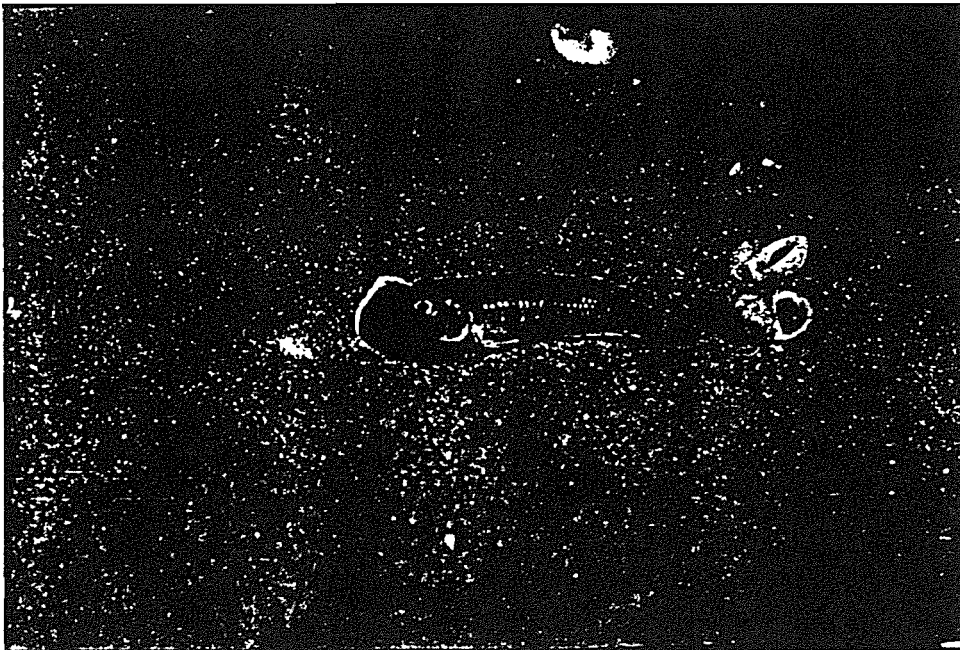


Figure 2.6 A male *L. ocellatus* at its principal shell with *Tanganyicia rufofilosa* shells on the surface. Small shells are not buried but are used by juveniles.

Table 2.5 Responses of fish to approach by divers.

	no.	>S1	>S2	> floor
<i>L. ocellatus</i>				
males	59	46	5	8
females	53	49	1	3
juveniles	21	18	1	2
<i>L. ornatipinnis</i>				
males	52	36	6	10
females	53	36	6	11
juveniles	20	7	0	13
<i>N. hecqui</i>				
adults *	51	24	10	17
juveniles	58	32	6	20
<i>L. laparogramma</i> (shells)				
males	57	17	3	37
females	54	17	3	34
juveniles	3	1	0	2
(holes)				
males	54	5	2	47
females	51	3	5	43
juveniles	56	1	2	53

>s1 fish moved and entered its principle shell, >s2 fish moved away from its principle shell and moved to the secondary shell, >floor the fish escaped across the lake substrate

* *N. hecqui* is not a dichromatic species so males and females were not distinguished.

- night-time.

Captive *L. ocellatus*, *L. ornatipinnis* and *L. laparogramma* normally sleep in depressions in the substrate near to their shells. In contrast, observations of wild shell-dwellers revealed that most were resting inside their shells at night. Active nocturnal predators included three *Crysiichthys* species (the most common was *C. sianenna*) and several mastecembelid eels.

Oviposition sites.

In *L. ocellatus* and *L. ornatipinnis* eggs are laid inside the female's snail shell. The site of egg laying is on the side wall and the floor one whorl around from the shell mouth (Figure 2.7). Very few shells collected contained eggs: shells used by four female *L. ocellatus* contained 23, 9, 10, 12 eggs (mean = 13.5, n = 4, SD = 5.6); and shells used by four female *L. ornatipinnis* contained 16, 27, 30, 49 eggs (mean = 30.5, n = 4, SD = 11.9).

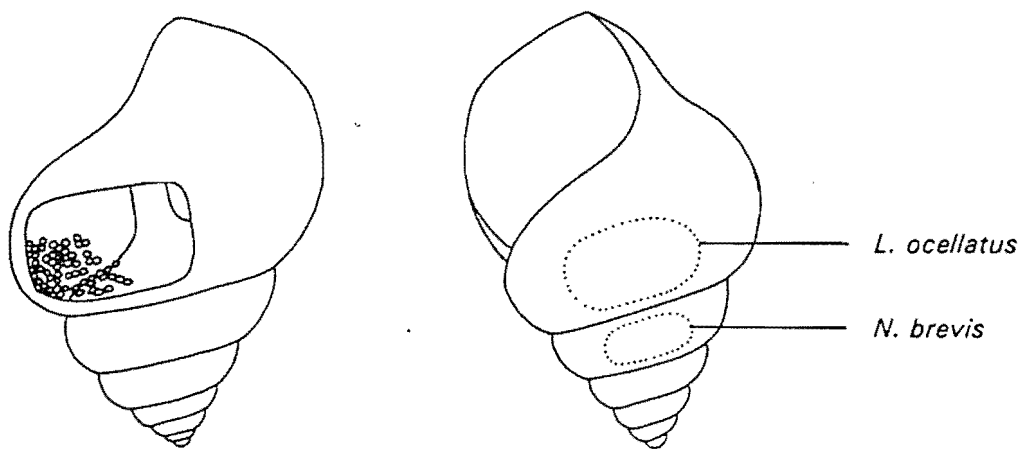


Figure 2.7 A diagram showing the oviposition site for *L. ocellatus* and *N. brevis*.

Neolamprologus brevis pairs share a single shell. Females lay their eggs deep inside the shell, 1.5 to 2.5 whorls from the mouth (Figure 2.7). Eggs from a single specimen numbered 40. Both *N. pleuromaculatus* and *L. attenuatus* lay their eggs in the shell mouth and on the outer surface of the shell (Figure 1.7). Eggs from single female *N. pleuromaculatus* numbered 146. Eggs were not found for either *N. hecqui* or *L. laparogramma*.

Feeding behaviour observations.

L. ocellatus mainly feeds from a hovering position above the substrate. Either individual prey are located and picked off the surface or a mouthful of sediment is taken into the mouth. The sediment is then sorted in the mouth and ejected through the gill rakers as well as being spat out of the mouth. Rarely individuals were observed lying on the substrate and engaging in sideways 'shuffling'. This behaviour disturbs the sediments and the fish dart forward when prey are located.

L. ornatipinnis and *L. laparogramma* both feed predominantly from a resting position on extended pelvic fins. The fins are tucked under the body and the fish bobs forward to either take individual prey from the substrate surface or to take in a mouthful of sediment. This is then 'chewed' with some being expelled through the gill rakers and some spat out of the mouth. All feeding takes place within territorial boundaries.

N. hecqui feeds from a hovering position above the substrate. Invertebrate prey are taken from the substrate surface or by 'chewing' through mouthfuls of sediment. Large adult *N. hecqui* were also seen to prey upon adult *N. multifasciatus* and juveniles of all other shell-dwellers. Often *N. hecqui* hunts in 'packs'. This is the only species in the soft substrate habitat which feeds outside its territorial boundaries.

N. brevis adults feed almost entirely on plankton. Feeding is usually carried out about 30-50cm above the shell, with females occurring lower in the water column than males. Analysis of stomach contents of a single specimen from Chezi showed the calanoid copepod, *Tropodiptomus simplex*, to be the dominant food item.

MOLLUSC SHELL DEPOSITS

Soft substrates contain a variety of shell deposits but are dominated in mass by the bivalve *C. burtoni* and the gastropod *N. tanganyicense*. Numbers range from a few individuals to several thousand per square meter. In all cases there are a mixture of species from rocky and soft substrates. How these mixed assemblages are produced is not fully understood at present (Cohen 1989). Species recorded from the main study site, Musende rocks, are shown in Table 2.6.

Shells used by cichlids. Only empty shells of the larger gastropod species, with mouth dimensions greater than 15mm high and 10mm wide, are used by fish as refugia and nesting sites (Table 2.6, Figure 2.8). Adult shell-dwellers almost exclusively use *N. tanganyicense*, while juveniles use any species which they can fit into. Juvenile *L. ocellatus* were commonly found using *L. thomsoni*, *L. grandis* and *T. rufofilosa*.

Table 2.6 Mollusc shells found in sediments at Musende Rocks.

Gastropoda	Bivalvia
<i>Lavigeria grandis</i> **	<i>Mutela spekei</i>
<i>Lavigeria</i> spp. *	<i>Brazzea anceyi</i>
<i>Limnotrochus thomsoni</i> **	<i>Caelatura burtoni</i>
<i>Paramelania iridescens</i> *	<i>Pseudospatha tanganyicensis</i>
<i>Reymondia</i> spp.	
<i>Spekia zonata</i>	
<i>Stormsia minima</i>	
<i>Tanganyicia rufofilosa</i> **	
<i>Tiphobia horei</i> *	
<i>Anceya</i> spp.	
<i>Martelia tanganyicensis</i>	
<i>Syrnilopsis</i> spp.	
<i>Neothauma tanganyicense</i> ***	
<i>Ferrissia tanganyicensis</i>	

Shells used by shell-dwelling fish: * occasionally used, ** regularly used by juveniles and small females, and *** the most commonly used by adult fish.

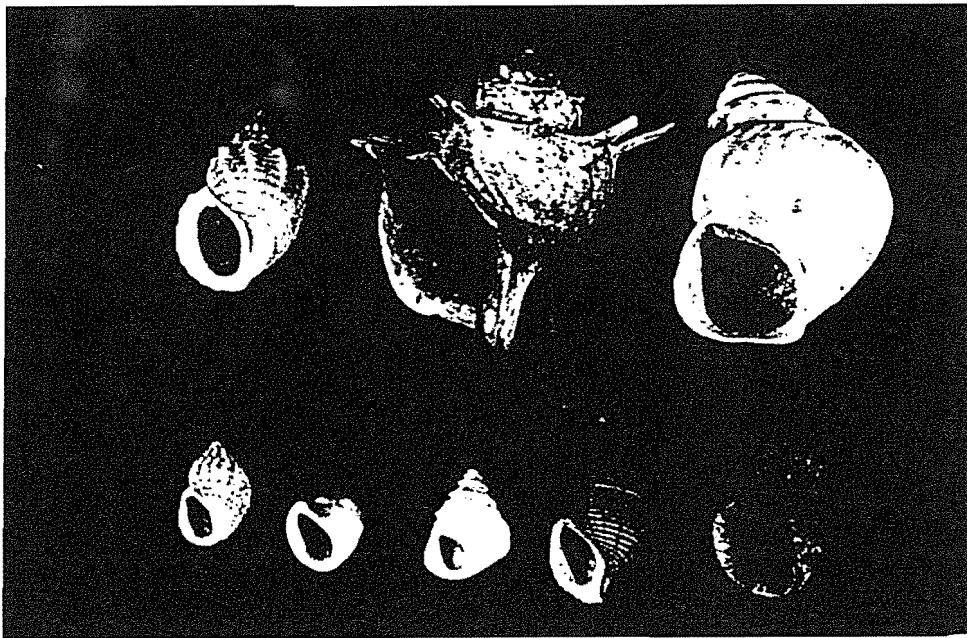


Figure 2.8 The eight gastropod shells most commonly used as refuges by shell-dwelling fishes. Clockwise from the top right they are: *Neothauma tanganyicense*; *Tiphobia horei*; *Paramelania* sp.; *Lavigeria grandis*; *Paramelania iridescens*; *Limnotrochus thomsoni*; *Tanganyicia rufofilosa*; *Lavigeria* sp.

Shell occupancy. Shells that were unburied and unoccupied by adult fishes had an occupancy level of 68% (Table 2.7). The dominant animals inhabiting these surface shells were decapod shrimps (83%, *Macrobranchium moorei*, CAW68A), while juvenile crabs (14%, *Platythelphusa maculata*, CAW 17A) and juvenile *P. typus* (3%, Bagridae, RUSI 38845) comprised the remainder of the occupants.

Surprisingly, shells occupied by adult fish had high numbers of additional heterospecific occupants. These were again dominated by shrimps (70%, Table 2.7). There were slightly higher numbers of shrimps in *N. hecqui* (Figure 2.9) shells, while the lowest numbers occurred in female *L. ocellatus* shells. This might be a function of shell size, since the larger shells having greater volumes for other occupants than smaller shells. Heterospecific juveniles were found cohabiting with adult male *L. ocellatus* and *L. ornatipinnis* (Figures 2.10 & 2.11).

Crabs did not share refuges with either shrimps or fishes. The crabs from Zambia and Burundi are tentatively identified as *Platythelphusa maculata* juveniles (Zambia - CAW 17A) and *P. polita* (Burundi - CAW 13A) (Cumberlidge, pers. comm., Figure 2.12). Some shells were inhabited by both

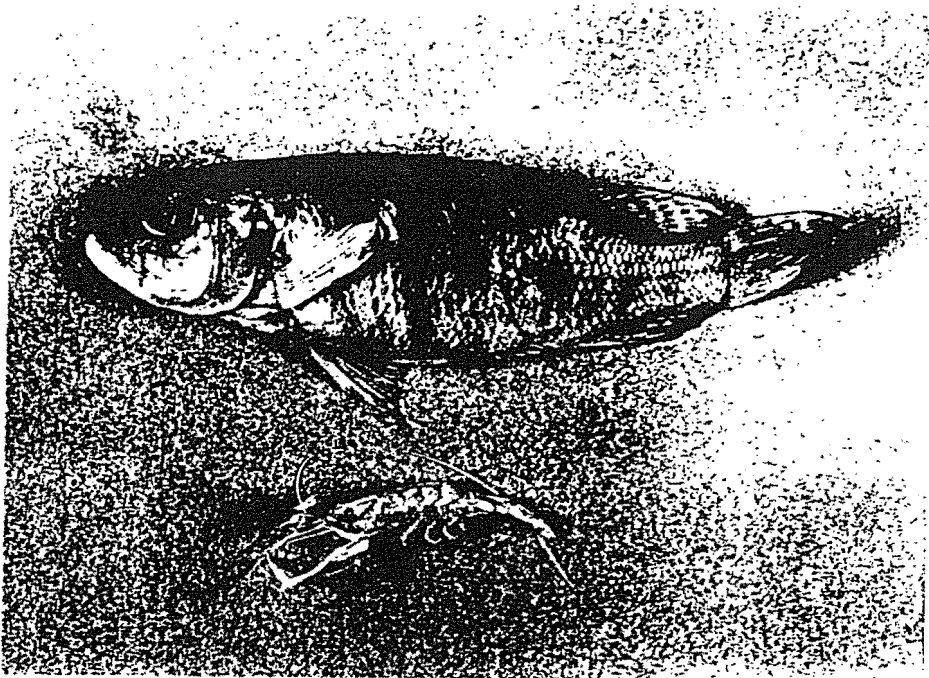


Figure 2.9 A male *N. hecqui* with co-habiting shrimp (*M. moorei*).

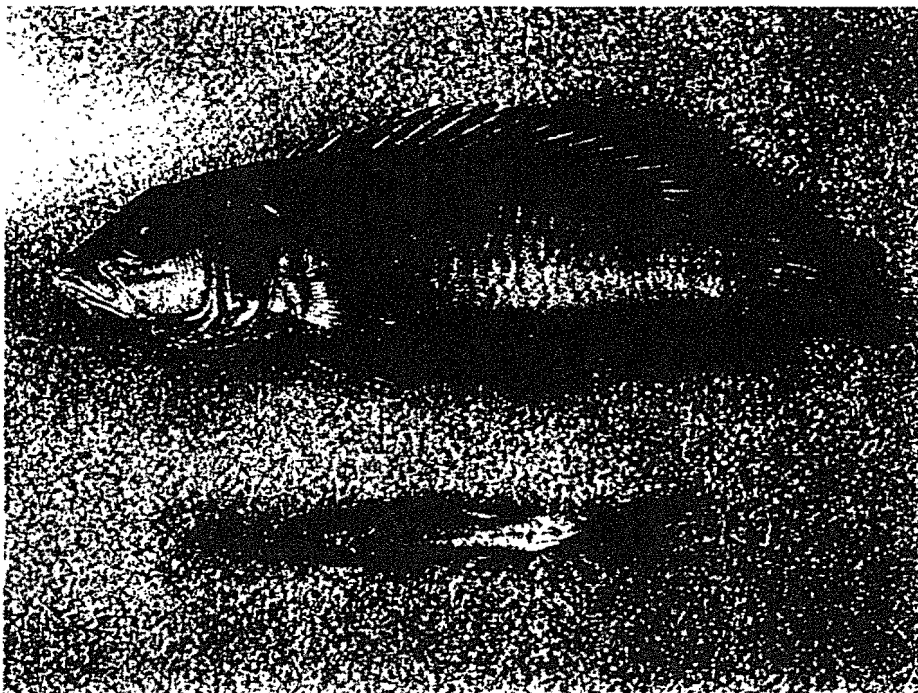


Figure 2.10 A male *L. ocellatus* with co-habiting juvenile *L. ornatipinnis*.

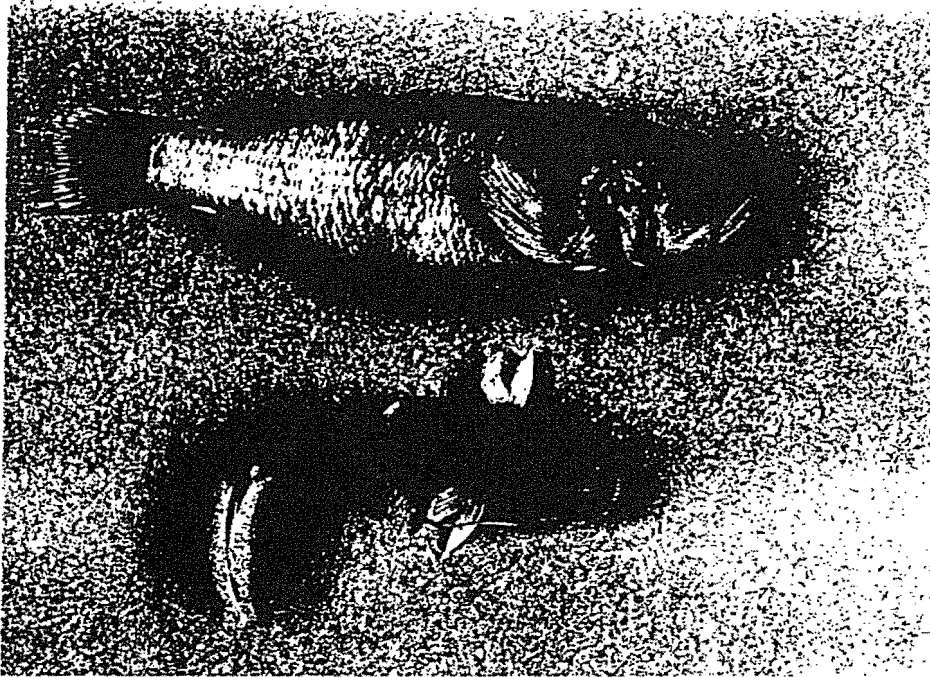


Figure 2.11 A male *L. ornatipinnis* with co-habitant juvenile catfish (*P. typus*).



Figure 2.12 Shell dwelling crabs: a) *P. maculata* from Mpulungu, Zambia; and b) *P. polita* from Gitaza, Burundi.

male and female *P. polita* and a few of these females were in berry. This indicates that *P. polita* attains a small adult size and may therefore be adapted to living in shells. *P. polita* had larger chelae than *P. maculata* (Figure 2.12) which may be of significance in shell defence (Chapter 6).

Table 2.7 Occupants of shells with and without resident fish (measurements in mm).

Main inhabitants species/no.	Fish CW	SL /	Shell height	Additional occupants				
	X ± sd		X ± sd	Cj	Hj	No	Sh	Cr
no adult fish (100)	-		41.3±5.2	0	2	32	59	10
<i>N. hecqui</i> (21)	44.6±9.7		47.8±4.0	0	0	4	25	0
<i>L. ornatipinnis</i> (23)	43.3±8.0		45.1±4.4	27	3*	6	11	0
<i>L. ocellatus</i> (21)	33.5±7.9		40.3±8.3	0	0	9	15	0
Crabs(23)	13.6±1.9		45.6±3.9	0	0	22	1	0

SL = fish standard length, CW = crab carapace width, (no.) = number sampled, Cj = conspecific juveniles, Hj = heterospecific juveniles (* all *Phyllonemus typus*), No = no residents, Sh = shrimps, Cr = crabs.

DESCRIPTIONS OF STUDY AND COLLECTION SITES

Musende Rocks, Zambia (8° 46' South, 31° 6' East)

This was the main study site. The majority of observations, collections and experiments (Chapters 3 & 4) were conducted in the central portion of the sandy area. The site is a submerged rock pinnacle (during 1991-93) about 150m offshore from the north east side of Musende Bay, Mpulungu (Figure 2.1). The rocky shore extends from just below the surface to about 18m depth on the north side. On the south-west side of the rocks, the rock intermediate habitat starts at about 9m and extends to 18m in the north-west (Figures 2.13 & 2.14). Soft substrates occur north and west of the rocks to approximately 20m depth, where shell beds occur. The different soft substrates, although patchy and often merging into one another, were generally distributed as follows and as in Figures 2.2 and 2.3.

The rock boundary. This boundary zone comprises three distinct microhabitats which vary in extent and are patchily distributed:

- a) the rock boundary;
- b) gravel patches with relatively few shells; and
- c) patches of shells.

Different shell-dwelling species are associated with each of these habitats. Amongst the rocks there are nest sites of *L. callipterus* (Figure 2.15), *L. attenuatus* and *N. tetracanthus*. Away from the rocks the commonest shell-dweller is *L. ornatipinnis*, while isolated colonies of *N. multifasciatus* also occur. Shell patches, often in elongated triangular shapes, may be comprised entirely of the bivalve *C. burtoni*. Where *T. vittatus* and *Altolamprologus* sp. occur gastropods (dominated by *N. tanganyicense*) are present.

Gravel slopes. Moving into deeper water away from the rocks coarse sand and shell fragments comprise the substrate. The gradient is relatively steep (20-30°), and surface shell numbers are usually high (>5 shells/m², Figure 1.3). This substrate forms a thin strip between the rock boundary and the sand substrate. The dominant shell-dweller is usually *L. ornatipinnis*.

Sand slopes. Gravel substrates grade into sand substrates. Accompanying this is a reduced gradient (10-20°), a decrease in particle size of the substrate, a general decrease in surface shell numbers (Figure 2.16) and a change in species composition of shell-dwelling fish. In this habitat shells were more evenly distributed than the rock boundary zone and gravel substrates. The shell-dwellers are dominated by *L. ocellatus* while *L. ornatipinnis* and *N. hecqui* are both common and may be locally dominant. *N. hecqui* is more abundant closer to shell beds and where there are high numbers of shells.

There are two types of excavation sites which are found in sand habitats:

- a) large (2-3m diameter, 1m depth), circular holes; and
- b) smaller, elongated, trough-shaped depressions.

It is unknown which species excavate these depressions. However, the most commonly observed fish associated with these holes were *A. occidentalis* (circular holes) and mouth-brooding *L. labiatus* ('troughs'). In and around these depressions there are higher numbers of shells compared to the surrounding areas and *N. hecqui*, *N. brevis* and *N. multifasciatus* are often locally dominant here.

Mud flats. Mud substrates occur around 18-20m depth and are associated with a further break in slope gradient (5-0°). Surface shells are rare or absent (Figures 1.5 & 2.17). The shell-dwelling fish are dominated by the facultative shell-dweller *L. laparogramma* (Figure 2.17). Other shell-dwelling species are rare. Two hole-nesting limnochromines, *Triglachromis otostigma* and *Limnochromis auritus* were also present but rare.

Shell beds. These are comprised of compacted shell gravel covered with surface shell deposits of over 100% cover (Figure 1.4). They extend from the north east (20-21m depth) in an irregular arc to the south west and continue into Musende Bay (Figure 2.14). The beds cover the majority of Musende Bay and reach 5m depth in some places. The species present are *N. multifasciatus*, *N. hecqui*, *Altolamprologus* sp. and *T. burgeoni*. The boundary zone may be abrupt where there are *N. multifasciatus* colonies or may extend over several meters. In the latter case *L. ornatipinnis* is usually dominant, although *N. hecqui*, *L. ocellatus* and *L. laparogramma* are also common.

Mbita Island, Zambia

North-east cliffs (8° 45' South, 31° 6' East).

This is a rocky shore with a slope to about 15m depth. Shell gravel slopes with high numbers of shells occur between 15-18m depths and are dominated by *L. ornatipinnis*. With increasing depth the substrate gradient decreases becoming more sandy and the shell density decreases. The dominant species on the sand is *L. ocellatus*. At 20m depth the substrate is flat mud with very low numbers of surface shells and is dominated by *L. laparogramma*. At 20-21m depth, shell beds occur extending in an arc from the east into the North Bay into the shallows up to about 5m depth.

North Bay (8° 45' South, 31° 5.5' East).

The site, about half way into the North Bay on the west side (Figure 2.1), is a rocky shore which slopes to 15m depth. The rock boundary gradually becomes deeper from the south end of the bay (5-7m depth) to the northern point (20m depth). The rock boundary has high numbers (50+ shells) of large *L. callipterus* nests which extend onto the rocky slopes. These nests were used by a variety of shell-dwellers such as *N. fasciatus*, *N. calliurus* and *T. vittatus*. On the gravel close to the rock

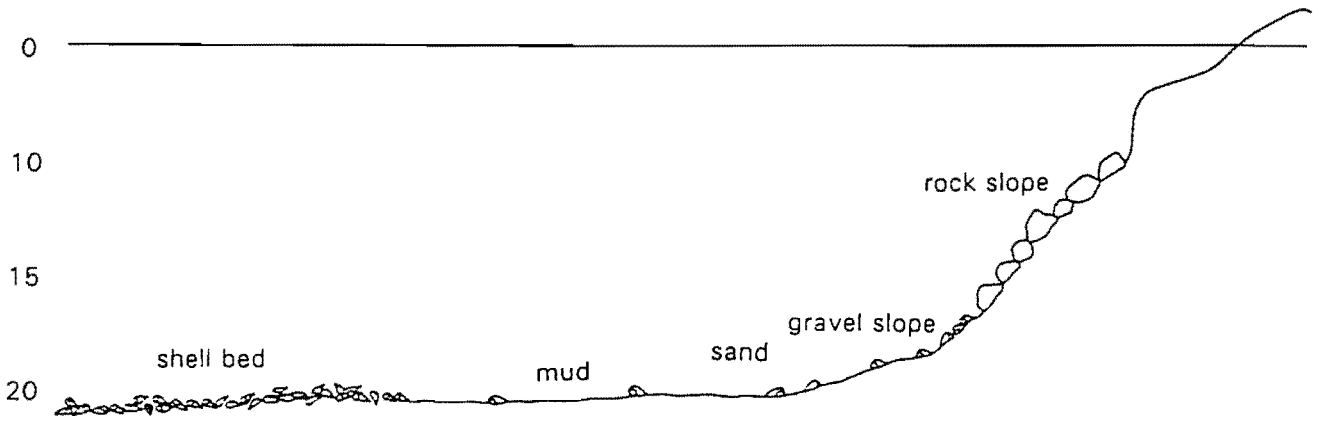


Figure 2.13 A diagram showing the slope and depth distribution of habitats at Musende Rocks.

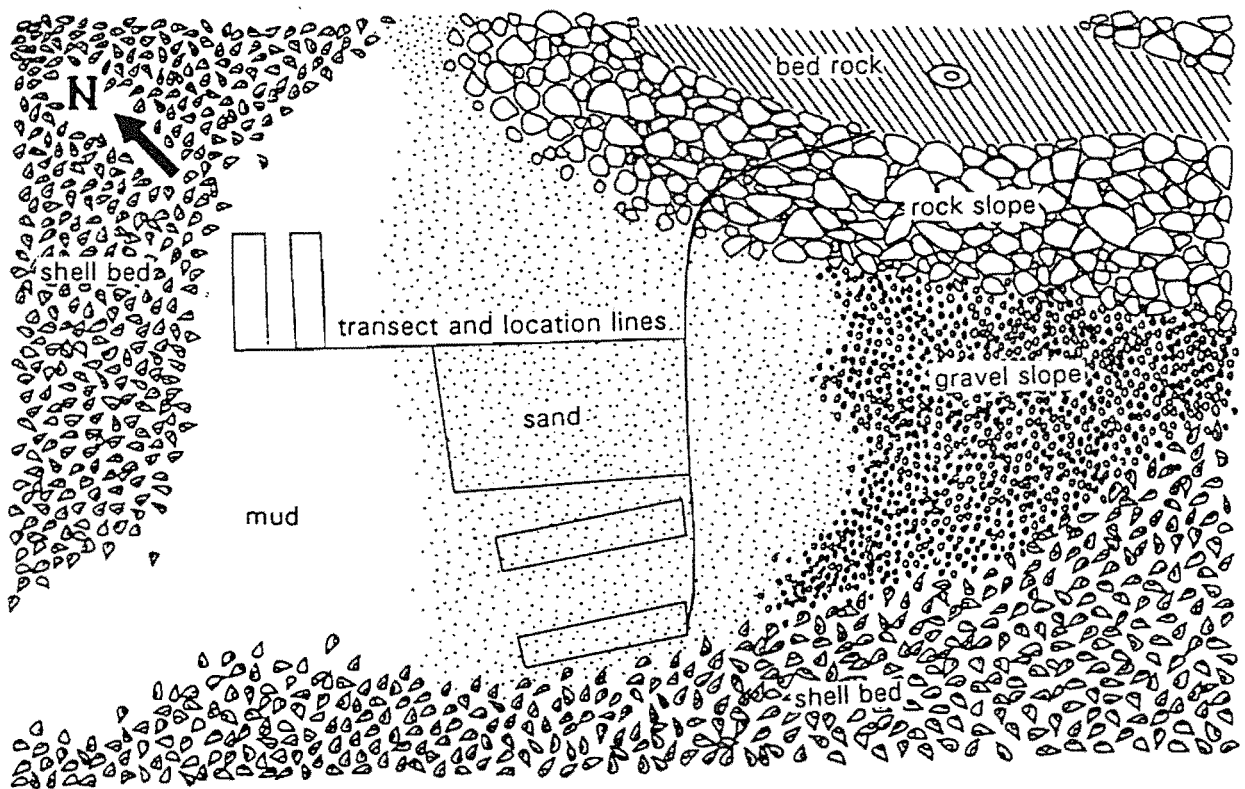


Figure 2.14 A diagram showing the distribution of habitats at Musende Rocks.

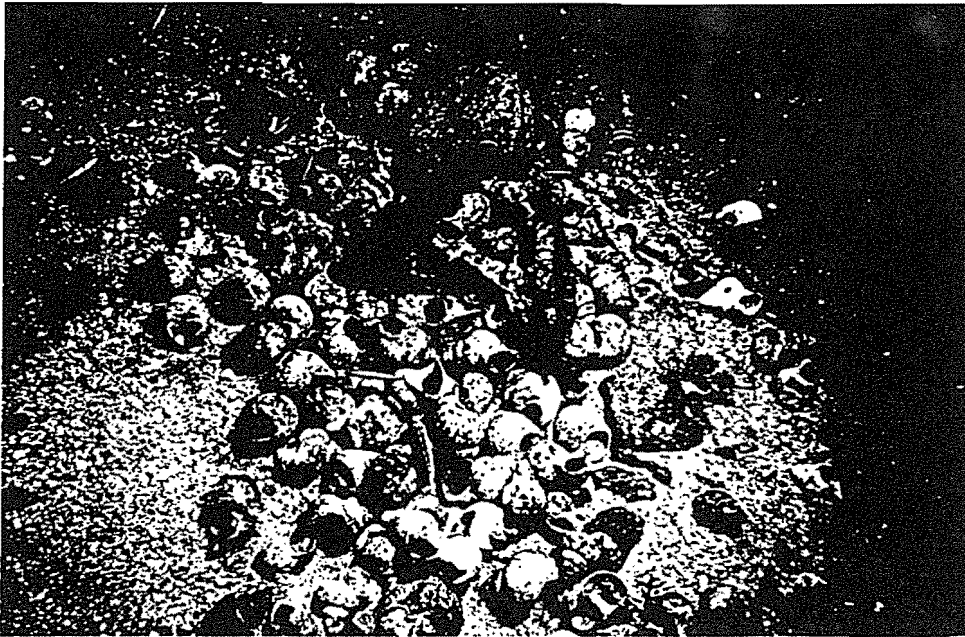


Figure 2.15 An *L. callipterus* nest site at the rock boundary.

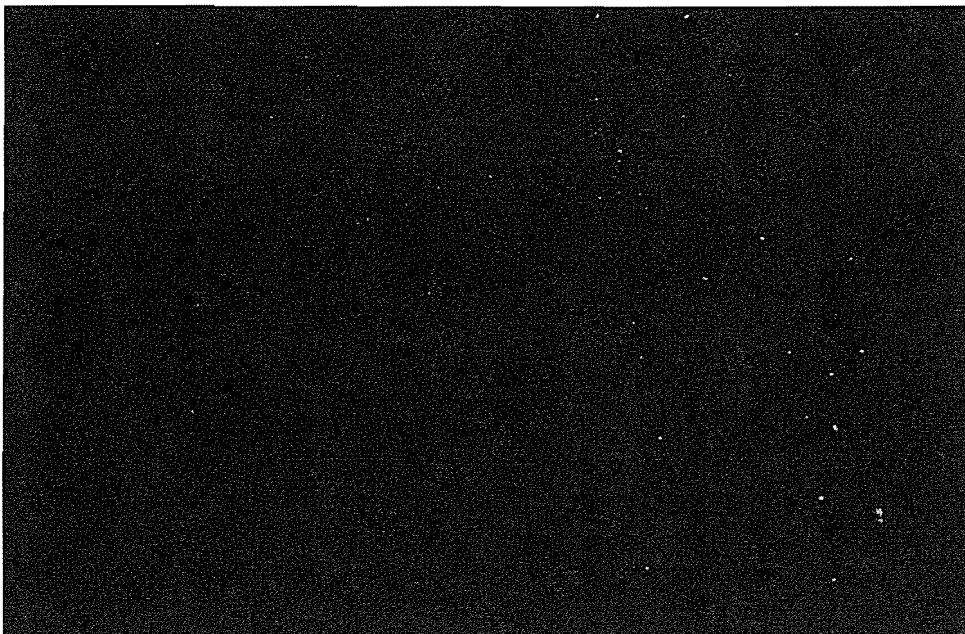


Figure 2.16 Low numbers of shells in low gradient sand substrates.

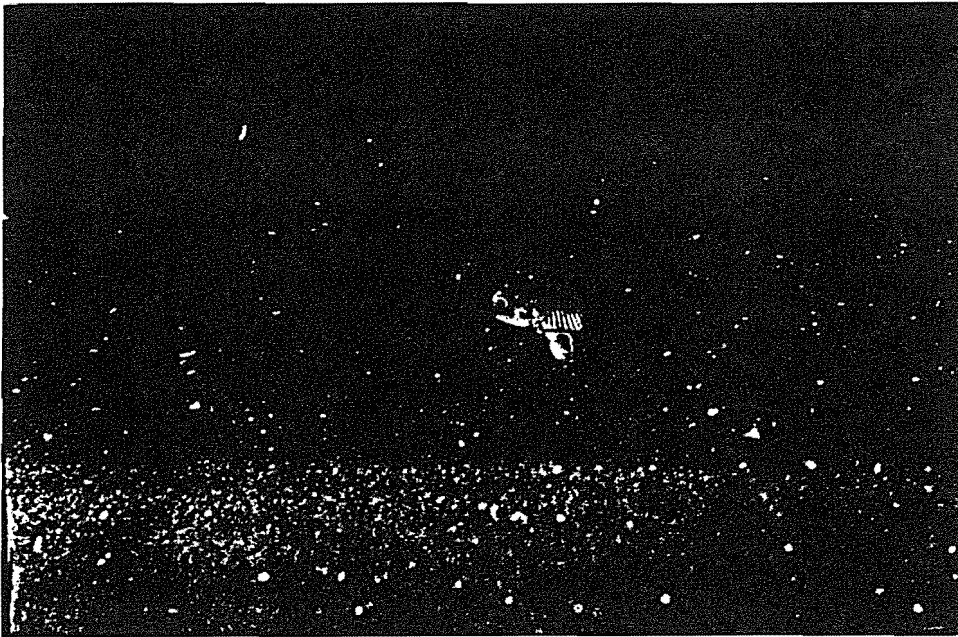


Figure 2.17 Flat mud substrate with no surface shells and *L. laparogramma* at its refuge hole.

patchy and *L. ornatipinnis*, *L. ocellatus*, and *N. hecqui* may be locally dominant. *N. brevis* was also present but rare. At 20m depth the substrate is a flat mud, dominated by *L. laparogramma*. Mud substrates give way to shell beds at about 22m depth. These shell beds extend south into the bay reaching 5m depth.

Chezi, Zambia (8° 47' South, 31° 1' East).

This site is just north of Chezi village on the Zambian south-west shore. It is a rocky slope to 10 meters depth and below this a sand slope to about 30m. Compared to the sand slopes in Mpulungu, Chezi is relatively steeper (about 20-30°); the sand is comprised of less shell material; and shells were less numerous. The only shell-dwellers were *L. ocellatus* (dominant) and *N. brevis* (rare). Over large areas *L. ocellatus* is the only shell-dwelling species present.

Gitaza, Burundi (29° 20' South, 3° 39' East).

This was a sand-mud substrate with varying shell densities between 10-15m depth. *L. ocellatus* was the most abundant species on sand occupying both *N. tanganyicense* and *P. damoni* shells. On mud

Gitaza, Burundi (29° 20' South, 3° 39' East).

This was a sand-mud substrate with varying shell densities between 10-15m depth. *L. ocellatus* was the most abundant species on sand occupying both *N. tanganyicense* and *P. damoni* shells. On mud *L. kungweensis* was dominant and used holes exclusively. Other species present on both sand and mud habitats and only occupying *N. tanganyicense* shell were *N. brevis* and *N. pleuromaculatus*.

SUBSTRATE GRAIN SIZES

Soft substrate habitats are not uniform in composition. Three types were distinguished: gravel; sand; and mud. These were usually associated with varying substrate gradients. In each substrate type sediment size composition (Table 2.8 & Figure 2.18), surface shell deposits and species composition of fish communities differed.

In the Mpulungu area there is usually a series of habitats (see Figures 2.13 & 2.14):

rocks <=> rock boundary <=> gravel <=> sand <=> gravel <=> shell bed; or

rocks <=> rock boundary <=> gravel <=> sand <=> mud <=> shell bed.

Gravel substrates occur at transition zones between the rock-soft areas and between the soft substrate-shell beds. Gravels are composed of a considerable amount of broken shell material. There are usually higher numbers of surface shells on gravel substrates than the sand and mud habitats.

Sand substrates are the most extensive type in water less than 20m depth. It occurred between gravels and gravel and mud substrates. Normally it is difficult to distinguish a clear transition between gravel and sand substrates. The sand-mud transition is usually accompanied by a change in slope and is also marked by the appearance of *L. laparogramma*.

Mud substrates are usually found in areas greater than 20m depth. Substrate gradients are low to flat and surface shell deposits are rare or absent.

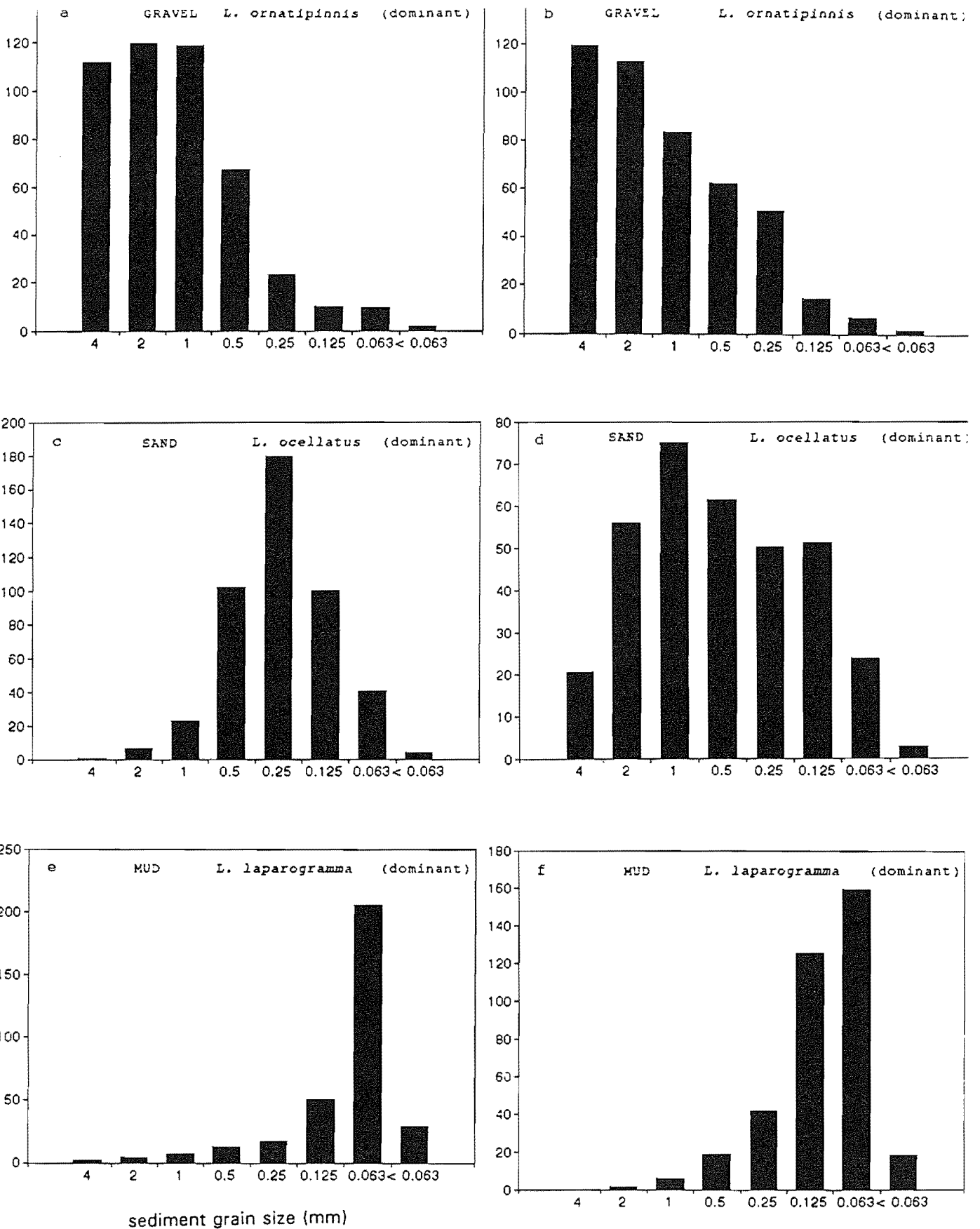


Figure 2.18 Graphs showing the size composition of substrate sediments from six sample sites: a) Mbita Island cliffs, 17m; b) Mbita Island north bay, 15m; c) Chezi, 25m; d) Musende Rocks, 17m; e) Mbita Island, 20m; f) Musende Rocks, 20m. The collection depths are given in meters.

Table 2.8 Grain size composition of substrates from different collection sites in Zambia.

site	size: > mm		> um	< um					total
	4	2	1	500	250	125	63	63	
Chezi - sand	1	6	23	103	180	100	41	4	456
Mbita - gravel	120	113	84	62	51	15	7	2	453
Mbita - mud	2	4	7	13	17	51	205	30	330
Mbita - gravel	112	120	118	67	24	10	10	2	463
Musende - sand	21	56	75	62	50	51	24	3	342
Musende - mud	1	2	6	19	42	126	160	19	373

Chezi - sand = Chezi-North Kombe, 25m depth, sand slope.

Mbita - gravel = Mbita Island, NW Bay collection site, 15m depth, sand substrate.

Mbita - mud = North west cliffs site, 20m depth, mud substrate.

Mbita - gravel = North west cliffs site, 16-18m depth, shell gravel-sand substrate.

Musende - sand = Musende rocks (transect lines), 17m depth, sand substrate.

Musende - mud = Musende rocks (transect lines), 20m depth, mud substrate.

REMARKS AND DISCUSSION

Shell-dwelling fish abundance. The varying abundance of *L. laparogramma* from 18/8/1990 to 9/11/1990 (Table 2.2) may be due to recruitment. This period is the warm-rainy season when most species breed. An alternative possibility is that this species holds territories only when food resources are economically defensible. Changing types and abundance of food resources during the year may alter the economics of territorial defence. This may only apply to *L. laparogramma* which is not dependant on shells as refuges. Obligate shell-dwellers are dependant on shells for refuges and so may be more permanent in their defence of territories. However, the number and distribution of shells used within territories may change with seasons. Other species were observed to maintain seasonal nests or breeding arenas e.g. *L. callipterus*, *A. dewindti* and *C. furcifer* (pers. obs.).

Territory sizes of shell-dwellers. Although territory sizes were not measured, inter-shell distances indicate that *L. ocellatus* and *L. ornatipinnis* have territories greater than the 0.25m²-1m² quoted in Walter and Trillmich (1994). This is considered a significant factor as territory size will affect the number of shells and the area of feeding substrate available to individuals.

Refuge use. Walter and Trillmich (1994) reported that captive male *L. ocellatus* used only one open shell and buried all others. In the wild, both male *L. ocellatus* and male *L. ornatipinnis* normally defend two open shells. Certain marine reef fish that use holes as night-time refugia also defend more than one hole (Shulman 1985). Shulman suggested that this behaviour resulted from predators and other hole-dwelling competitors evicting the resident from its hole. In either case the possession of a second hole enables the resident to immediately retreat to safety. Shell-dwellers in general have two options:

- a) To come out of the shell and fight or to flee the attacker. This increases the risk of being eaten, injured in a fight or losing the shell.
- b) To go deeper into the shell and avoid the attackers.

At night, option b) seems to be the most common choice (pers. obs.). During the day both options are used. It would be interesting to test the effects of different intruder species on resident responses.

Another reason for males having more than one open shell may be that foraging close to refugia is possible over a larger area of territory if two or more shells are open. Why then are not more shells used? Presumably there is a trade-off between rising costs of defending open shells and increased benefits from extended foraging areas. Interestingly when juveniles are present more shells are uncovered and juveniles spread out between these shells. It is my hypothesis that, by opening greater numbers of shells when juveniles are present, adults improve their reproductive success in two ways:

- a) Sibling competition for benthic invertebrates is reduced between dispersed juveniles and so they mature and leave parental territories more quickly than those in single-shell territories.
- b) Spreading juveniles between several shells will reduce the fry lost during successful raids by predators.

Oviposition sites and female post-breeding behaviour. In *L. ocellatus*, *L. ornatipinnis* and *L. callipterus*, eggs are laid in shells occupied by the female.

In *L. callipterus*, females enter a male's nest and use a shell as a breeding site (Sato 1994). Females usually choose the largest shells available. Other species are found in nests of *L. callipterus* and one of these, *T. vittatus*, is an egg-eater. Interestingly, once female *L. callipterus* have spawned they remain inside their shells or at the mouths of shells during egg incubation (pers. obs.). I suggest that this is an anti-predator strategy against *T. vittatus*.

In *L. ocellatus* and *L. ornatipinnis* males use larger shells than females. Few of the smaller shells contained additional animals. By using smaller shells females may exclude shrimps and juvenile fish from shells and thus safeguard their eggs (see Chapter 4). Although *L. ocellatus* females often enter shells and fan eggs they do not remain inside shells whilst eggs are present. This may be due to the absence of egg predators such as fish and shrimps.

Feeding. Preliminary observations of feeding behaviour indicate that *L. ornatipinnis*, *L. ocellatus*, *L. laparogramma* and *N. hecqui* are predominantly substrate feeders whilst *N. brevis* is a planktivore. With the exception of *N. hecqui*, all of these species feed within the boundaries of their territories. This contradicts Walter and Trillmich (1994) who stated that *L. ocellatus* mainly feeds on plankton, quoting Brichard (1989) as their source. However, this is incorrect as Brichard (1989) simply stated that *L. ocellatus* is a 'microfeeder' and did not specify what types of food are eaten or where feeding occurs. It is not known if Brichard examined the stomach contents of *L. ocellatus*. Poll (1956) reported that the diet of *L. ocellatus* comprised small shrimps. The assumption that *L. ocellatus* is a plankton feeder is significant, as Walter and Trillmich (1994) concluded that food resources are not defensible. Based on my behavioural observations I suggest that *L. ocellatus*, *L. ornatipinnis* and *L. laparogramma* all defend feeding territories. Stomach contents analysis of several species are presently in progress in order to determine if this hypothesis is true.

Knowledge of aspects of the ecology and behaviour of these shell-dwelling fish in their natural habitats has enabled the formulation of a series of questions concerning shell burial and use. These questions, mainly relating to shell burying in *L. ocellatus* and *L. ornatipinnis*, were tested by conducting experiments in the lake (Chapters 3 and 4).

CONCLUSIONS

1. The main predators of *L. ocellatus* and *L. ornatipinnis* and *L. laparogramma* are: day-time - *L. callipterus* and *L. cunningtoni*; and night-time - masticembelid eels and *Crysichthys* species.
2. Although several species are often present at any one site certain species were dominant on substrates: *L. ocellatus* - sand; *L. ornatipinnis* - gravels along rock and shell bed boundaries; *N. hecqui* - along shell bed boundaries; and *L. laparogramma* - mud.

3. Territory sizes for both *L. ocellatus* and *L. ornatipinnis* are above 2m².

4. *L. ocellatus*, *L. ornatipinnis* and *L. laparogramma* eat predominantly benthic invertebrates and they maintain feeding territories. In contrast *N. hecqui* forages outside its territorial boundaries.

5. Exhumation of old shells and the arrival of new shells within territories appear to be common. New surface shells are usually buried within one to two hours of detection by residents.

6. There are interspecific differences in behaviour patterns, for example oviposition sites and the numbers of shells in territories.

7. In addition to cichlid fishes other animals use shells as refuges such as bagrid catfish, crabs and shrimps.

CHAPTER 3

EXAMINATION OF SHELL BURIAL BEHAVIOUR IN *Lamprologus ocellatus* AND *Lamprologus ornatipinnis*

BY UNDERWATER EXPERIMENTS IN NATURAL HABITATS.

INTRODUCTION

The use of gastropod shells as refuges and breeding sites by fishes is not unique to Lake Tanganyika. Shell-dwelling fish occur in marine habitats (Breder 1950 & 1954, McLean 1983 & others) and in Lake Malawi (Burgess 1976, Ribbink et al. 1983, Konings 1988). These species use shells for refuges and breeding sites. However, behaviour patterns related to shell use appear more complex and diverse in Tanganyikan cichlids compared to shell-dwelling fishes of other regions. Shells are used opportunistically as temporary refuges, for example by *Telmatochromis vittatus* and *L. lemairii* (Figure 1.6), and as permanent refugia and breeding sites, for example by *L. ocellatus* (Figure 1.8). Sato (1989a) termed these different shell users facultative and obligate shell-dwellers respectively. Facultative shell-dwellers use shells opportunistically and may be found using other refugia or breeding sites, such as rock crevices, when shells are not available. Obligate shell-dwellers are exclusively associated with shells, as refugia and/or breeding sites, for a period in their life histories.

Lamprologus ocellatus, uses gastropod shells as refugia for the whole of their life history and adults spawn exclusively inside shells (Konings 1988). *Lamprologus callipterus* and *Neolamprologus brevis*, also exclusively spawn inside shells, but only use shells as refuges for limited periods during their life histories (Konings 1988). The definitions place *L. ocellatus*, *L. callipterus* and *N. brevis* within the obligate shell-dwelling group.

The obligate shell-dwellers which occur in soft substrate habitats show particularly complex behaviours relating to shell use. Territories comprising one to many shells are actively defended; those

shells in use may be buried or excavated; while those not in use may be moved or hidden. Shell-burying behaviour in *L. ocellatus* has been described by Paulo (1986), Konings (1988), and in greater detail by Haussknecht & Kuenzer (1990). These studies concentrated on the process of shell burial while the underlying reasons for burial were not investigated. Suggestions were made that shells are buried to reduce predation (Konings 1988, Haussknecht & Kuenzer 1990) or to prevent theft of shells by *L. callipterus* (Konings 1988). Haussknecht & Kuenzer (1990) supported their hypothesis with the observation that juveniles bury shells before sexual maturity.

Personal field observations (Chapter 2) contradict Haussknecht & Kuenzer's finding. For example, in natural habitats *L. ocellatus* juveniles rarely bury their shells, juveniles of *Lamprologus lemairii* and *Neolamprologus hecqui* adults excavate depressions around shells, and adult *N. brevis* often bury shells incompletely. Furthermore, the antipredation hypothesis does not account for why excess shells within territories are buried and 'hidden' (see Chapter 2). Exposed excess shells could draw the attention of predators away from shells in use and thus reduce predation.

The hypothesis that shells are buried by *L. ocellatus* to avoid theft by *L. callipterus* (Konings 1988) is also unlikely to be correct. Territorial male *L. callipterus* gather shells and place them in large circular nests. These nests may contain up to 100 shells and exclusively occur at the rock-sand boundary (Sato 1989a). *L. callipterus* males are only able to carry shells over short distances (<5m, pers. obs.) and so the area of soft substrate which is affected by this species is limited. The majority of the shell-burying fish occurring in sand habitats are situated far from *L. callipterus* nest sites. Thus it seems improbable that a species wide evolutionary change could be effected when only part of a population is exposed to that competition.

The process of shell burial is costly in terms of both energy and time expended. Individuals could use unburied shells and spend more time and energy foraging, in territorial defence, mating and other activities. How then does shell burial improve the fitness of the resident fish? My hypothesis is that the burying of shells by *L. ocellatus* and *L. ornatipinnis* is a strategy for reducing competition for shells between other shell-dwellers. In contrast to Konings (1988), I suggest that the competitors are those which are syntopic with the burying species such as *L. laparogramma*, *L. ornatipinnis*, *L.*

ocellatus, *N. hecqui*, *N. pleuromaculatus* and *N. brevis*. By burying shells residents may prevent intruders from obtaining information about shells such as shell quality, size, territorial shell densities and thus also territory value. The objective of this chapter is to test this hypothesis and to determine how shell burial may improve the competitive ability of residents.

In this context I will use the phrase 'improved competitive ability' to indicate that fish enhance their ability to repel intruders (shell-dwelling competitors) during conflicts over shell refuges by adopting certain behaviour patterns e.g. burying shells or orientating shells vertically. This is synonymous with increased fitness as longer retention of territories will also lead to increased reproductive outputs and a higher recruitment rate of offspring.

Experiments were conducted to answer five questions.

1. Can shell quality be determined? For example will all shells within a territory be buried regardless of their condition or will only intact, useable shells be buried?
2. Do fish respond differently to shells of varying size? For example are responses to shells of varying size the same or are there preferred size ranges?
3. Does shell abundance affect fish behaviour? For example are there no differences in shell use and treatment between the first and last shells added to a territory or do fishes' responses to additional shells change?
4. Does shell abundance affect numbers or species composition of shell-dwelling communities? For example will the addition of shells to the site have no effect on the fish present or will there be an increase in fish number and/or a change in species composition?
5. If shells are prevented from being buried, will they be occupied by residents or will residents be replaced by species which prefer unburied shells?

MATERIAL AND GENERAL METHODS

Due to the time-consuming nature of this work it was not possible to examine all of the species in soft substrate habitats. Work concentrated on *L. ocellatus* and *L. ornatipinnis* and while *L. laparogramma*, *N. hecqui* and crabs (*Platythelphusa* spp.) were also observed.

Experiments and observations were conducted using SCUBA. Territories of *L. ocellatus*, *L. ornatipinnis* and *L. laparogramma* were located and marked with lines and metal tags (Figure 3.1). After the addition of lines, these areas were allowed to recover for several days prior to the start of the experiments. The term 'principal shell' refers to that shell at which the fish was observed to spend most of its time. Additional shells and objects were placed 20cm away from the principal shells (Figure 3.1), left for between 24-48 hours and then revisited to record the fishes' responses. Except in Experiment 2, which examines fishes' responses to shells of varying size, all added shells were of medium size (mean shell height 43mm \pm 3.2mm). All added shells were placed on the surface of the sediments with the mouth facing upwards.

Data analysis

Shell usage. Territories were observed for approximately 2 minutes and shells were recorded as: in use (IU) if the resident fish was present at the shell; unused (UU) if absent; and not present (NP) if they were not located.

Shell treatment. Responses to shells were varied and results were recorded as the number of shells that were: not present (NP); unburied (UB); pushed over into the mouth down position (MD); partially buried (PB, Figure 4.8); buried (clear of sediments and in use, B, Figure 5.2); hidden (filled and covered with sediments and not useable, H, Figure 5.3); moved (M); unused (UU); and in use (IU).

Not present (NP) shells may have been stolen by neighbours or removed by residents.

Unburied (UB) shells were those remaining 'mouth-up' on the substrate surface.

'Mouth-down' (MD) shells were shells found lying 'mouth-down' on the substrate surface.

Partially buried (PB) shells were found in a variety of stages of burial ranging from a single small depression to almost complete burial.

Buried (B) shells are fully buried with only the shell mouth visible and they were recorded as 'in use' (IU).

Hidden (H) shells are buried and filled in so that no part of the shell is visible. They are easily located if the covering over process is recent, as digging lines in the substrate are visible. Hidden shells were considered:

- i) 'in use' (in storage for later use) if they were in the species' preferred orientation, and
- ii) 'unused' if not in the species' preferred orientation.

Where shells were relocated within territories and buried they were noted as 'in use' (IU) and where removed as 'unused' (UU).

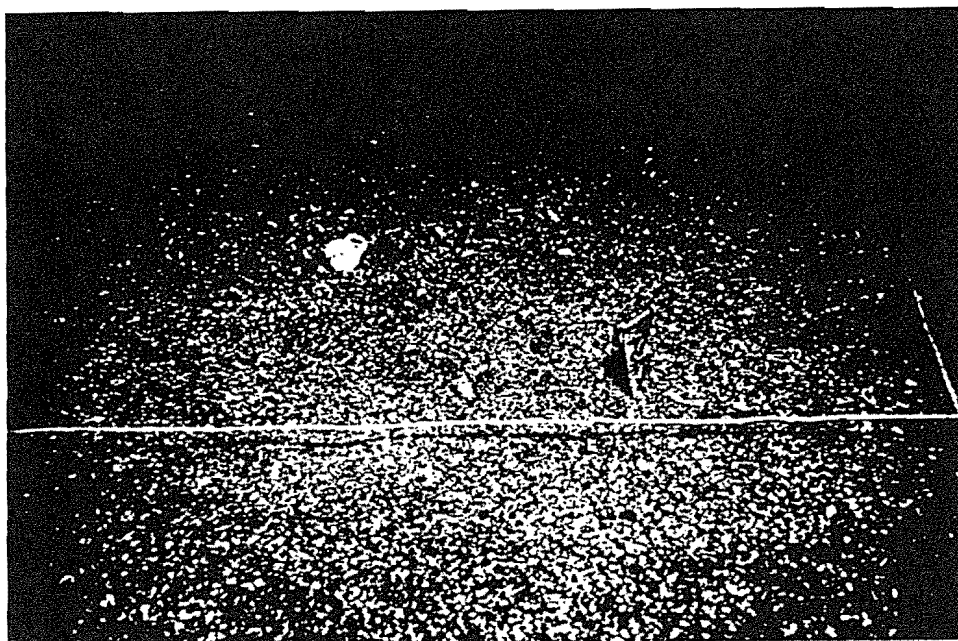


Figure 3.1 Location lines marking fish territories under study. A shell has been added close to the principal shell of an *L. ocellatus* and a metal marker peg indicates the position of the added shell.

EXPERIMENTS AND RESULTS

Experiment 1. Can fish determine shell quality?

Methods

Three types of shell were added to territories: high quality-shells (with side walls intact); disintegrating shells (with most of the side walls lost); and blocked shells (the mouth was filled with silicone glue) (Figure 3.2). Blocked shells were only partially filled with silicone and a small hole was made in the shell wall to vent air when underwater. After 24-48 hours the territories were revisited and fish responses to additional shells recorded.

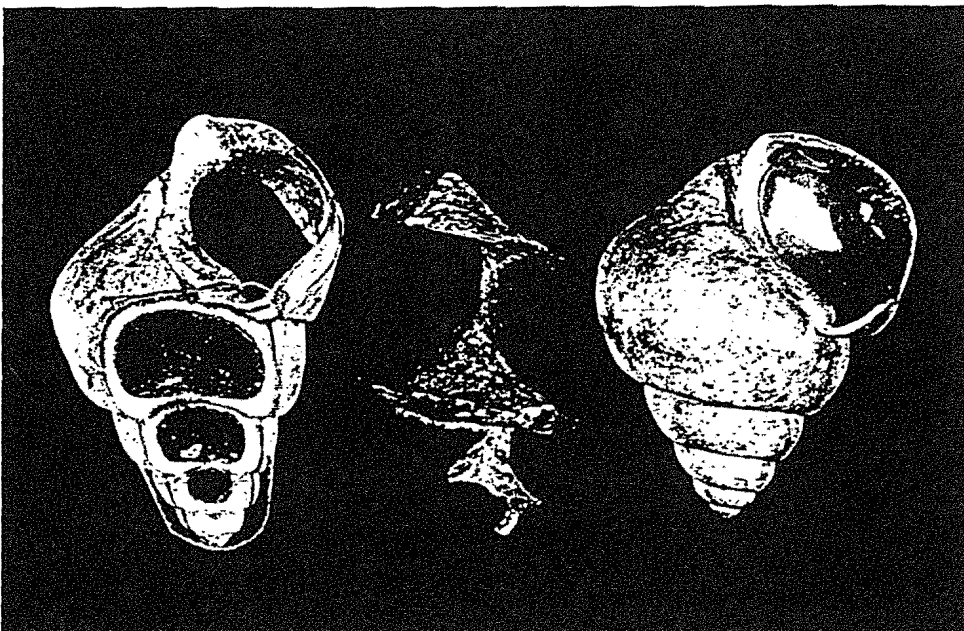


Figure 3.2 Shells used in Experiment 3.1: an 'intact' glass sided shell (for internal shell observations); a 'disintegrating' shell and a 'blocked' shell.

Responses to shells were varied and results were recorded as the number of shells that were: not present (NP); unburied (UB); pushed over into the mouth down position (MD); partially buried (PB); buried (B); hidden (H); moved (M); unused (UU); and in use (IU). A contingency table (Table 3.1) was constructed from results and subjected to chi-square analysis.

Contingency tables were constructed from results and subjected to chi-square analysis. The significance level of $p < 0.05$ (5% error) was chosen.

Results (Table 3.1 and summary Table 3.2).

* Control shells were mostly buried and used by both *L. ocellatus* and *L. ornatipinnis*.

There was no difference in shell use between the two species ($\chi^2 = 2.3$, $df = 1$, $p = 0.13$).

There were significant differences in shell treatment between the two species ($\chi^2 = 19.8$, $df = 6$, $p = 0.003$). *L. ocellatus* completed burying 75% of added shells compared to 25% in *L. ornatipinnis*. 50% of shells added to *L. ornatipinnis* territories were moved while only 5% of shells added to *L. ocellatus* territories were moved.

Table 3.1 Responses by *L. ornatipinnis* and *L. ocellatus* to additions of disintegrating, blocked and intact (control) shells.

Shell added	No	Shell: treatment							use	
		NP	UB	MD	PB	B	H	M	UU	IU
<i>L. ornatipinnis</i>		q								
disinteg	20	2	18	0	0	0	0	5 x	20	0 a
blocked	20	0	17	2	1	0	0	9 x	20	0 a
control	20	0	5	2	8	2	3	10 y	7	13 b
<i>L. ocellatus</i>		q								
disinteg	21	3	17	1	0	0	0	5 x	21	0 a
blocked	22	1	6	3	8	3	1	3 y	19	3 a
control	20	1	1	0	3	9	6	1 z	2	18 b

Abbreviations: not present (NP); unburied (UB); unburied, mouth down (MD); partially buried (PB); buried (B); hidden (H); moved (M); unused (UU); and in use (IU). Different letters to the right of rows indicate statistically significant differences ($p < 0.05$, chi square).

- * Disintegrating shells were all unused and unburied.

There were significant differences in the use of control and disintegrating shells in *L. ocellatus* ($\chi^2=30.1$, $df=1$, $p=0.000$) and *L. ornatipinnis* ($\chi^2=16.4$, $df=1$, $p=0.000$).

The treatment of control and disintegrating shells also differed significantly in *L. ocellatus* ($\chi^2=36.8$, $df=6$, $p=0.000$) and in *L. ornatipinnis* ($\chi^2=25.8$, $df=6$, $p=0.000$).

L. ocellatus and *L. ornatipinnis* showed no differences in their treatment of disintegrating shells ($\chi^2=1.21$, $df=3$, $p=0.75$).

- * Blocked shells were mainly unused by both species.

Three female *L. ocellatus* were small enough to use the vent holes (see methods) of blocked shells. These fish buried shells with vent holes uppermost i.e. in positions uncharacteristic for the species.

The use of blocked and control shells differed significantly in *L. ocellatus* ($\chi^2=21.5$, $df=1$, $p=0.000$) and *L. ornatipinnis* ($\chi^2=16.4$, $df=1$, $p=0.000$).

The treatment of blocked and control shells differed significantly in *L. ocellatus* ($\chi^2=16.2$, $df=6$, $P=0.01$) and *L. ornatipinnis* ($\chi^2=17.0$, $df=5$, $p=0.004$).

There were also differences in treatment of blocked shells between *L. ocellatus* and *L. ornatipinnis* ($\chi^2=18.7$, $df=6$, $p=0.004$).

In *L. ornatipinnis* 45% of blocked shells were moved and 95% remained unburied. In *L.*

ocellatus 55% of blocked shells were either partly or completely buried.

* Shells in varying states of disintegration through age and predator damage, and shells blocked by smaller shells, broken shell material and other shell-dwellers such as crabs were all frequently observed in the study area.

* Low-quality shells were used by juveniles and small, un-paired individuals. These shells were rarely buried and residence times, although not measured, appeared to be short.

Table 3.2 A summary of responses by *L. ornatipinnis* and *L. ocellatus* to the addition of disintegrating, blocked and intact (control) shells.

	<i>L. ocellatus</i>	<i>L. ornatipinnis</i>
<u>DISINTEGRATING SHELLS</u>		
Usage:	all unused	all unused
Treatment:	81% unburied, 25% moved	90% unburied, 25% moved
<u>BLOCKED SHELLS</u>		
Usage:	90% unused	all unused
Treatment:	55% partly or completely buried	95% unburied, 45% moved
<u>CONTROL SHELLS</u>		
Usage:	90% used	65% used
Treatment:	75% completely buried 5% moved	25% completely buried 50% moved

Experiment 2. Do fish respond differently to varying sized shells?

Methods

Shells of three different sizes (20 of each type) were added to territories (Figure 3.3). Mean shell heights (with standard deviation and sample size) were as follows: 'small' shells = 21.1mm (SD = 2.18, n = 20), 'medium' shells = 43.3mm (SD = 3.18, n = 20) and 'large' shells = 56.5mm (SD = 4.0, n = 20). Shell height was the maximum distance between the shell spire and mouth and was measured with vernier callipers. A single shell was added to each fish territory, left for 48 hours and then revisited. Residents' responses to additional shells were recorded (Table 3.3) and results were analysed in the same way as in Experiment 3.1.

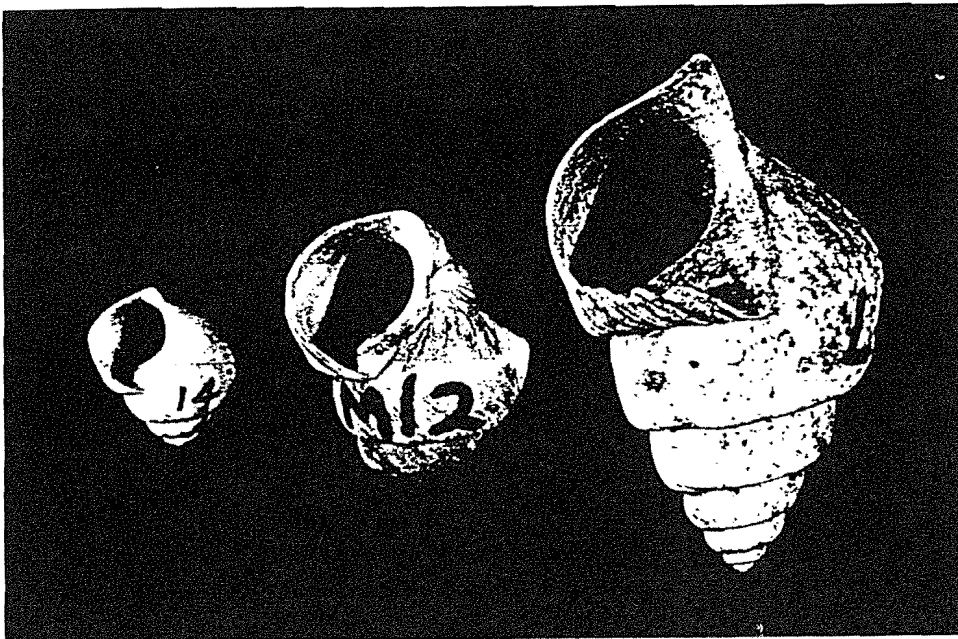


Figure 3.3 Small, medium (this size used in experiment 3.1) and large shells used in Experiment 3.2.

Results (Tables 3.3 and 3.4).

L. ornatipinnis

* Medium and large shells were mainly used (both 60%). Medium and large shells which were in use were in varying stages of burial and their treatment did not differ ($\chi^2 = 8.47$, $df = 6$, $p = 0.21$).

* Small shells were mainly unused and unburied (90%) and a high proportion (60%) were moved. This resulted in differences both in the use and treatment between small and medium shells and between small and large shells:

use of small-medium shells differed ($\chi^2 = 8.9$, $df = 1$, $p = 0.002$) as did their treatment ($\chi^2 = 25.4$, $df = 6$, $p = 0.000$); and

use of small and large shells differed ($\chi^2 = 8.9$, $df = 1$, $p = 0.000$) as did their treatment ($\chi^2 = 22.6$, $df = 6$, $p = 0.000$).

L. ocellatus

* *L. ocellatus* showed a distinct preference for shell size using 80% of medium sized shells, 33% of small shells and 20% of large shells. There were differences in shell use and treatment between the different shell sizes:

use of small and medium shells differed ($\chi^2 = 7.26$, $df = 1$, $p = 0.000$) as did their treatment ($\chi^2 = 14.72$, $df = 6$, $p = 0.02$);

use of medium and large shells differed ($\chi^2 = 12.1$, $df = 1$, $p = 0.000$) as did their treatment ($\chi^2 = 16.34$, $df = 6$, $p = 0.01$).

There was no difference between the use ($\chi^2=0.37$, $df=1$, $p=0.54$) or treatment ($\chi^2=9.04$, $df=6$, $p=0.17$) of small and large shells in *L. ocellatus*.

Table 3.3 Responses by *L. ornatipinnis* and *L. ocellatus* to small, medium and large shells.

Abbreviations: not present (NP); unburied (UB); unburied, mouth down (MD); partially buried (PB); buried (B); hidden (H); moved (M); unused (UU); and in use (IU). Different letters to the right of rows indicate statistically significant differences ($p<0.05$, chi square).

Shell added	No.	Shell treatment							Shell use	
		NP	UB	MD	PB	B	H	M	UU	IU
<i>L. ornatipinnis</i>		q								
small	20	0	14	4	0	1	1	12 x	18	2 a
medium	20	5	1	2	7	2	3	10 y	8	12 b
large	20	3	4	1	6	6	0	6 y	8	12 b
<i>L. ocellatus</i>		r								
small	21	1	11	2	1	4	2	8 x	14	7 a
medium	20	1	2	1	3	8	5	1 y	4	16 b
large	20	0	13	1	3	3	0	1 x	16	4 b

L. ocellatus and *L. ornatipinnis*

* There was no difference in *L. ocellatus*' and *L. ornatipinnis*' response to small shells (use: $\chi^2=2.0$, $df=1$, $p=0.15$, treatment: $\chi^2=5.8$, $df=6$, $p=0.44$). 78% of small shells were unused with 61% unburied and 50% moved (*L. ocellatus* and *L. ornatipinnis* combined).

* *L. ornatipinnis* moved more, and buried and hid fewer, shells than *L. ocellatus* ($\chi^2=15.28$, $df=6$, $p=0.02$). However, *L. ocellatus* and *L. ornatipinnis* used medium shells equally ($\chi^2=1.07$, $df=1$, $p=0.3$).

* *L. ornatipinnis* used, buried and moved more large shells than *L. ocellatus* (shell use: $\chi^2=5.10$, $df=1$, $p=0.02$, shell treatment: $\chi^2=12.95$, $df=5$, $p=0.02$).

* Juvenile *L. ocellatus* were frequently observed using small shells (< 25mm) of several species of gastropod (Table 2.2). These were rarely buried and appeared to be used as transient refuges.

Table 3.4 A summary of the responses by *L. ocellatus* and *L. ornatipinnis* to shells of varying size being added to territories.

	<i>L. ocellatus</i>	<i>L. ornatipinnis</i>
<u>SMALL SHELLS</u>		
Usage:	67% unused	90% unused
Treatment:	52% unburied, 38% moved	70% unburied, 60% moved
<u>MEDIUM SHELLS</u>		
Usage:	76% used	60% used
Treatment:	76% partly or completely buried, 5% moved	60% partly or completely buried, 50% moved
<u>LARGE SHELLS</u>		
Usage:	76% unused	60% used
Treatment:	62% unburied, 5% moved	60% partly or completely buried, 30% moved

Experiment 3. Does shell abundance affect fish behaviour?

Methods

Due to restricted dive times and the length of setting up this experiment, only eight *L. ocellatus* and thirteen *L. ornatipinnis* territories were located and marked. Five shells were added to each territory over a ten-day period (one shell every two days). The first additional shell was denoted as Sa1 through to the fifth additional shell Sa5. Fish's responses to each shell were recorded after two days and then

the next shell was added. The behaviour of *L. ocellatus* and *L. ornatipinnis* appeared different, and so the two data sets were not combined to increase cell frequencies. Responses were recorded (Table 3.5) and analysed in the same way as Experiments 3.1 and 3.2.

Results

* During the course of this experiment, resident fish were not always observed. Initially open shells were thought to indicate fish residency. However, by the end of the experiment it was clear that two good indicators of the original resident being absent were:

- i) the presence of other fish at open shells, and
- ii) low numbers of shells within territories.

On this basis, six territories were considered deserted, two of *L. ocellatus* and four of *L. ornatipinnis*. In three territories other fish were present (two juvenile *L. ocellatus* and one adult *N. hecqui*) and in three there were no fish and 0 to 3 shells (none of which were buried).

* *L. ocellatus* differed in its treatment of shells during the experiment. The numbers of shells buried decreased as shells added to the territory was increased ($\chi^2 = 20.5$, $df = 4$, $p < 0.01$).

* Despite this, by the end of the experiment, there was no change in the percentage of buried shells (79%) within *L. ocellatus* territories. This was partly due to residents 'catching up' with shell burial at the end of the experiment and partly due to thefts of unburied shells by non-residents.

* In *L. ornatipinnis* there were no differences in the treatment or use of shells during the experiment.

* The mean number of shells in territories and percentage shell use before and after shell additions is shown in Table 3.6. There was a difference in the number of shells removed from and

Table 3.5 Responses by *L. ocellatus* and *L. ornatipinnis* to increasing numbers of new shells.

Added shells	Shell treatment						Shell use	
	NP	UB	PB	B	H	M	UU	IU
<i>L. ocellatus</i> (6)								
start	-	0	0	11	0	-	0	11
Sa1	0	0	0	6	0	1	0	6
Sa2	0	0	1	3	2	0	1	5
Sa3	0	1	2	3	0	0	2	4
Sa4	0	1	2	3	0	0	2	4
Sa5	1	2	0	2	1	1	3	3
end	-	5	0	27	2	-	5	29
<i>L. ornatipinnis</i> (9)								
start	-	3	6	15	0	-	9	15
Sa1	4	2	1	1	1	7	7	2
Sa2	1	2	2	1	3	3	4	5
Sa3	0	1	2	3	3	3	2	7
Sa4	1	2	3	1	2	7	5	4
Sa5	1	3	5	0	0	1	5	4
end	-	18	11	26	12	-	24	43

Abbreviations: not present (NP); unburied (UB); unburied, mouth down (MD); partially buried (PB); buried (B); hidden (H); moved (M); unused (UU); in use (IU); Sa1 = first additional shell; and Sa2 = second additional shell etc.

remaining in occupied territories ($\chi^2 = 46.4$, $df = 1$, $p < 0.01$) but not in unoccupied territories ($\chi^2 = 0.54$, $df = 1$, $p > 0.05$, Table 3.7).

* Two individuals, immediately after shell additions, were observed to hide their principal shells and move to secondary shells. By the next shell addition these fish had returned and opened the principal shell. Although rarely observed, this behaviour was also noted in Experiments 3.2 and 3.5.

Table 3.6 The number of shells present and in use in *L. ocellatus* and *L. ornatipinnis* territories before and after Experiment 3.3.

Shells in territory	start			end		
	mean & SD	no	% use	mean & SD	no	% use
<i>L. ocellatus</i>	1.9 ± 0.9	8	100	5.7 ± 0.8	6	85
<i>L. ornatipinnis</i>	2.2 ± 1.4	13	68	7.4 ± 1.8	9	64

Mean & SD = numbers of shells in fish territories, no = number of fish territories, % use = percentage of shells in use by residents of each territory.

Table 3.7 The number of shells removed from and remaining in occupied and deserted territories during Experiment 3.3 (Data for *L. ocellatus* and *L. ornatipinnis* was combined).

shells	occupied (n = 15x5)	unoccupied (n = 6x5)
removed	8	17
remaining	67	13

Experiment 4. Does shell abundance affect numbers or species composition of shell-dwelling communities?

Methods

Eight 10m x 1m transects were permanently fixed to the substrate. The transects were set up in mud habitats where shell abundance was low (<1 shell/m²). Two hundred and forty shells were added to four 'experimental' transects (60 each) and no shells were added to the other four 'control' transects. Fish and shell numbers were counted before and three months after shell additions. As shell burial is an energy- and time-consuming process a period of three months was chosen to allow the fishes present in the transect areas to bury shells. Due to the low numbers of fish present, the eight transects' data were pooled into 'control' and 'experimental' groups. The species and numbers present, before and after shell additions, were compared with contingency tables (Table 3.8) and chi-squared analysis.

Results

- * At the start of the experiment there were no differences between the communities of shell dwellers in 'control' and 'experimental' transects ($\chi^2 = 6.0$, $df = 3$, NS).

- * The movement of shells by male *L. ornatipinnis* resulted in shell numbers decreasing in 'experimental' transects and increasing in 'control' transects. The control transects therefore became experiments where low numbers of shells were added.

- * In the 'control' transects there was an increase in average shell abundance from 8 to 53 shells (Table 3.8). However, there were no changes in fish numbers, species composition ($\chi^2 = 5.8$, $df = 4$, NS) or in visible numbers of shells. Resident fish buried all the new shells of which 83% were hidden.



Figure 3.4 A crab (*Platythelphusa maculata*) occupying a shell buried by *L. ocellatus*. Its claw is extended from the shell mouth in defence.

Table 3.8 Species compositions of transects at Musende Rocks, Mpulungu, before and after shell additions.

Transect nos.	Shell nos. (hidden)	Species present				
		ocel	ornat	laparo	hecqui	crabs
CONTROL						
start	8 (0)	0	2	27	0	1
after 3 months	53 (44)	3	2	27	1	5
60 SHELLS ADDED						
start	8 (0)	3	0	26	0	0
after 3 months	179 (44)	4	4	22	4	93

Species present: ocel = *Lamprologus ocellatus*, ornat = *L. ornatipinnis*, laparo = *L. laparogramma*, hecq = *N. hecqui* and crabs = *Platythelphusa maculata*.

* In 'experimental' transects shell numbers had decreased from 240 to 179. 61 shells had been removed and 44 shells hidden. The majority of remaining shells (135) was unburied on the sediment surface. These unburied shells were mainly occupied by juvenile crabs (*Platythelphusa maculata*, Figure 3.4).

* In the 'experimental' transect there was a change in the species composition after three months ($\chi^2=65.9$, $df=4$, $p<0.001$). There was also a difference between the 'experimental' and 'control' transects after three months ($\chi^2=48.1$, $df=4$, $p<0.001$). With the exception of *L. laparogramma* all shell dwelling species in the 'experimental' transect had increased in abundance. The number of crabs had increased from 0 to 93 and these were the dominant shell dwellers.

Experiment 5. What if shells are prevented from being buried?

Methods

Shells, which were glued to metal plates to prevent burial or movement, were added to territories. Shells were orientated flat, as they would lie on the surface of the substrate. The species and sex of the original residents and immigrants present at 'metal plate shells' (referred to subsequently as MP shells) and control shells were recorded. This experiment was conducted at two sites: Musende Rocks (Table 3.9); and Gitaza (Table 3.10).

Results

- Musende Rocks, Zambia.

* Many of the shells glued to metal plates were inspected and occupied by intruders, as well as by the original territory holders. Whilst residents were usually the first to inspect new shells, they were

often followed by a series of other fish, usually larger than residents, which were sometimes in groups. Intruders were dominated by *N. hecqui* and males of *L. ornatipinnis* and *L. ocellatus*. When larger intruders inspected shells, residents hovered close by displaying erect fins but only rarely attacked.

* There was a significant difference in the number of original residents and immigrants between fish given metal plate shells and control shells for both *L. ocellatus* ($\chi^2 = 13.1$, $df = 2$, $p = 0.001$) and *L. ornatipinnis* ($\chi^2 = 17.1$, $df = 2$, $p = 0.001$) (Table 3.9). Thirty nine fish (98%) which were given control shells remained in their territories. In contrast only 18 fish (45%) given metal plate shells remained in territories. Nineteen fishes immigrated into territories where metal plate shells were added of which 11 (58%) were heterospecifics. In the control shell additions there was only one (heterospecific) immigrant.

* Responses to metal plate shells were varied:

- i) MP shells were ignored and residents continued to use their principal shells;
- ii) residents occupied both MP and principal shells;
- iii) principal shells were filled in and MP shells adopted as new principal shells;
- vi) residents hid principal shells, ignored MP shells and moved to secondary shells;
- iv) residents were chased away from territories and immigrants occupied MP shells;
- v) territories were abandoned and MP shells remained unoccupied; and
- vi) residents used principal shells and immigrants used MP shells.

* *L. ocellatus* and *L. ornatipinnis* did not differ in their response to metal plate shells ($\chi^2 = 0.4$, $df = 2$, $p = 0.83$).

* Males and females (*L. ocellatus* and *L. ornatipinnis* combined) differed in their response to metal plate shells ($\chi^2 = 15.4$, $df = 2$, $p = 0.000$). 70% of males remained in their territories defending metal

plate shells. In some instances males appeared to have left their principal shell and be resident at the metal plate shell. In contrast, 80% of females had either moved to secondary shells or abandoned their territories. Where immigrants were conspecific males the females did not leave shells.

Table 3.9 Responses of *L. ocellatus* and *L. ornatipinnis* to the addition of shells glued to metal plates (Musende Rocks, Zambia).

Species/ sex	number of fish	Fish present after 24 hours			Immigrant species
		Resident	Immigrant	none	
<i>L. ocellatus</i>					
female	10	3	7	3	8Nhe,2Loc
male	10	7	2	1	2Nhe
Total	20	10	9	4	10Nhe,2Loc
Control	20	19	1	0	1Nhe
<i>L. ornatipinnis</i>					
female	10	1	7	2	3Nhe,4Lor
male	10	7	0	3	-
Total	20	8	7	5	3Nhe,4Lor
Control	20	20	0	0	-
Total females	20	4	14	5	11Nhe,4Lor, 2Loc
Total males	20	15	2	4	2Nhe

(Nhe = *Neolamprologus hecqui*, Loc = *Lamprologus ocellatus* & Lor = *L. ornatipinnis*)

- Gitaza, Burundi.

* The shell dwelling community near Gitaza (Burundi) consisted of *L. ocellatus*, *N. brevis*, *N. pleuromaculatus* and the crab *Platythelphusa polita* (Table 3.10). Twenty four hours after the addition of metal plate shells 40% of the original residents remained in territories. All immigrants (seven) were

larger than original residents and four (57%) of the immigrants were *N. pleuromaculatus*.

Table 3.10 Responses of *L. ocellatus* to the addition of shells glued to metal plates at Gitaza, Burundi.

Species & sex	Resident fish present	Immigrant fish present	Immigrant species
<i>L. ocellatus</i>			
female	2	5	2Npl, 1Nbr, 1Loc, 1crab
male	3	2	2Npl
Total	5	7	4

(Npl = *Neolamprologus pleuromaculatus*, Loc = *Lamprologus ocellatus*, Nbr = *N. brevis*)

* *N. hecqui* (Mpulungu) and *N. pleuromaculatus* (Burundi) are the largest shell dwellers in their respective communities and both excavate depressions around shells rather than burying them.

* Several females, in response to the addition of metal plate shells, hid principal shells and moved to secondary shells. At the end of the experiment, metal plate shells were retrieved. With the removal of MP shells females returned and opened the hidden principal shells.

DISCUSSION

Can fish determine shell quality?

Both *L. ocellatus* and *L. ornatipinnis* are able to assess shell quality and size. Their responses to shells vary according to these assessments.

Shell burial by *L. ocellatus* and *L. ornatipinnis* is a complex behaviour consisting of inspection,

digging in and covering over phases (Hausknecht & Kuenzer 1990). The time an individual takes to bury a shell varies with fish and shell size and probably motivation, from less than an hour to several days. Several hundred acts of inspection, digging and covering over are conducted during the course of shell burial. Thus the costs in time and energy expended, and the increased possibility of predation whilst occupied in digging, must be high. Where the cost of using a resource is high, the importance of inspection behaviour should be dependant on the reasons for shell burial and the resource variability. If all shells are buried or there is no variation in shell quality, inspection is clearly unnecessary. If only certain shells are used and those shells encountered are of variable quality, inspection behaviour becomes essential if the individual is to be efficient in its allocation of time and energy.

The quality of shells in natural habitats is variable, with some having disintegrated through old age, some being partially broken from crab predation (West et al. 1991, Chapter 2) and intact shells may be blocked with shell debris, gravel and crabs. Experiments and observations of wild fish have shown that *L. ocellatus* and *L. ornatipinnis* are able to assess shell quality (Tables 3.1 and 3.2) and thus the null hypothesis is rejected. In general, only high quality shells were buried. Some fish did initiate burial of blocked shells and this is discussed in Chapter 6.

The assessment process in the cichlids studied here is different from that of marine hermit crabs. Hermit crabs occupy and use single shells and do not hold territories. When a hermit crabs is presented with a new shell, the occupied and new shells are compared. The result of the inspection behaviour is that the shell which fits best or is of higher-quality will be accepted and the poorer fitting or lower-quality shell will be rejected. In contrast to hermit crabs, *L. ocellatus* and *L. ornatipinnis* defend territories over 1m² in area. All shells in these territories, providing they are within broad size or quality ranges, are buried. Comparisons of shells may be made once a new shell is buried. Inspection behaviour in *L. ocellatus* and *L. ornatipinnis* occurs throughout the burial process (Hausknecht & Kuenzer 1990, pers. obs.). The assessment of many factors may be essential to territory maintenance

and responses to individual shells may depend on factors unrelated to shell quality or size. The proximity of mates, neighbours and regional shell abundance may all be assessed and affect an individual's response to a shell (see Chapter 6).

Do fish respond differently to varying sized shells?

Fishes' responses to added shells indicates that *L. ocellatus* prefers 'medium' (43.3mm) shells and *L. ornatipinnis* prefers 'medium' to 'large' (43.3mm-56.5mm) shells. Several factors may contribute to this:

a) the costs of burying shells was shown by Hausknecht and Kuenzer (1990) to increase with increasing shell size;

b) by choosing shells of close fit, individuals may restrict the size and number of competitors for shells; and

c) 'small' (21.1mm) shells may be ignored or used unburied because they are only occupied by small individuals temporarily.

Thus for *L. ocellatus* the higher costs of burial and increased competition may outweigh the benefits of using larger shells. Field observations (Chapter 4) indicate that shell and fish sizes are related.

Does shell abundance affect fish behaviour?

In *L. ornatipinnis* the use and treatment of shells did not change with increasing numbers of shells added. In *L. ocellatus* the only change which occurred was that the percentage of shells buried decreased (77%) with increasing shells added. However, two days after the end of the experiment the majority of shells (79%) in *L. ocellatus* territories were buried. I suggest that the change in the number

of shells buried by *L. ocellatus* during the course of the experiment was caused by fatigue from burying five shells in 10 days. Both species actively reduce visible, high-quality shells within territories. This strategy does not appear to change with increasing shell numbers tested although the ability of individuals to bury shells may be reduced.

In areas of where shell abundance is high, such as near the rock and shell-bed interfaces, *L. ornatipinnis* is generally more abundant than *L. ocellatus*. This may be because increased numbers of shells may be too costly to bury and that the larger species (*L. ornatipinnis*) is more capable of defending exposed shells. Results indicate that residents actively defend both buried and unburied shells within territories (Table 3.7).

It was expected that once the fish had accumulated enough shells for refuges and breeding, any excess shells would be ignored. Although there were some instances of large male *L. ornatipinnis* carrying shells to the peripheries of territories, most fish are not capable of moving shells. Therefore the only option smaller fish have to reduce shell numbers is to bury and hide them. It seems that territorial space in soft substrate habitats is limiting. As territories are centred around shells, competition for space can be reduced by removing shells, either by movement or hiding.

Does shell abundance affect numbers or species composition of shell-dwelling communities?

My null hypothesis was that shell abundance would not alter the fish community. An alternative hypothesis was that shell numbers would add numbers and diversity to the ecosystem and thus effect changes in fish numbers and species composition.

When small numbers of extra shells were added, residents were able to bury and hide all shells and so maintain the original number of exposed shells on the surface. There was no change in either

fish abundance or species composition.

When higher numbers of shells were added residents were apparently unable to bury all the new shells. Some of the consequences were: an increase in the numbers of visible shells; an increase in abundance of shell dwellers; and a change in the species composition; a change in the dominant species. The new dominant species was the crab, *P. maculata*, which mainly occupied unburied shells. Crabs defend their shells by extending their larger chela into the shell mouth (Figure 3.4), thus preventing fish from burying shells (see Experiment 4.5). All species increased in number with the exception of the originally dominant species *L. laparogramma*.

These results indicate that shells are buried to reduce competition for shells and that unburied shells are more difficult to defend. Buried shells probably attract less attention from other shell-dwellers and thus intrusions into territories may be reduced. Also intruders may fight for shorter times where shells are not fully visible so that proper assessments of quality and size are not possible.

Changes in species composition with varying shell abundance has conservation implications. Regular seine netting of sublittoral, soft-substrate habitats occurs lake-wide. The disturbance of bottom sediments by seine nets may alter shell distributions and abundance with consequent changes in fish abundance and species composition.

What if shells are prevented from being buried?

A high proportion of shells that were prevented from being buried were occupied by immigrants. As with the increased shell density experiment, this indicates that there is both intra- and interspecific competition for shells. On numerous occasions intruders were observed entering territories and inspecting unburied shells. Therefore the burying of shells seems to enhance the ability of *L.*

ocellatus and *L. ornatipinnis* to defend shells. As would be expected, males (larger individuals) are more capable of defending shell resources than females (smaller individuals). This was reflected by the occurrence of fewer immigrants in males' territories. Females probably rely heavily on males for territorial defence of joint male-female territories.

Why are shells buried?

The responses of fish to shells of varying quality and size suggests that the reason for burying shells is not related to predation. Most shells that are valuable as refuges are buried, often when occurring in excess of resident's refuge needs, which implies that burial is a method of preventing other shell-dwellers access to shells. Why then prevent shell access if the shells are in abundance?

Although feeding ecology has not been examined, cursory feeding observations (Chapter 2) of *L. ocellatus*, *L. ornatipinnis* and *L. laparogramma* indicate that the majority of feeding is from the substrate. Territories are used for feeding and food is a finite and defensible resource. As shells form the focal point of territories fish can reduce competition for space and food by restricting access to shells.

Buried and hidden shells are detectable by other fishes so how can shell burial help in reducing competition for shells? When two competitors fight for a resource the victor should be the one with the highest ratio of resource value to cost of contesting and maintaining that resource (Maynard Smith 1974). A major component of the cost is the difference in fighting ability, usually determined by size, between the two individuals which affects the probability of incurring injury. In most animal conflicts both the values and costs vary for each contestant i.e. there are asymmetries (Maynard Smith & Parker 1976, Hammerstein 1981, Parker & Rubenstein 1981). Territory holders, fighting over resources, usually have an advantage over intruders (Hammerstein 1981, Enquist & Leimar 1987). In territorial

species the strategy 'respect ownership status if the difference in fighting ability is below a critical value, and respect fighting ability for larger differences' seems to be common (Hammerstein 1981). Several reasons may account for this: stronger individuals may accumulate if the resource is long lived; the resource value may be higher for the owner than the intruder; role asymmetries (owner-intruder) may be enough if there are no other asymmetries (reviewed in more detail by Leimar & Enquist 1984, Enquist & Leimar 1987).

My hypothesis is that the burying and hiding of shells by *L. ocellatus* and *L. ornatipinnis* is related to increasing asymmetries in resource value between residents and intruders. By burying shells residents can reduce the information, concerning territorial resources (shell numbers and quality), available to intruders. This may be achieved in two ways.

1. Shell burial reduces the stimulus of a visible 'shell' to 'shell mouth' or in hidden shells simply a 'mound of sand'. This may cause intruders to be less motivated to inspect shells particularly when these are defended by residents. Where shells are approached inspections will be incomplete because thorough external and internal inspections are not possible. Motivation to fight for a buried shell should be lower compared to an unburied shell. Hausknecht & Kuenzer (1990) showed that inspection is a necessary precursor to accepting and burying shells and it may also be true for contesting over a shell.
2. Hidden shells do not have to be defended and they may increase the value of territories for residents. Intruders, disputing ownership of a single shell, will be unaware of hidden shell resources and thus the total value of territories.

This agrees with Enquist & Leimar (1987) who stated that resource value is likely to be the most important variable in fighting ability after individual size. Their model predicts that contestants will take higher risks for higher rewards and that individuals with more to gain will win more frequently. Results in Experiment 5 support this hypothesis (Table 3.9). Shells which could not be buried (MP shells) were occupied by intruders more (37.5%) than shells which could be buried (control shells).

During these experiments some shells became occupied by heterospecifics and *L. ornatipinnis* stole shells from neighbouring con- and heterospecifics. Competition for shell resources between both con- and heterospecifics therefore appeared to be intense. There were also interspecies differences in responses to shell additions. Differences in both behaviour patterns and responses to shells between *L. ocellatus* and *L. ornatipinnis* are investigated in Chapter 4.

CHAPTER 4

INTERSPECIFIC COMPETITION FOR SHELL RESOURCES

INTRODUCTION

Shell-dwelling cichlid communities in Lake Tanganyika usually comprise several species. During the course of initial observations (Chapter 2) and experiments (Chapter 3) interspecies differences in fish behaviour patterns were noted. Differences in shell burial methods between *L. ocellatus* and *N. brevis* were first reported by Pauló (1986).

Specifically, differences between *L. ocellatus* and *L. ornatipinnis* in methods of shell burial, shell orientation and the sizes of shells used were observed (Chapter 2 & 3). The purpose of this chapter is to:

1. report some of these interspecific differences in behaviour patterns; and
2. examine how certain behaviour patterns may affect interspecies competition for shell resources.

As in Chapter 3, the main species examined were *L. ocellatus* and *L. ornatipinnis*. Observations and experiments were conducted to answer five questions.

1. Are there interspecific differences in shell sizes used? For example are shells of varying size used randomly as they are encountered or do fish of each species select shells of specific size ranges?
2. Are there interspecific differences in methods of shell use? For example will shells be used by all species in the same way or will each species exhibit distinct methods of shell use?
3. Does shell orientation affect which species use shells? For example if a fish finds a shell buried in an undesirable position will it use the shell as it finds it, dig it up and reposition it before use, or not use it?

4. If residents are removed from territories but shells are left, which species will recolonise the shells? For example will recolonisation of shells be random with respect to species or will immigrants be of similar size and the same species and sex as those removed.

5. How do residents respond to heterospecific shell-dwelling intruders? For example will intruders be ignored or will con- and heterospecifics be attacked with equal vigour?

MATERIAL AND GENERAL METHODS

Due to the time-consuming nature of this work it was not possible to examine all of the species. In most cases *L. ocellatus* and *L. ornatipinnis* were studied. When time permitted limited observations were made of *L. laparogramma*, *N. hecqui* and juvenile crabs (*Platythelphusa* spp.).

Experiment 1. Are there interspecific differences in shell sizes used?

Methods

Shell-dwelling fishes and crabs, together with their shells, were collected and individually bagged underwater. Upto twenty five specimens of each species were collected, although at some sites certain species were rare. Collections were made at four sites in Zambia: 1. Kombe; 2. Mbita Island; 3. Musende Rocks; 4. Musende Rocks; and one in Burundi 5. Gitaza (see Table 4.1).

Total and standard length and body depth were measured. However, this last parameter was considered unreliable due to barotrauma. Crabs were measured for maximum width across the carapace, minimum width between the eye sockets and carapace length (anterior to posterior). Shells were measured for maximum height and width and mouth height and width. These data (Table 4.2) were plotted on scatter graphs with regression lines (Figures 4.1 to 4.5).

Table 4.1 Details of the collection sites for fish size-shell size correlation analyses.

Site	Kombe	Mbita	Musende	Musende	Gitaza
Country	Zambia	Zambia	Zambia	Zambia	Burundi
Substrate	sand	gravel-sand	mud	shell-bed edge	sand
Depth (m)	10-20	10-20	20	20	10-20
Shell abundance	< 1/5m ²	> 5/m ²	< 1/5m ²	> 200/m ²	1-5/m ²
Shell-dwellers (d = dominant, p = present, - = absent)					
<i>L. ocellatus</i>	d	d	p	p	d
<i>L. ornatipinnis</i>	-	p	p	p	-
<i>L. laparogramma</i>	-	-	d	p	-
<i>N. hecqui</i>	-	p	p	p	-
<i>N. brevis</i>	p	-	-	-	p
<i>N. pleuromaculatus</i>	-	-	-	-	p
crabs	-	p*	p*	p*	p**

* *P. maculata*, ** *P. polita*

Results

* Kombe (Sand slope, Figure 4.1). *L. ocellatus* attained a larger size and used larger shells at this site than at any of the other sites (Table 4.1).

* Mbita Island (Figure 4.2). Fish standard length showed a high correlation with shell refuge size for *L. ornatipinnis* ($n = 29$, $r^2 = 58.7$, $p < 0.0001$) and *L. ocellatus* ($n = 31$, $r^2 = 64.8$, $p < 0.0001$). *N. hecqui* was weakly correlated with shell size ($n = 27$, $r^2 = 27.6$, $p = 0.004$).

* Musende Rocks (mud flats, Figure 4.3). *L. laparogramma* was the only facultative shell-dweller at this site. *L. laparogramma* SL was weakly correlated with shell height ($n = 38$, $r^2 = 17.1$, $p < 0.009$).

In contrast the other common species of shell-dwellers were highly correlated with shell height (*L. ornatipinnis*, $n=19$, $r^2=63.4$, $p<0.001$ and *L. ocellatus*, $n=34$, $r^2=60.3$, $p<0.001$). Only three specimens of *N. hecqui* were collected and the resulting correlation is not significant ($n=2$, $r^2=57.7$, $p=0.45$).

* Musende Rocks (sand-gravel slope, Figure 4.4). There was a high correlation between fish SL and shell height for *L. ocellatus* ($n=21$, $r^2=69.7$, $p<0.001$) and for *L. ornatipinnis* ($n=23$, $r^2=61.3$, $p<0.001$). *N. hecqui* SL showed a moderate correlation with shell height ($n=21$, $r^2=43.1$, $p<0.01$). Crab size showed negligible correlation with shell height ($n=23$, $r^2=9.2$, $p=0.16$).

* Gitaza, Burundi (Figure 4.5). The low numbers of *N. pleuromaculatus* and *N. brevis* resulted in non-significant correlations. There was a moderate correlation between fish SL and shell size for *L. ocellatus* ($n=49$, $r^2=47.8$, $p<0.0001$) and *P. polita* ($n=28$, $r^2=44.8$, $p<0.0001$).

If all the fishes are combined (Figure 4.5) as a community, fish SL shows a strong correlation with shell size ($n=74$, $r^2=69.4$, $p<0.0001$).

* At all the sites there is a hierarchy of fish sizes with adult male *N. pleuromaculatus* (Burundi) and *N. hecqui* (Zambia) being the largest fish and using the largest shells. Female and juvenile *L. ocellatus* were the smallest shell-dwellers and they used the smallest shells (Figures 4.1 to 4.5).

* *Platythelphusa maculata* (Zambia) and *P. polita* (Burundi) differed in the sizes of their chela although this was not measured (Figure 2.19). Some *P. polita* shared shells with mates with the larger males always being in the outer section of the shell. A few females were found carrying eggs indicating that this species matures at a small size.

Table 4.2 The average fish and shell sizes from collection sites.

Species / site	no	Fish SL \pm S.D.	Shell ht \pm S.D.
Kombe (sand, 10-20m depth)			
<i>N. brevis</i>	5	44.4 \pm 2.1	54.7 \pm 2.6
<i>L. ocellatus</i>	34	39.0 \pm 9.4	44.7 \pm 9.9
Mbita Island (gravel, 10-20m depth)			
<i>N. hecqui</i>	28	49.5 \pm 7.2	51.2 \pm 4.2
<i>L. ornatipinnis</i>	30	38.1 \pm 8.2	47.4 \pm 7.1
<i>L. ocellatus</i>	32	30.6 \pm 7.0	39.3 \pm 7.9
Musende Rocks (mud, 20m depth)			
<i>N. hecqui</i>	3	43.1 \pm 7.0	44.1 \pm 4.8
<i>L. ornatipinnis</i>	20	39.5 \pm 9.1	42.1 \pm 5.3
<i>L. laparogramma</i>	38	32.2 \pm 4.5	40.1 \pm 4.9
<i>L. ocellatus</i>	35	31.7 \pm 7.2	36.8 \pm 8.6
Musende Rocks (shell bed edge, 18-20m depth)			
<i>N. hecqui</i>	21	44.6 \pm 9.7	37.0 \pm 2.4
<i>L. ornatipinnis</i>	23	43.3 \pm 8.0	35.7 \pm 3.5
<i>L. ocellatus</i>	21	33.5 \pm 7.9	31.5 \pm 6.1
Crab (<i>P. maculata</i>)	23	13.6 \pm 1.9	35.3 \pm 2.7
Gitaza (sand-mud, 11-18m depth)			
<i>N. pleuromaculatus</i>	10	50.2 \pm 3.0	51.2 \pm 4.7
<i>N. brevis</i>	15	39.4 \pm 2.1	47.6 \pm 2.5
<i>L. ocellatus</i>	50	30.3 \pm 6.5	36.7 \pm 5.1
Crab (<i>P. polita</i>)	25	14.4 \pm 3.1	40.0 \pm 6.2

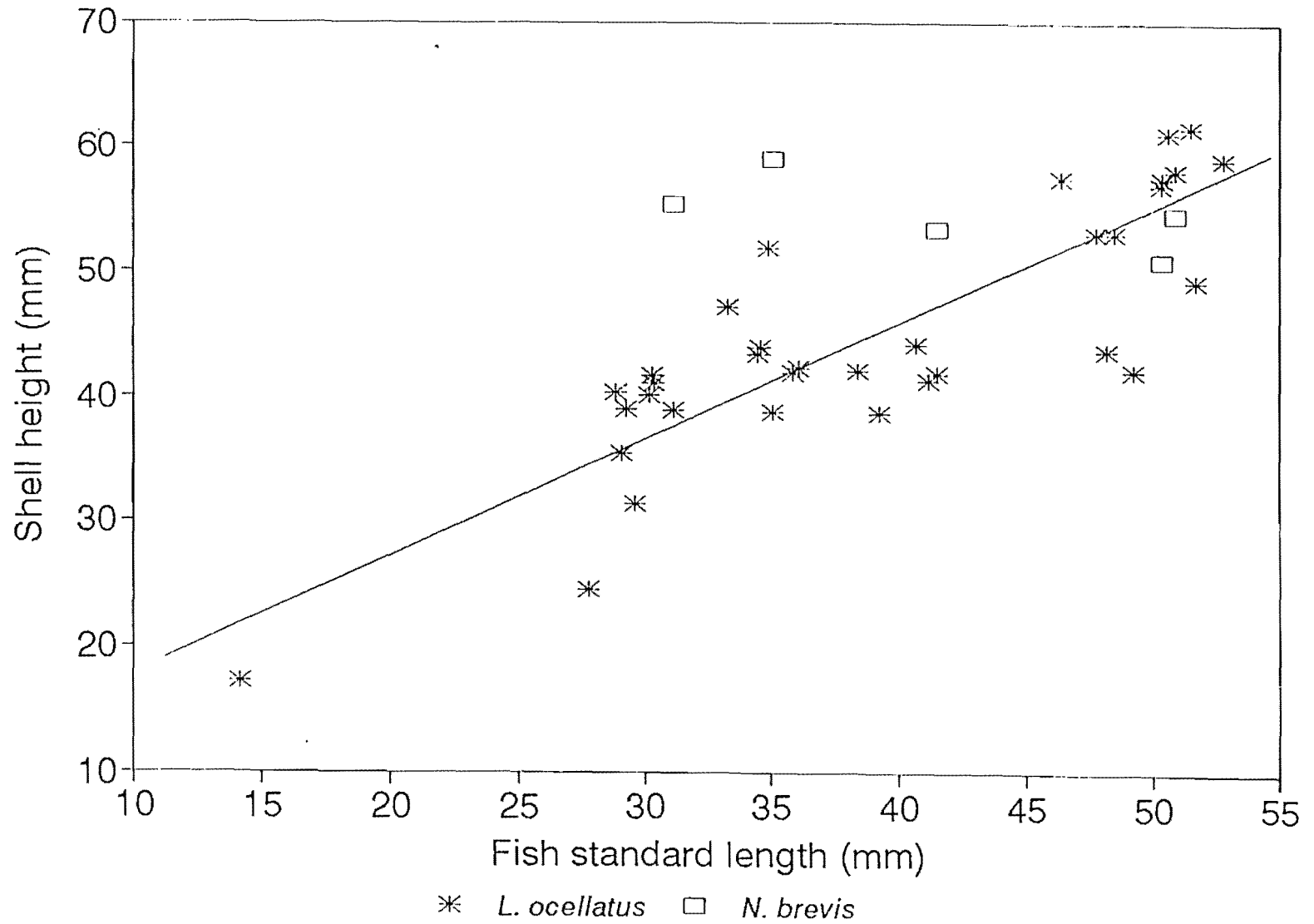


Figure 4.1 Relation between shell-dweller size (fish SL or crab carapace width) and refuge shell size (shell height) at Kombe, Zambia. Collection site: sand, 20m depth. Regression line for combined shell-dwelling fish community: $y = 9.0 + 0.9x$

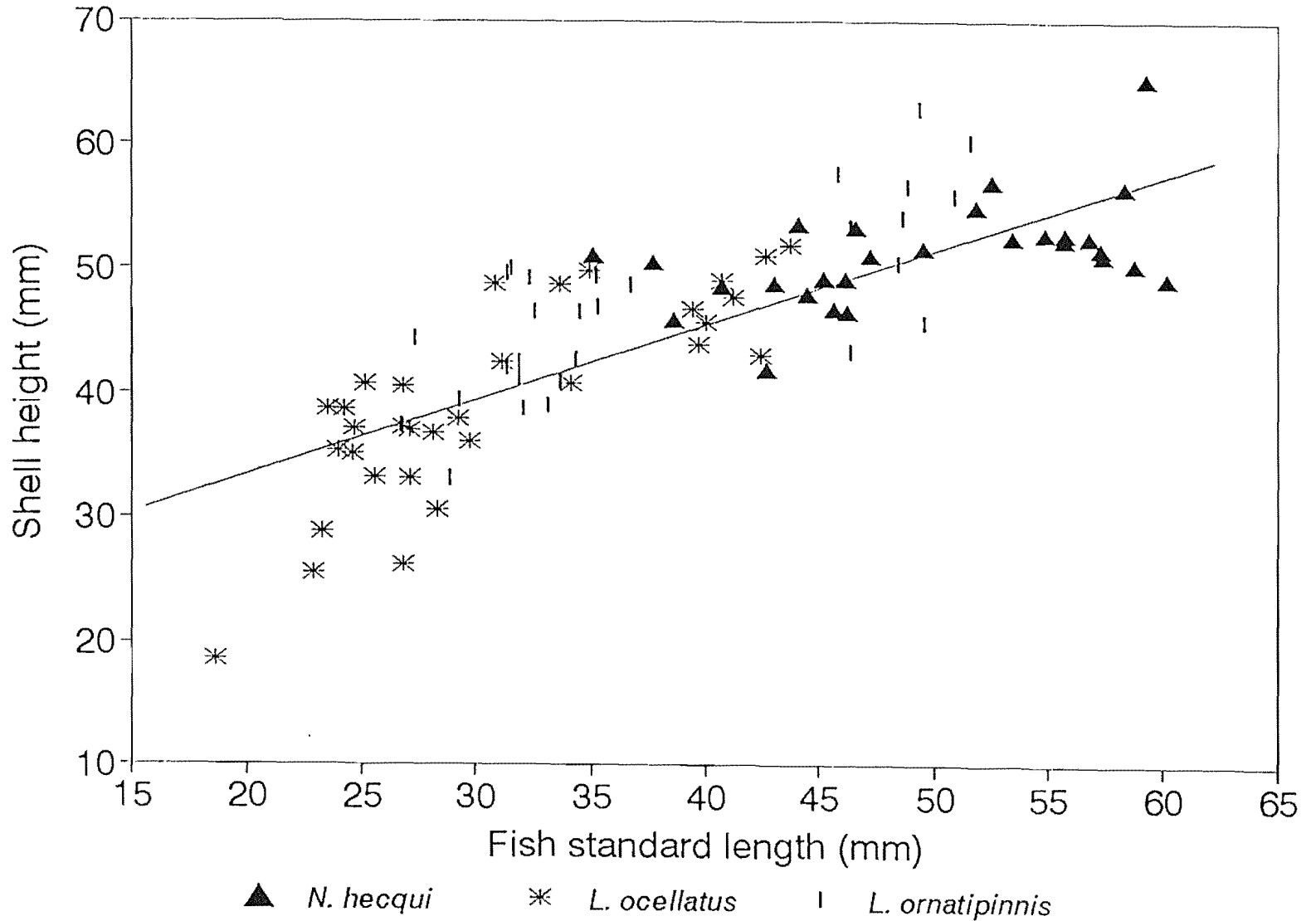


Figure 4.2 Relation between shell-dweller size (fish SL or crab carapace width) and refuge shell size (shell height) at Mbita Island, Zambia. Collection site: shell gravel, 10-20m depth. Regression line for combined shell-dwelling fish community: $y = 21.2 + 0.6x$

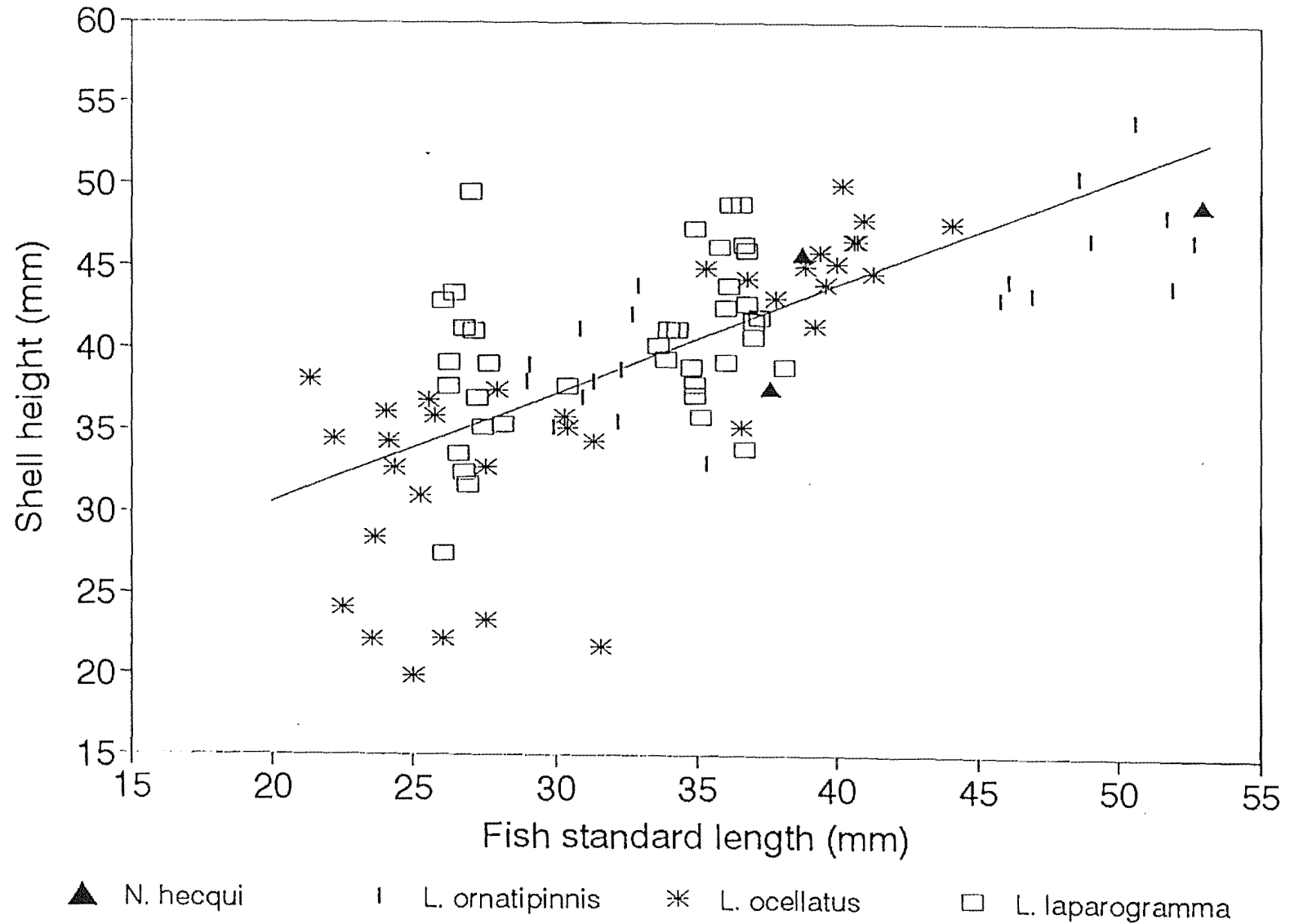


Figure 4.3 Relation between shell-dweller size (fish SL or crab carapace width) and refuge shell size (shell height) at Musende Rocks, Zambia. Collection site: mud, 20m depth. Regression line for combined shell-dwelling fish community: $y = 18.4 + 0.6x$

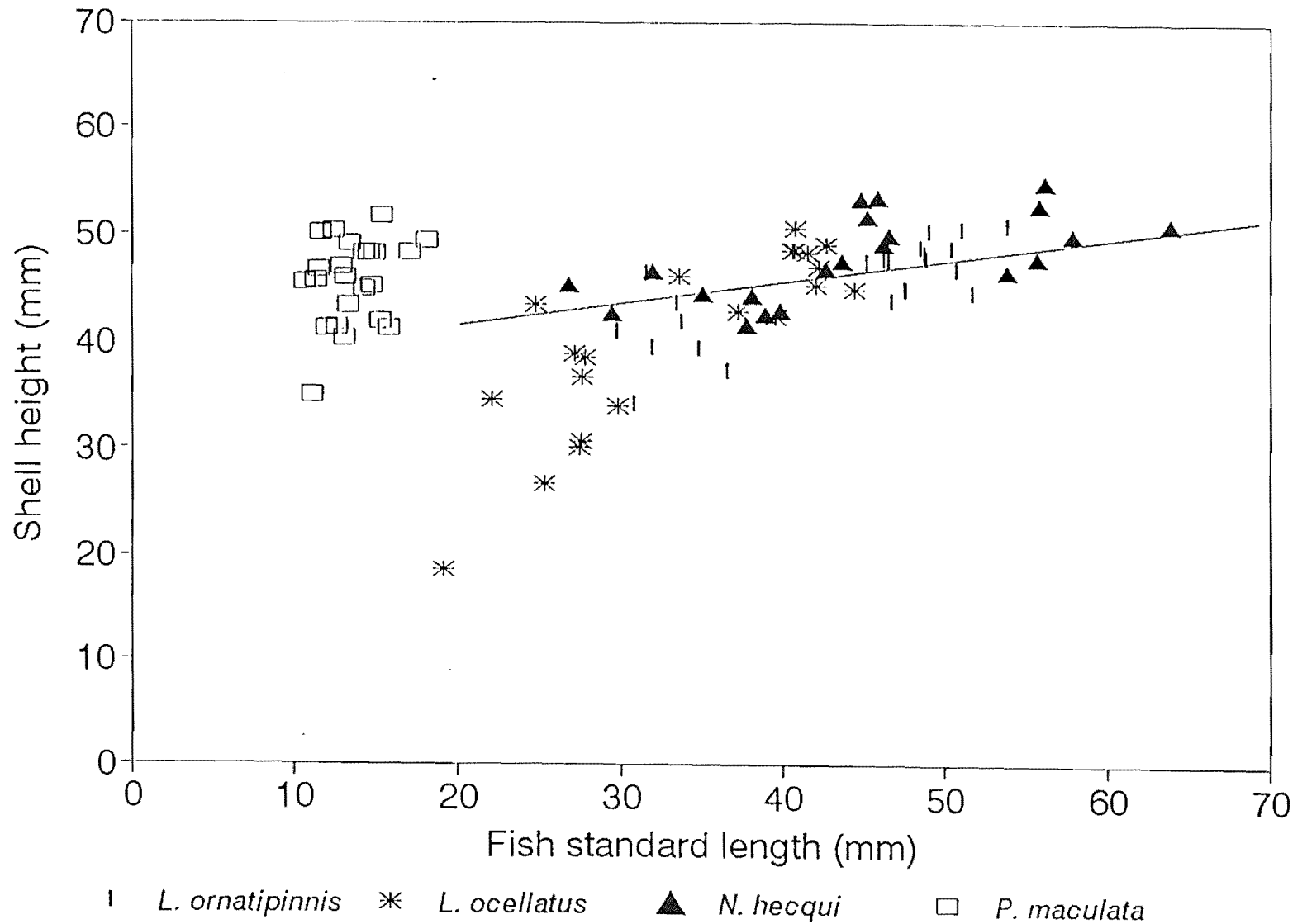


Figure 4.4 Relation between shell-dweller size (fish SL or crab carapace width) and refuge shell size (shell height) at Musende Rocks, Zambia. Collection site: shell-bed-soft substrate boundary zone, 15-20m depth. Regression line for combined shell-dwelling fish community: $y = 39.8 + 0.15x$

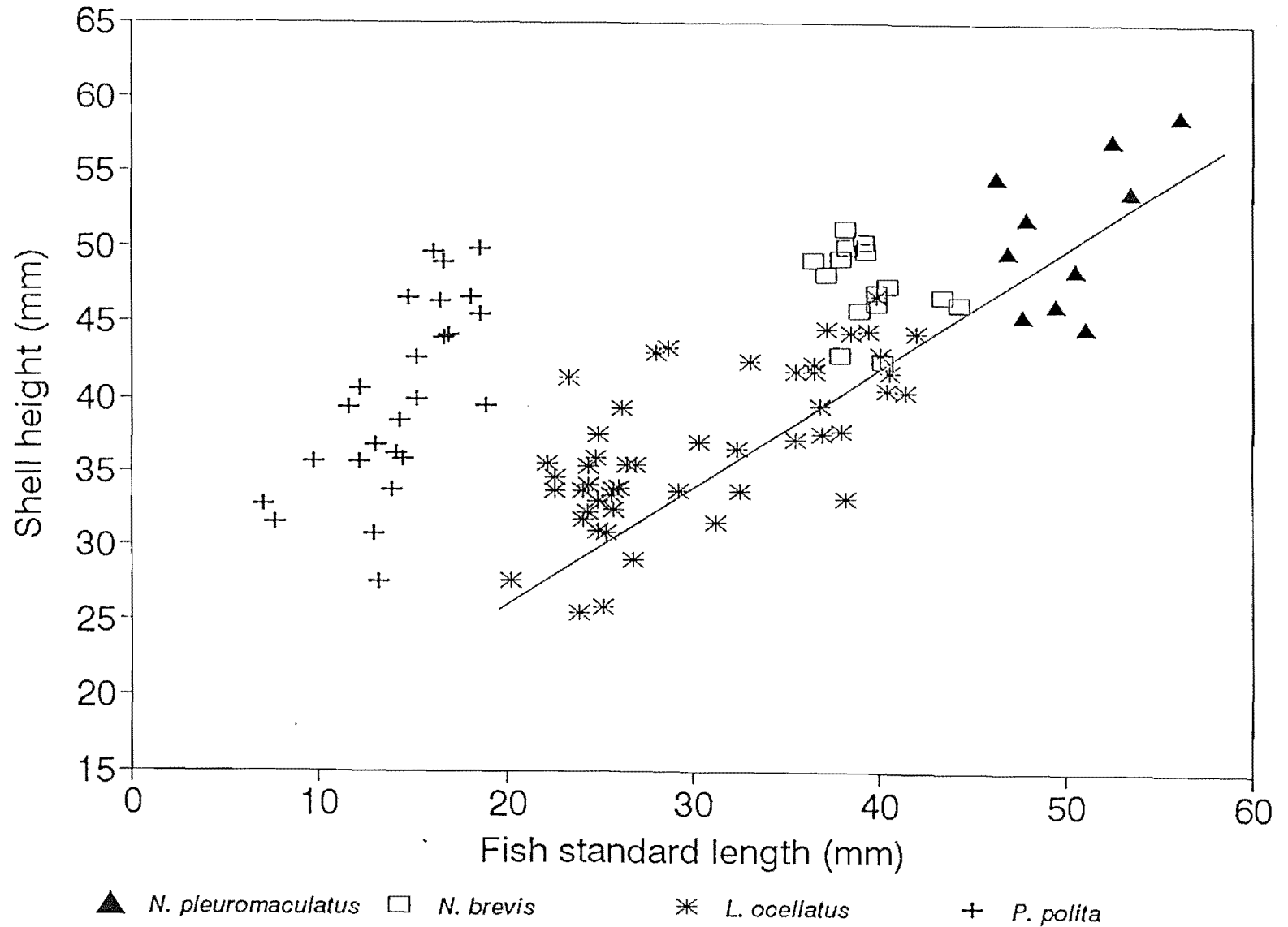


Figure 4.5 Relation between shell-dweller size (fish SL or crab carapace width) and refuge shell size (shell height) at Gitaza, Burundi. Collection site: sand-mud, 11-18m depth. Regression line for combined shell-dwelling fish community: $y = 16.4 + 0.7x$

Experiment 2. Are there interspecific differences in the methods of shell use?

Methods

Wild-caught *L. ocellatus* and *L. ornatipinnis* were placed into 15 litre plastic fish tanks (one fish per tank) with 10cm depth of sand and a single *N. tanganyicense* shell. The fish were allowed to settle for one week prior to observations. After one week the shell was dug up, the sand levelled and the shell left, mouth facing up on the sand surface. The fish was then observed until shell burial was complete. The behaviour patterns are described but not quantified.

Shell burial has been described and the frequency of specific patterns quantified in detail for *L. ocellatus* by Haussknecht & Kuenzer (1990). Their terminology for behaviour patterns has been adopted with the exception of 'shell building' which I term 'shell burying'.

Fish were also observed in the wild and the orientation of shells in use noted. Shells were recorded as being buried vertically; horizontally with mouth sideways; or horizontally with mouth upwards. Results were examined using chi-squared contingency analysis.

Results

- * There are differences between *L. ocellatus* and *L. ornatipinnis* in aspects of each phase.

Inspection phase.

- * The inspection behaviour, prior to shell use or rejection, is the same for both species (Figure 4.6). Shells are inspected from outside by swimming around it and inside by entering it. *L. ornatipinnis* appeared to take longer than *L. ocellatus* to inspect shells and initiate digging, both in tanks and in the field. This was not measured but is supported by higher numbers of unburied shells in *L. ornatipinnis* territories in all of the experiments.

Digging-in phase.

* *Lamprologus ocellatus* digs at the spire of the shell and at a single point in the sand (Figure 4.7). As the hole develops the shell sinks into it spire first. Due to shell shape, burying the shell on its apex results in *L. ocellatus* holes having to be deeper than those of *L. ornatipinnis* (Table 4.3). At this stage the shell rests on its apex and is relatively easy to move. The fish may reposition it by grasping the shell rim in its mouth and swimming forwards vigorously (Figure 4.8). This may be done 10-20 times before the desired position is achieved.

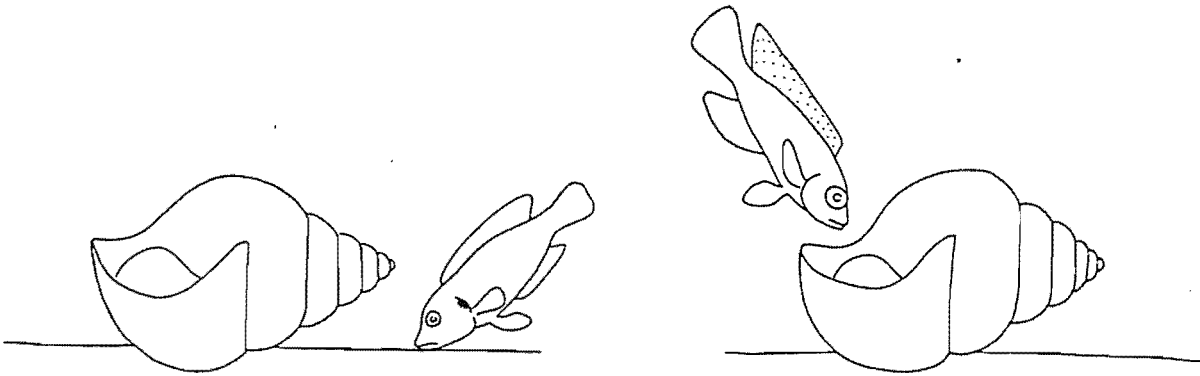


Figure 4.6 *L. ocellatus* and *L. ornatipinnis* inspecting the inside and outside of new shells.

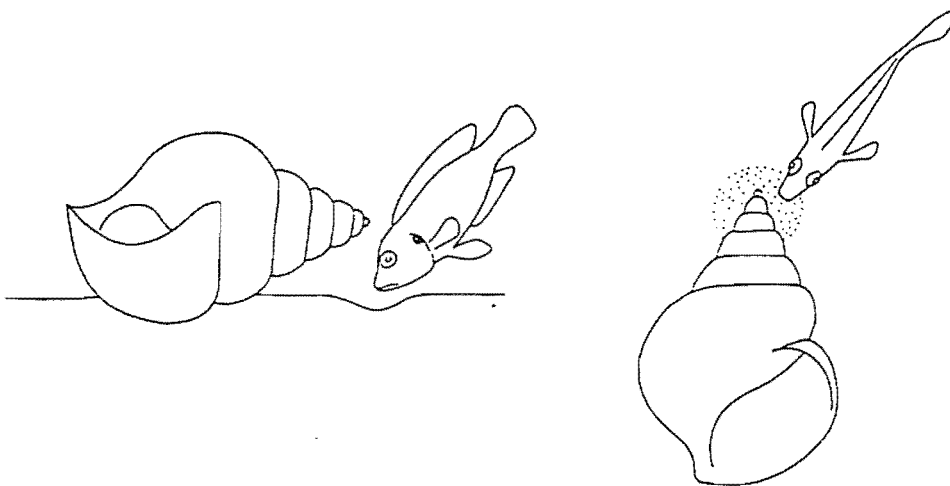


Figure 4.7 *L. ocellatus* digs at the spire of the shell (side and above views).

* *Lamprologus ornatipinnis* concentrates its digging activity around the shell mouth. Digging may occur in several places on either side of the shell (Figure 4.9). The hole which develops is broader and shallower than that for *L. ocellatus* (Table 4.3) and the shell sinks horizontally into it. When the sand has been dug away from the shell sides, and it is supported only by a sand pedestal, it may be moved by larger males. Shell manipulation is effected by the fish resting on the lip of the shell mouth and swimming down (Figure 4.10). This is rapid movement forces the shell to rotate downwards. Shell repositioning in *L. ornatipinnis* usually occurs only once, after which digging continues.

* Throughout the digging-in phase both species carry out inspections (Figure 4.11).

Oversanding phase.

* Covering of the shell is effected entirely by horizontal digging (Hausknecht & Kuenzer 1990). This involves the fish facing away from the shell and swimming down into the sand. This results in sand being swept backwards by the fins onto the shell. There are small differences between the species in this process.

L. ocellatus opens its mouth and swims vigorously into the sand. The movement ends when half the fish's body is covered in sand (Figure 4.12).

L. ornatipinnis does not open its mouth or go as deep into the sand (Figure 4.13).

Final shell position.

* *L. ocellatus*-buried shells are positioned apex down with the posterior lip of the mouth protruding from the sand (Figure 4.14).

* *L. ornatipinnis*-buried shells are buried on their sides (Figure 4.15). There are also differences in mouth positions between shells buried by males and females. Males push shell mouths down into the sand resulting in the mouth facing sideways. Females were not observed to reposition shells and

mouths were usually positioned facing upwards.

* Observations in the lake indicate that these orientations are characteristic for species ($\chi^2 = 71.8$, $df = 1$, $p < 0.001$) and sex in *L. ornatipinnis* ($\chi^2 = 12.2$, $df = 1$, $p < 0.001$, Table 4.4).

Table 4.3 The average hole depths during shell burial for *L. ocellatus* and *L. ornatipinnis* (degrees of freedom = 26).

	no	mean	SD	't' statistic	p
Shell size mm					
height	14	43.9	3.01	} 7.54	0.0000
depth	14	34.5	3.32		
Hole depth					
<i>L. ocellatus</i>	14	33.4	3.96	} 4.58	0.0001
<i>L. ornatipinnis</i>	14	27.0	3.00		
% of shell buried					
<i>L. ocellatus</i>	14	75.9	7.19	} -0.86	0.399
<i>L. ornatipinnis</i>	14	78.7	9.20		

Table 4.4 *Lamprologus ocellatus* and *L. ornatipinnis* shell orientations in natural habitats.

shell orientation	<i>L. ornatipinnis</i>		<i>L. ocellatus</i>	
	♂	♀	♂	♀
horizontal	19	21	1	1
vertical	0	0	20	20
mouth position				
upwards	4	16	1	1
sideways	15	5	20	20

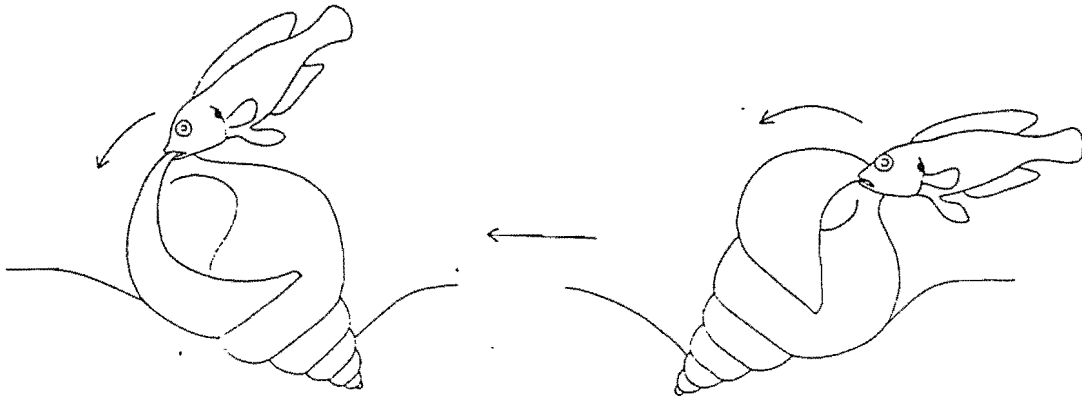


Figure 4.8 *L. ocellatus* repositions shells after partial excavation by grasping the lip of the shell and swimming forwards.

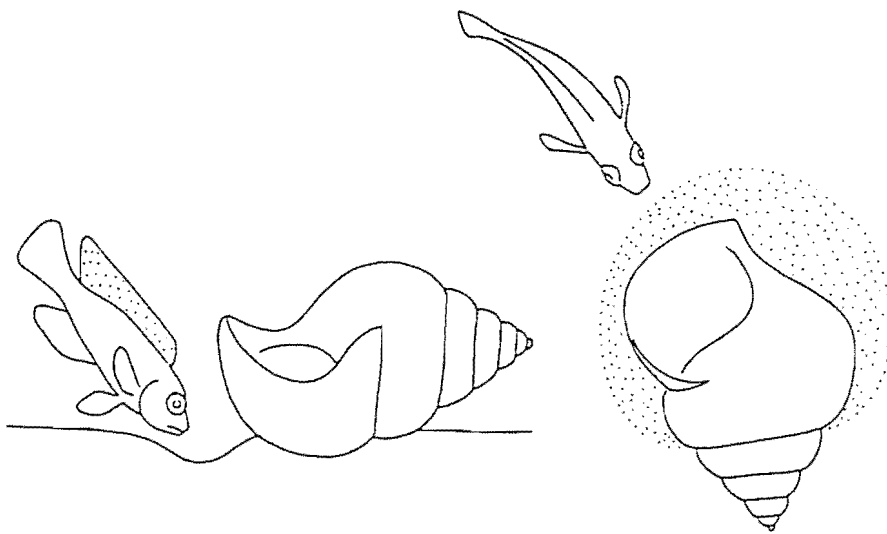


Figure 4.9 *L. ornatipinnis* digs all around the shell but more at the mouth and first whorl area (side and above views).

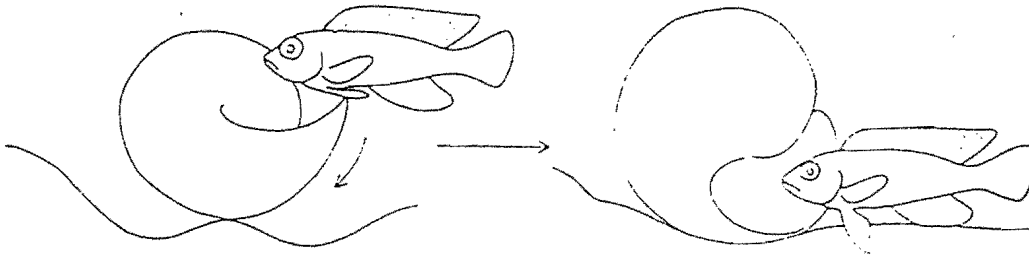


Figure 4.10 *L. ornatipinnis* repositions the shell after partial excavation by resting on shell lip and swimming downwards.



Figure 4.11 *L. ocellatus* rests between digging actions on the shell. This activity was termed CONT (Haussknecht & Kuenzer 1990).

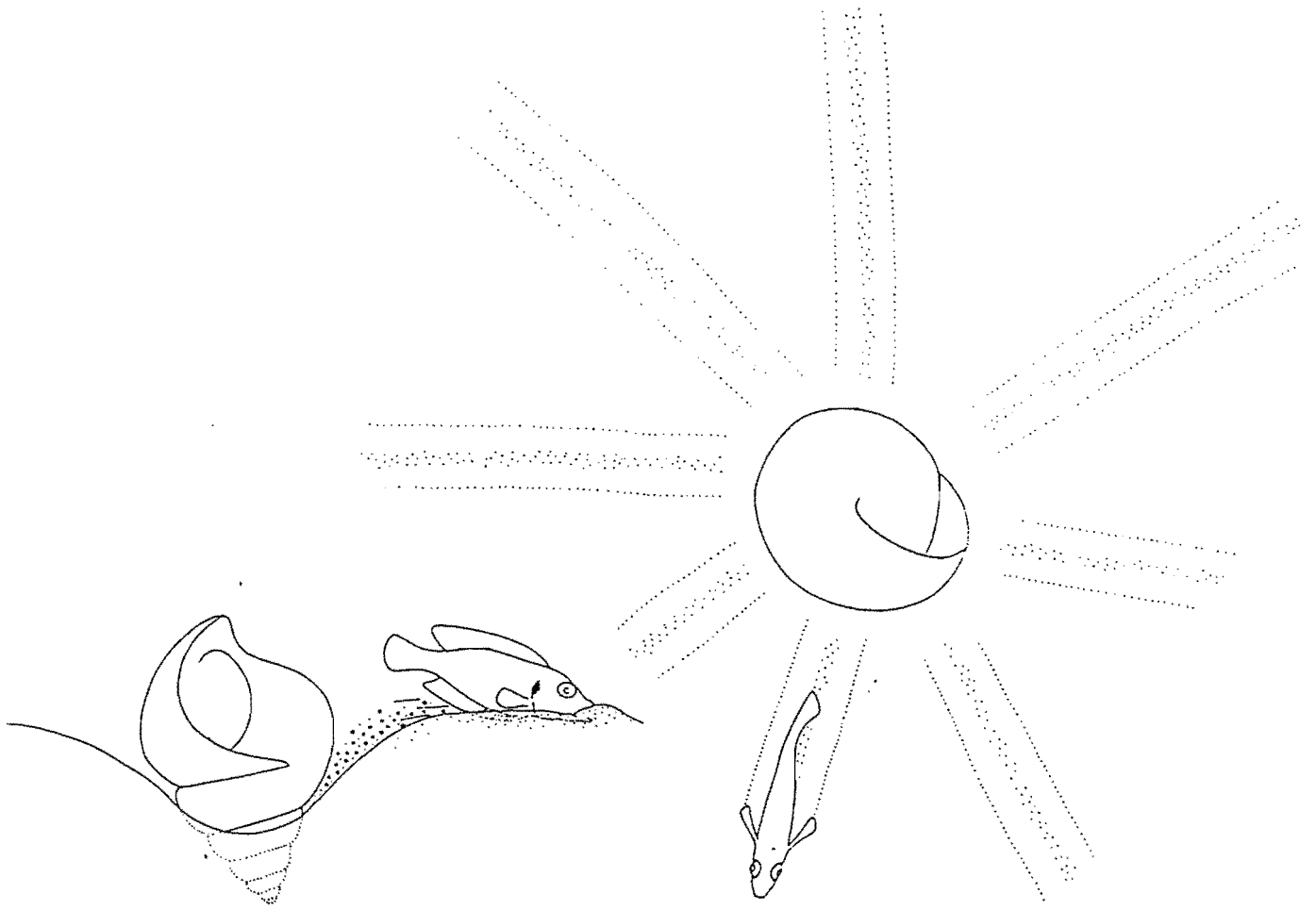


Figure 4.12 *L. ocellatus* covers the shell by 'horizontal digging'.

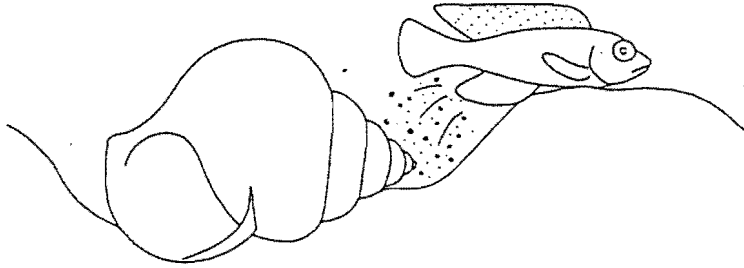


Figure 4.13 *L. ornatipinnis* covers the shell by 'horizontal digging'.

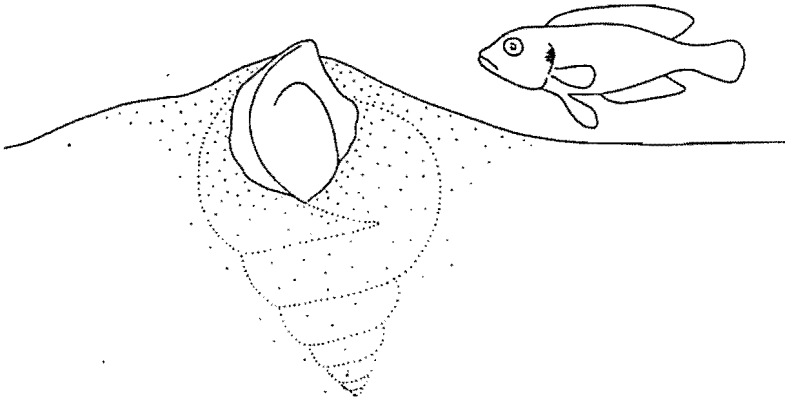
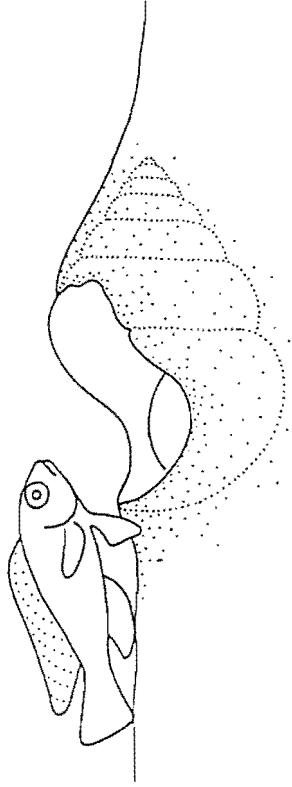


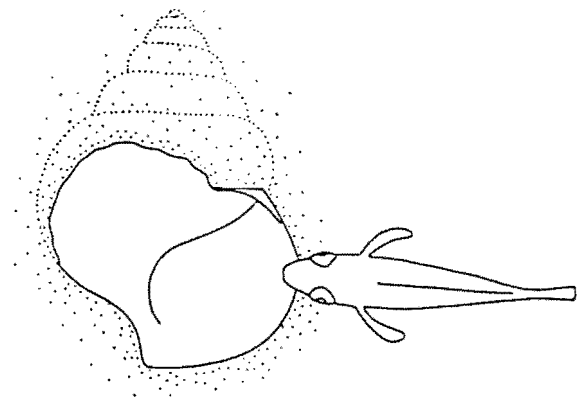
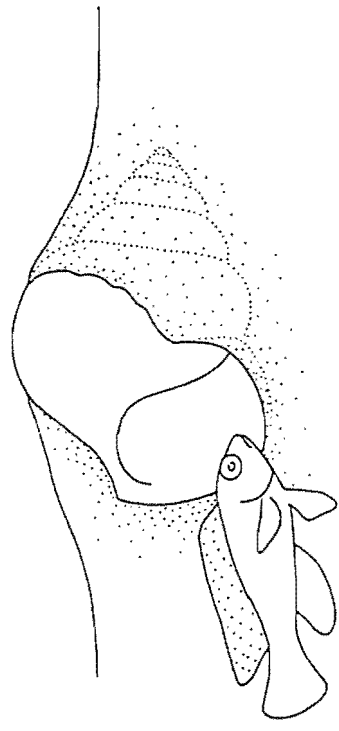
Figure 4.14 The final shell position in *L. ocellatus*.

females



side view

males



above view

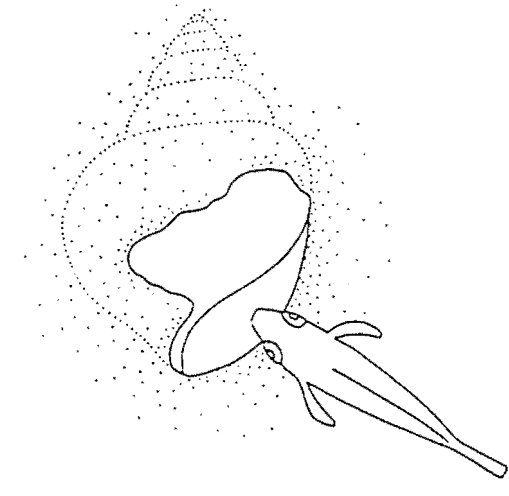


Figure 4.15 The final shell positions in *L. ornatipinnis* (side and above views for males and females).

Experiment 3. Does shell orientation affect which species use shells?

Methods

Twenty individuals of *L. ocellatus* and *L. ornatipinnis* were located and their territories marked with lines and metal tags (Figure 3.1). As part of the experimental procedure new shells were then added to territories or existing shells were manipulated as follows.

- a) Principal shells were pulled out of the substrate and reburied in the orientation characteristic for the other species.
- b) New shells were added and buried in the orientation preferred by the other species.
- c) New shells were buried in the species' preferred orientation.
- d) Results were compared with responses to shells added unburied and mouth up (Experiment 3.2).

Responses to shells were varied and results were recorded and compared in the following way: as the number of shells that were in use (IU); unused (UU); vertically buried (V); horizontally buried (H); partially buried (PB); not present (NP); or moved (M). These results were recorded as a contingency table (Table 4.5) and subjected to chi-square analysis.

Results

Responses to the reorientation of principal shells.

- * 40% of *L. ornatipinnis* and 32% of *L. ocellatus* deserted their territories after their principal shells were experimentally reorientated (Table 4.5). This was considered a disturbance effect rather than due to a change of shell orientation. Consequently later experiments were modified, leaving principal shells undisturbed and using added shells in preferred and unpreferred orientations.

Unburied control shells.

* Control shells showed that the differences in shell orientation between *L. ocellatus* and *L. ornatipinnis* (Figures 4.14 & 4.15) are highly significant when shell treatments are compared ($\chi^2=31.3$, $df=4$, $p<0.001$).

* *L. ocellatus* used vertically buried and control shells equally and showed no differences in the treatment of shells ($\chi^2=0.3$, $df=3$, $p=0.96$). Shells which were experimentally added horizontally to *L. ocellatus* territories were dug up, reorientated and buried vertically. In many cases this was done within one to two hours. The result was that shells buried horizontally and control shells were used equally ($\chi^2=0.19$, $df=1$, $p=0.68$) and treated similarly ($\chi^2=4.28$, $df=4$, $p=0.37$). There were no differences between shells buried vertically (preferred) and horizontally (unpreferred) in either use ($\chi^2=0.91$, $df=1$, $p=0.34$) or treatment ($\chi^2=5.45$, $df=4$, $p=0.24$). Two *L. ocellatus* which did not reorientate shells had juveniles present.

* *Lamprologus ornatipinnis* used horizontally buried and control shells equally and there were no significant differences in treatment ($\chi^2=3.2$, $df=2$, $p=0.20$). Vertically buried (unpreferred) shells were used least (25%) and none were reorientated into preferred positions by the end of the experimental period. Consequently there were significant differences between vertically buried and control shells in use ($\chi^2=4.95$, $df=1$, $p=0.03$) and in treatment ($\chi^2=20.12$, $df=4$, $p<0.001$). There were also differences between vertically and horizontally buried shells in use ($\chi^2=5.57$, $df=1$, $p=0.02$) and treatment ($\chi^2=20.9$, $df=4$, $p=0.003$)

Interspecific differences.

* If provided with shells buried in unpreferred orientations, both species dug them up and repositioned them. However, *L. ocellatus* reorientated shells more quickly than *L. ornatipinnis*. During

the experimental period *L. ocellatus* dug up, reorientated and completely reburied 60% of horizontally added shells. In the same period no *L. ornatipinnis* had completed this process for vertically buried shells.

* The addition of shells buried in unpreferred orientations resulted in reduced shell use. *L. ocellatus* used 16% fewer shells while *L. ornatipinnis* used 64% fewer shells than those fish given shells in preferred orientations.

Table 4.5 Responses by *L. ornatipinnis* and *L. ocellatus* to shells added in varying orientations.

Experiment/ species	No	Shells					IU	UU
		V	PB	H	NP	M		
<i>L. ornatipinnis</i> (preferred orientation is horizontal)								
S1 vertical	20	11	1	4	4	4	12	8
Sa vertical	20	8	5	0	7	10	5	15
Sa horizontal	21	0	4	12	5	7	14	7
Control (unburied)	20	* 0	7	5	5	10	13	7
* 3 unburied								
<i>L. ocellatus</i> (preferred orientation is vertical)								
S1 horizontal	22	13	2	7	0	0	15	7
Sa horizontal	20	12	4	3	1	3	16	4
Sa vertical	20	17	2	0	1	1	19	1
Control (unburied)	20	* 15	3	0	1	1	18	2
* 1 unburied								

V = buried vertical (figure), PB = partially buried, H = buried horizontally, NP = shell not present, M = total moved shells, IU = in use, UU = unused.

Experiment 4. If residents are removed from territories but shells are left which fish will recolonise the shells?

Methods

At Musende Rocks, territories of *L. ocellatus* and *L. ornatipinnis* were located and marked. Fish were then captured using nets. Shells were not disturbed. After one week territories were revisited and any new fish, together with their shells, were collected. Resident and immigrant fishes were measured for total length, standard length and body depth. Shells were measured for maximum height and width and mouth height and width. Results are in Appendix 2 (raw data) and summarised in Tables 4.6 and 4.7.

The original and new residents were compared for size using Kolmogorov-Smirnov two-sample tests (Siegel & Castellan 1988). Fish immigrants and resident behaviour were compared by chi-squared tests.

Results

* Original residents and new immigrants showed no significant differences in size:

L. ocellatus

males ($t=0.55$, $df=5$, $p>0.10$; $K-S=0.74$, $n_1=10$, $n_2=6$, $p=0.65$)

females ($t=-0.7$, $df=5$, $p>0.10$; $K-S=0.45$, $n_1=10$, $n_2=6$, $p=0.99$)

L. ornatipinnis

males ($t=1.47$, $df=7$, $p>0.10$; $K-S=0.89$, $n_1=10$, $n_2=8$, $p=0.40$)

There was only one immigrant into *L. ornatipinnis* female's shell and this was the resident male.

* Immigrants were mainly of the same species ($\chi^2=0.11$, $df=1$, $p>0.05$) and of the same sex ($\chi^2=0.04$, $df=1$, $p>0.05$) as the original resident.

* Males and females behaved differently towards vacated shells (*L. ocellatus* and *L. ornatipinnis*)

combined, $\chi^2 = 13.1$, $df = 2$, $p = 0.0014$, Table 4.7). Females left vacant male's shells open and appeared less able to defend shells against larger fish. This resulted in males of other species colonising several shells. In contrast males hid all shells not immediately colonised by immigrant females. No other species entered shells where males were present. There were 6 female *L. ocellatus* and no female *L. ornatipinnis* immigrants.

Table 4.6 The sizes of original residents, sizes and species composition of immigrants after the removal of residents.

Original residents	<i>L. ocellatus</i>		<i>L. ornatipinnis</i>	
Number	10	10	10	10
Sex ($\delta/\text{♀}$)	δ	♀	δ	♀
Size (mean)	38.4	25.2	48.0	32.0
S.D.	± 4.0	± 2.3	± 1.6	± 1.8
Shell height	39.2	25.2	47.2	43.6
S.D.	± 7.2	± 7.5	± 3.1	± 3.5
New fish residents				
Number	6	6	8	1
Sex ($\delta/\text{♀}$)	5 δ / 1 ♀	2 δ / 4 ♀	7 δ / 1 ♀	1 δ
Size (mean)	36.3	26.1	46.4	56.8
S.D.	6.8	4.0	2.9	-
New immigrant species				
<i>L. ocellatus</i>	4	6	0	0
<i>L. ornatipinnis</i>	1	0	5	1
<i>N. hecqui</i>	1	0	3	0
Crabs (<i>P. maculata</i>)	1	0	0	0

Table 4.7 The treatment of shells after residents were removed.

fish / shell	open	hidden	not present
<i>L. ocellatus</i>			
♂	8	1	1
♀	6	4	0
total	14	5	1
<i>L. ornatipinnis</i>			
♂	9	1	0
♀	1	7	2
total	10	8	2
Sexes combined			
all ♂	17	2	3
all ♀	7	11	0

Experiment 5. How do residents respond to heterospecific shell-dwelling intruders?

Methods

Interference competition was induced by adding crabs (*P. maculata*) to *L. ocellatus* and *L. ornatipinnis* shells and territories. Crabs were used because they are less mobile than fish and were considered less likely to immediately desert territories. They are also frequent competitors for shell refuges (Chapter 3).

a) Initial observations.

Crab fidelity to refuges was investigated by locating and tagging shells containing crabs. Shells were then observed the next day, collected and smashed open to determine residency. Overnight fidelity to shells was not high (see below), so this, coupled with diving restrictions, determined the four-hour

interval between experiments. The experiment consisted of two components.

b) Adding crabs to principal shells.

Fish territories were located and residents were carefully chased away from their principal shells but not out of territories. Crabs were introduced into shells with their larger claws outermost. Crabs were given two minutes to settle before the fish were allowed back to shells. Crabs were added to principal shells in 20 *L. ocellatus* and 20 *L. ornatipinnis* territories (10 male, 10 female).

In both treatments fish territories were revisited four hours later. The presence of the fish at the principal, additional or secondary shells, and the presence of the crab were recorded. These results were compared to those from adding open shells buried in species preferred orientations (Experiment 4.3).

c) Adding crabs in new shells into territories close to the principal shells.

Crabs together with their shells were collected and moved into fish territories. The shells were buried in the orientation preferred by the resident fish species. Crabs and shells were added to 20 *L. ocellatus* and 20 *L. ornatipinnis* (10 male, 10 female) territories.

Results

a) Initial observations.

* Crab fidelity to shells over a 24 hour period was 32% (n = 50). Thus crabs appear to use shells as day-time refuges, forage at night on the lake floor and find new refuges the following day. This may be a contributing factor in why crab and shell sizes are not correlated (see section 4.1).

* Crabs introduced to territories were always attacked by fish. They were either driven away from shells or picked up by their legs and carried away to the edge of the territory (Figure 4.16). If crabs were added to shells with their smaller claw outer most they would come out of the shell and turn around. When fish approached shells the resident crab would extend its claw in the shell mouth (Figures 3.4 & 4.16).

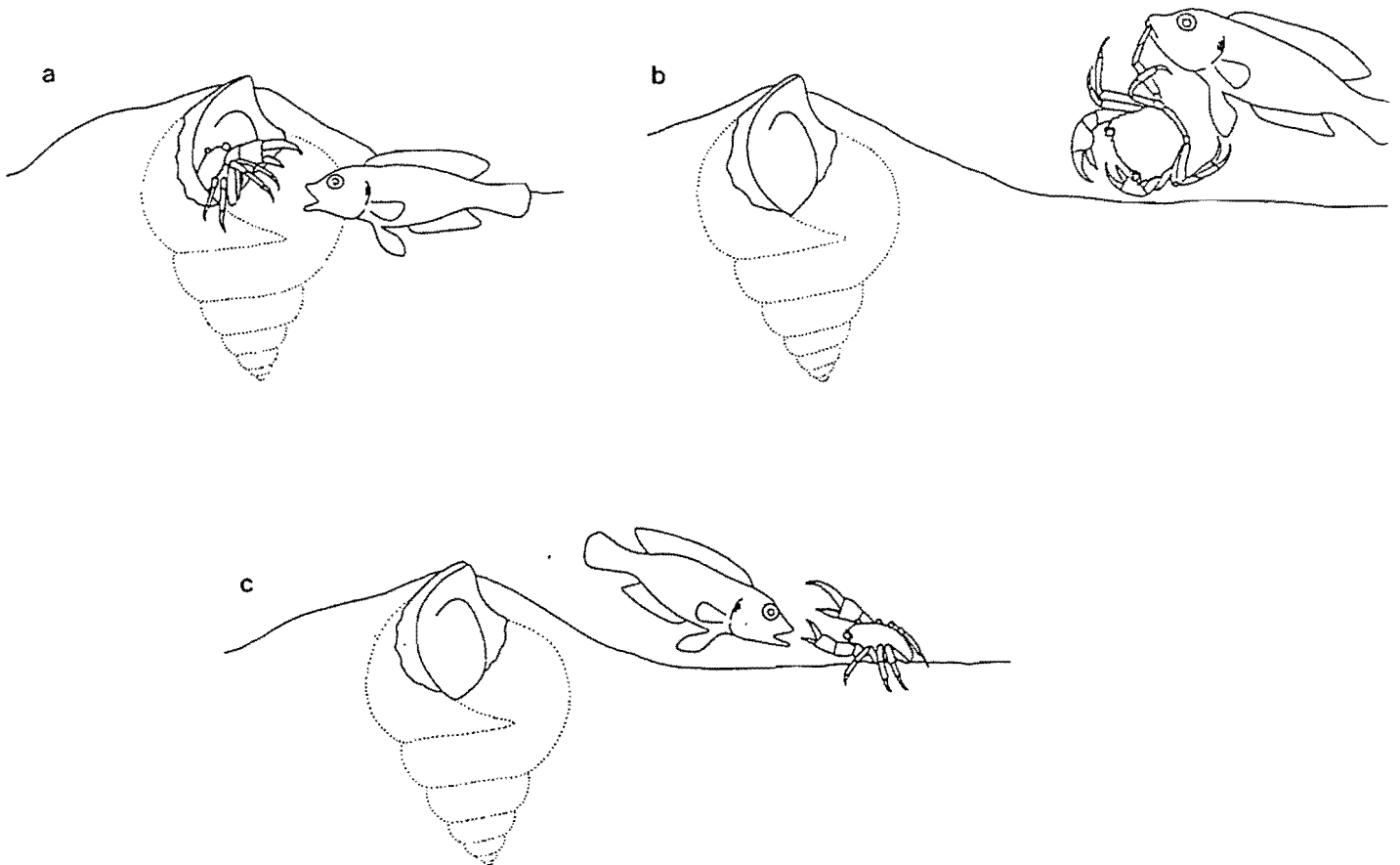


Figure 4.16 An *L. ocellatus* a) pulling the crab out of a shell by its legs, b) carrying a crab out of the territory and c) pushing a crab away from a shell.

* Once fish were allowed back to shells, they first attempted to enter the shell. Having detected the crab they then tried to pull the crab out by its legs (Figure 4.16). This was attempted numerous times. Where females failed to remove crabs, their mates would also try. Larger fish appeared to be better at removing crabs from shells than smaller fish. Crabs were grasped by their longer walking legs, pulled out of the shell and carried up to a meter away and dropped. Where crabs were not removed fish either left territories or moved to secondary shells. Shells where crabs remained were either left open or hidden by resident fish. Hiding did not seem to result in immediate vacation of shells by crabs as some crabs were found in hidden shells. Crabs are also commonly found buried in the substrate where there are no shells.

b) Crabs added to principal shells (Table 4.8).

* After four hours 72.5% of the principal shells were open and 47.5% of the crabs were absent. Several crabs were observed to have been pulled out of shells by resident fishes.

* Observations indicate that small individuals (e.g. female *L. ocellatus*) were less capable of removing crabs than large individuals (e.g. male *L. ornatipinnis*). However, there were no significant differences between females *L. ocellatus* and male *L. ornatipinnis* ($\chi^2=4.4$, $df=2$, $p>0.10$).

* There was no difference between *L. ocellatus* and *L. ornatipinnis* in the numbers of fish and crabs present at shells ($\chi^2=1.2$, $df=2$, $p=0.55$).

* In both species when residents or their mates were unable to evict crabs, the resident either moved to a secondary shell or left the territory. When males deserted territories, females usually ignored the male's, crab-occupied shell. When females deserted territories males usually hid female's, crab-occupied shell. Despite this apparent trend there were no intersexual differences in the treatment of shells added to *L. ocellatus* territories ($\chi^2=0.2$, $df=1$, $p=0.63$, Table 4.8). Male and female *L.*

ornatipinnis did differ in their treatment of shells (see above, $\chi^2 = 6.7$, $df = 2$, $p = 0.04$). There was no difference between the two species (male and female data combined) ($\chi^2 = 1.27$, $df = 2$, $p = 0.53$).

Table 4.8 Responses by *L. ocellatus* and *L. ornatipinnis* to crabs (*P. maculata*) being added to their principal shells.

Species	<i>L. ocellatus</i>		<i>L. ornatipinnis</i>	
	♂	♀	♂	♀
Number	10	10	10	10
Shells buried:				
excavated	0	0	0	1
open	8	6	10	5
hidden	2	4	0	4
Fish at:				
principle shell	4	1	5	3
secondary shell	2	3	2	4
Crab at S1	5	7	3	6

c) Crabs and shell additions (Table 4.9).

* In both species there were no sexual differences and shell treatments were the same. There were also no significant sexual differences with regard to fish and crab presence for *L. ocellatus* ($\chi^2 = 0.8$, $df = 2$, NS) and *L. ornatipinnis* ($\chi^2 = 1.2$, $df = 2$, NS). This contrasts with the previous experiment and is explained by males responding to all additional shells whether placed close to male's or female's shells.

Table 4.9 Responses of fish when shells, containing crabs (*P. maculata*), were added to territories buried in the species' preferred orientation.

Species	<i>L. ocellatus</i>		<i>L. ornatipinnis</i>	
	♂	♀	♂	♀
Number	10	10	10	10
Added shells:				
excavated	1	0	0	0
open	9	9	5	5
hidden	0	0	5	5
Fish present at:				
principle shell	3	3	9	6
secondary shell	7	4	1	2
Crab present at shell	3	4	1	2

Table 4.10 The treatment of shells by *L. ornatipinnis* and *L. ocellatus* after crabs (*P. maculata*) were added to principal shells (S1 + crab) and where shells with (Sa + crab) and without (Sa open) crabs were buried in territories.

Experiment	Shell treatment			
	no	excavated	open	hidden
<i>L. ornatipinnis</i>				
S1 + crab	20	1	15	4
Sa + crab	20	0	10	10
Sa (open)	21	9	9	3
<i>L. ocellatus</i>				
S1 + crab	20	0	14	6
Sa + crab	20	2	18	0
Sa (open)	20	3	15	2

* There were interspecific differences for both shell treatment ($\chi^2 = 14.3$, $df = 2$, $p < 0.001$) and for fish-crab presence ($\chi^2 = 9.9$, $df = 2$, $p < 0.01$). This resulted from *L. ocellatus* responding differently to added shells by actively occupying new shells. *L. ornatipinnis*, as in the previous experiment, continued to occupy its original shell and hid 50% of added shells.

A comparison with empty buried shells.

* The treatment of shells buried with and without crabs was compared (Table 4.10). *L. ocellatus* shows no significant difference ($\chi^2 = 2.47$, $df = 2$, NS); while *L. ornatipinnis* does show significant differences in behaviour ($\chi^2 = 12.8$, $df = 2$, $p < 0.01$). The presence of crabs in shells inhibits the excavation and movement of shells and increases shell hiding in *L. ornatipinnis*. *L. ocellatus*, which does not move shells, appears to be unaffected by the presence of crabs.

DISCUSSION

1. Are there differences in shell sizes used between species?

Generally there is a relationship between fish size and shell refuge size (Table 4.2, Figures 4.1 to 4.5). Large fishes use large shells and small fish use small shells. However, correlations varied within species at different sites and also between species at the same site. From these results I conclude that shell use is not random but that shell size is one of several factors which affect shell use.

The relationship of fish and shell size for individual species is affected to some extent by fish life histories. For example *L. ocellatus* uses shells throughout its life while *N. brevis* only uses shells when ready to spawn. At each site there is a hierarchy of adult sizes.

Size differences in *L. ocellatus* between Kombe and other sites may be due to two factors. Reduced competition for shells. The absence of other shell-dwelling competitors at Kombe may give *L. ocellatus* access to larger shells. *Lamprologus callipterus* females were also found to attain larger size where larger shells were available (Sato 1989b). Reduced predation levels. Lower fish abundance

at Kombe may result in lower predation levels, fishes living longer and thus attaining larger sizes. The community age structure at each site could be determined by collecting fishes and examining scales and otoliths. Another method would involve block netting a portion of lake floor and removing all species except *L. ocellatus*. These could be left for six months to one year and their sizes compared before and after the experiment and with fishes outside the netted area.

I suspect that differences in crab size/shell size correlations between *P. maculata* (Zambia) and *P. polita* (Burundi) may be due to differences in chela sizes. Crabs with larger chela should be able to block shell mouths more effectively and thus prevent fish from pulling them out of shells. Conversely, improved competitive ability of *P. polita* may be responsible for *L. ocellatus* SL having its lowest correlation with shell size at the Gitaza site, where *P. polita* and *L. ocellatus* overlap almost completely in the size of shells used. Presumably if *L. ocellatus* is less capable of removing *P. polita* from shells it will be forced into using a wider size and quality range of shells. If Experiment 4.5 was repeated at Gitaza, the competitive ability of *P. polita* and *L. ocellatus* could be tested and compared with the Zambian *P. maculata* and *L. ocellatus*.

Experiment 2. Are there differences in methods of shell use between species?

Throughout every phase of the shell burial process there are differences between *L. ocellatus* and *L. ornatipinnis*. Some of the behavioural sequences are very similar and the species exhibit only subtle differences such as the duration of inspection times (discussed further in Chapter 6) or in the depth of horizontal digging. There is only one species-specific behaviour exhibited by each species. This is the means of shell manipulation (Figures 4.8 & 4.10). However, the behaviour which results in the most significant difference in final shell position is the location of digging activity. This results in a difference in shell orientation of about 90° between the two species (Table 4.4).

These differences may have evolved in response to interspecific competition for shell resources. It is my hypothesis that they have evolved under conditions of interspecific competition for shell resources. The selection of these behaviours has resulted in individuals with better competitive abilities. Some of these differences and behaviour patterns are discussed below while others are discussed

further in Chapter 6.

These differences would appear to have a genetic basis. This is supported by observations from sites where only *L. ocellatus* is present and where shell and fish numbers are very low e.g. Kombe-Mwella. At these sites *L. ocellatus* still buries shells vertically despite the absence of other shell-dwelling competitors.

Inspection-assessment behaviour.

Assessment of the shell position, where fish rest in the shell mouth, was termed 'Cont' by Haussknecht & Kuenzer (1990). Although 'Cont' occurs throughout the digging-in phase, these authors considered its function was to enable the fish to decide when to stop digging-in and to start covering the shell. It seems improbable, however, that 'Cont' should be necessary at the start of and throughout the digging-in phase if its purpose is to decide when to stop digging. I suggest that 'Cont' occurs throughout the digging-in phase because it is related to precise shell orientation. Regular repositioning of shells (by *L. ocellatus*) or changing of digging location (by *L. ornatipinnis*) during the digging phase supports this hypothesis. I would agree that 'Cont' is necessary at the end of the digging phase to determine when covering should start.

Alternatively 'Cont' may also be an act of resting between digging actions. By resting in the shell mouth other shell dwellers may be prevented from entering the shell while the fish remains ready to enter the shell in case of attack by predators.

Digging methods.

During the digging-in phase two methods are used for moving sand: mouth digging and horizontal digging. Haussknecht & Kuenzer (1990) recorded a ratio of one horizontal digging:146 digging acts in *L. ocellatus*. In many shell burials I did not witness horizontal digging behaviour during the digging-in phase. In contrast during the covering-over phase horizontal digging is the only method of sand movement. It would seem that horizontal digging is a more efficient method of moving sand. Why then is it not used more frequently during the digging-in phase?

A possible reason for this may relate to shell orientation. For preferred shell orientations to be achieved digging activity has to be in precise locations around the shell. This can be done by mouth digging but not by horizontal digging. During the covering over phase accuracy is not essential and the more efficient method of horizontal digging predominates. This is discussed further in Chapter 6.

3. Does shell orientation affect which species use shells?

These experiments confirm earlier observations that *L. ocellatus* and *L. ornatipinnis* bury shells in species-specific ways. The two species did not respond in the same way to shells buried within their territories.

L. ocellatus used the majority of buried shells regardless of their orientation: shells buried in preferred orientations were used as found; and shells buried in unpreferred orientations were dug up and repositioned.

L. ornatipinnis used the majority of shells in preferred orientations. Prior to use, however, 33% of shells were dug up, moved and buried. Why this was done is unknown. Possibly *L. ornatipinnis* requires its shell resources to be evenly distributed rather than clumped within territories. Shells buried in unpreferred orientations had a negative effect upon shell use with 75% of existing shells being unused. This is a striking difference between all the other shell additions for *L. ornatipinnis* and compared to *L. ocellatus*.

Why do *L. ocellatus* and *L. ornatipinnis* differ in their ability to reorientate shells? If a shell buried horizontally is to be reorientated *L. ocellatus* must dig at the apex of the shell (Figure 4.17). As *L. ocellatus* buries shells deeper than *L. ornatipinnis* the amount of digging necessary for reorientating shells is no more than when burying a surface shell.

In contrast if a vertically buried shell is to be reorientated by digging at the shell mouth the shell will be deeper than normally preferred by *L. ornatipinnis* (Figure 4.17). Also the amount of digging would be greater compared to a surface shell. Two possible solutions to this are: dig some sand away, pull the shell out of the sand, allow it to fall horizontally back into the original depression and bury it;

and dig the shell up, move it away from the original position and start the burial process afresh. These options for reorientating shells imply that *L. ornatipinnis* must do more work than *L. ocellatus*. To be able to move shells individuals have to be above a certain size. This precludes all but the largest males from reorientating and moving shells.

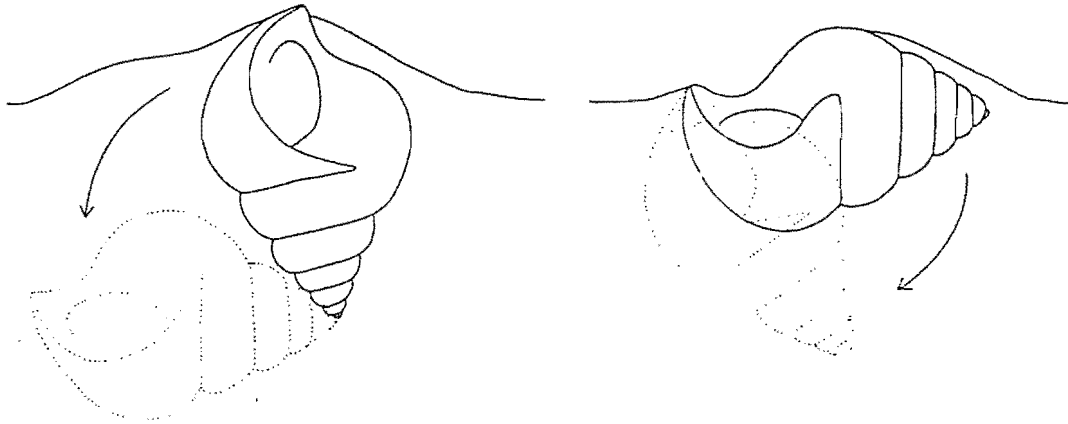


Figure 4.17 Scenarios for reorientating vertically and horizontally buried shells.

4. If residents are removed from territories but shells are left, which species will recolonise the shells?

When a fish is removed or preyed upon the remaining mate has several options regarding its shell resources.

- a) It may ignore open shells of its ex-mate and allow random recolonisation by other shell-dwellers.
- b) It may defend the territory allowing only acceptable immigrants, such as females ready to spawn, access to open shells.
- c) It may hide open shells and uncover them only when suitable mates enter the territory.
- d) It may remove shells from the territory thus preventing immigration of other shell-dwellers.
- e) It may leave the territory in search of a new mate.

All of these options are used. However, the recolonisation of vacant shells is not random. The species and sex of immigrants is probably affected by several factors: shell orientation; shell size; and the behaviour of remaining fish (sections 4.1 to 4.3). Species and sexes differ in their behaviour. Why are there differences, between species and sexes, in responses to vacant shells?

Most females (of both species) ignore shells vacated by males and were unable to defend territories against larger male immigrants. Due to sexual dimorphism females use smaller shells than their mates. Haussknecht & Kuenzer (1990) showed for *L. ocellatus* that there was a significant increase in costs of shell burial with increasing shell size (Figure 4.18, line 1). Females probably do not bury or hide male shells because they are too large and therefore too costly to bury.

Male *L. ornatipinnis* hid a higher proportion of shells than *L. ocellatus*. These differences between males of may be related to levels of competition for shells (shell and competitor abundance), availability of mates and the costs of various behaviours.

As female *L. ocellatus* use the smallest shells, the likely recolonists will therefore be female *L. ocellatus* or immature individuals of other species. *L. ocellatus* are also abundant and so new mates may be encountered rapidly. Therefore male *L. ocellatus* may leave small shells open because the cost of hiding them outweighs the cost of their defence (Figure 4.18).

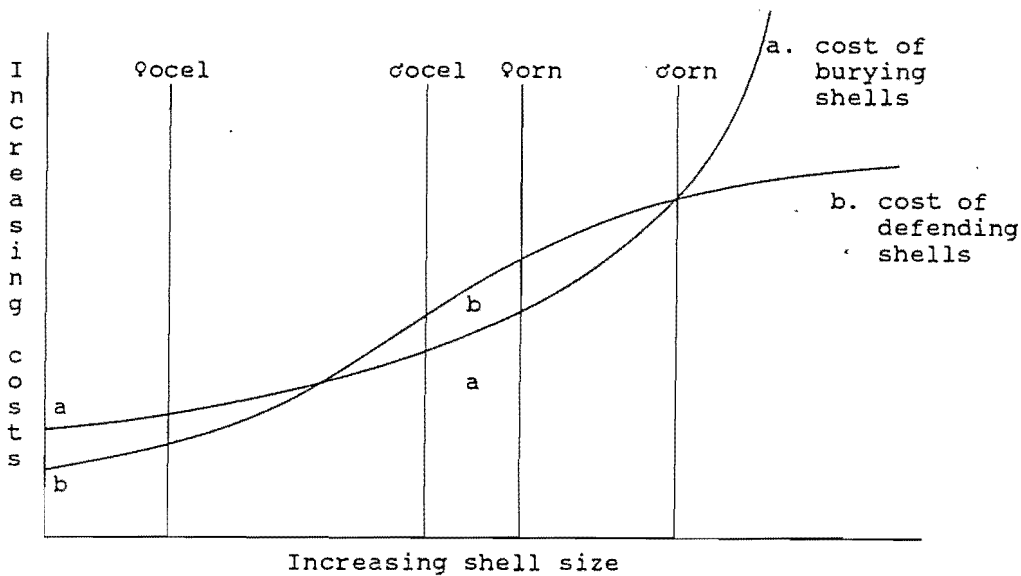


Figure 4.18 A model representing the decision to leave open, hide or move shells in *L. ocellatus* and *L. ornatipinnis*. (a = cost of burying shells, b = cost of defending shells, vertical lines indicate mean sizes of males and females of *L. ocellatus* and *L. ornatipinnis*)

However, *L. ornatipinnis* females use shells within the size range used by adult male *L. ocellatus*, *L. laparogramma* and *N. hecqui* (Table 4.2). For male *L. ornatipinnis* therefore the possibility of shells being used by males of other species is high. Female *L. ornatipinnis* are also less abundant than *L. ocellatus* and so encountered less frequently. It may be less costly to hide shells and uncover them only when a new female enters the territory than defend an open shell for a long time.

I propose that the two species use the same strategy of 'least costs' in responding to open shells vacated by ex-mates. The costs of various factors are dominated by individual fishes' size which affects the ability to bury shell, defend shells, attract mates etc. (Figure 4.18).

There was a difference between *L. ocellatus* and *L. ornatipinnis* females in the number of recolonised open shells. Six female *L. ocellatus* migrated into territories where females had been removed while there were no female *L. ornatipinnis* immigrants. This may be accounted for in several ways.

a) *L. ocellatus* was numerically more abundant in most areas and so mate encounter rates must be considerably higher for this species.

b) Female *L. ornatipinnis* may move over shorter distances in search of new refuges than female *L. ocellatus*.

c) Male *L. ornatipinnis* may be more choosy than male *L. ocellatus*.

I consider a) the most probable as *L. ocellatus* was numerically dominant at the study site (Table 4.1).

5. How do residents respond to heterospecific shell-dwelling intruders?

During the early observational work of this study hidden shells were often found to contain crabs. This gave me the idea that fish may be hiding shells in order to evict crabs. Experiment 5 tested this idea.

L. ocellatus and *L. ornatipinnis* react to crabs by pulling them out of shells by their legs and carrying them out of territories (Figure 4.16). Males also hide shells containing crabs. However, shell

hiding appears to be elicited by the absence of females rather than the presence of crabs (see section 4.4).

In previous experiments the digging up and moving of shells by *L. ornatipinnis* was a characteristic feature of this species. Crabs inhibit this behaviour. This may be effected in two ways:

- a) by preventing internal inspection (which may be a precursor to moving); or
- b) by antagonistic behaviour such as extending chela from the shell mouth.

The latter possibility seems unlikely because if the crab extends its claw out of the shell it risks exposure and removal. It is also improbable that the crab could prevent the fish from digging the shell up.

In captivity *L. ocellatus* both external and internal inspection was found to be necessary before digging was initiated (Hausknecht & Kuenzer 1990). Therefore the hiding of shells (or the onset of horizontal digging) should be preceded by shell inspection. This was not the case with crab-blocked shells. In both experiments some individuals (of each species and sex) initiated digging of some sort. Either the onset of digging does not require internal shell inspection as a cue or the fish may assess that if there is a crab in the shell it is a satisfactory refuge. In the case of crabs added to principal shells the fish was already familiar with the shell and presumably remembers its internal size and quality.

CONCLUDING REMARKS

L. ocellatus and *L. ornatipinnis* compete with con- and heterospecific fish and crabs for shell refuges. This is done by a variety of behaviours which enhance competitive ability and result in partitioning of shell resources. Behaviour is particularly complex and often there may be several possible responses to similar situations. Behavioural differences appear to have a genetic basis e.g. *L. ocellatus* orientates shells vertically even when other species are not present.

SUMMARY

1. The shell-dwelling fish which occur in soft substrate habitats attain different adult sizes. Consequently different species and sexes use different size ranges of shells. Despite this there is considerable overlap in the sizes of shells used between species.
2. There are distinct differences between species in methods of shell burial and shell use resulting in species-characteristic shell orientations. These appear to have a genetic basis as they are exhibited by species with lake-wide distributions.
3. Shell orientation does affect other species' use of shells.
4. Where individuals are removed from territories shell size and orientation and remaining fish behaviour affect the recolonising fishes size, sex and species.
5. Behavioural responses to shell-dwelling competitors are complex and species-specific.

CHAPTER 5

PHYLOGENETIC ANALYSIS OF SHELL-DWELLING BEHAVIOURS IN THE GENUS *LAMPROLOGUS*

INTRODUCTION

The lamprologine shell-dwellers exhibit a suite of unique behaviour patterns associated with shell use (Chapters 3 & 4). Species in soft substrate habitats steal shells from other fish, excavate depressions around shells, hide, move and bury shells. In most instances the species inhabiting a territory may be identified from the distribution, number and orientation of shells without seeing the fish. During the course of experiments in Chapters 3 and 4, I became interested in how certain behaviour patterns evolved within the shell-burying and hole-digging species. In this chapter I examine the phylogenetic distribution of five behaviour patterns within the genus *Lamprologus*: digging around the shell; shell orientation; shell hiding; shell moving; and hole digging.

A phylogenetic tree was constructed using a variety of independent characters. The five behaviour patterns to be examined were then fitted to the tree. These five behaviour patterns were not used in the generation of the tree. The phylogenetic distribution and the evolution of these behaviour patterns is discussed.

THE FIVE BEHAVIOUR PATTERNS

1. Digging around the shell - excavation or burial (eb).

Species which occur in shell bed habitats (*Altolamprologus cf. compressiceps*) and at the rock-sand intermediate zone (*T. vittatus* and *L. callipterus*, Figure 2.15) use shells on the substrate surface. All of the species occurring in soft substrate habitats either excavate depressions around shells (*N. hecqui* Figures 2.4 and 5.1) or bury shells (*L. ocellatus* Figures 2.10 and 5.2b). As shell excavation is a first step towards burying shells, it could be argued that excavation preceded shell burying. However, it is unknown if this occurred or if the two behaviour patterns evolved in different lineages.

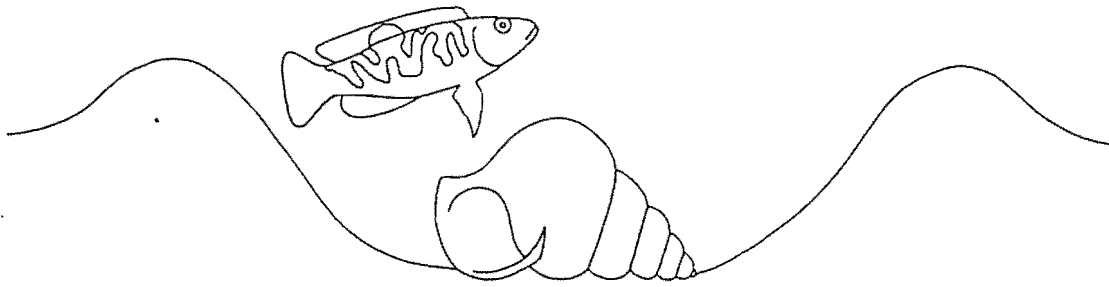


Figure 5.1 A shell excavated by *N. hecqui*.

2. Shell orientation (or).

Prior to burial, shells lie on the substrate in a horizontal orientation (Figure 4.6). All of the excavators and all but one of the shell buriers orientate shells horizontally. Only *L. ocellatus* buries shells in a vertical orientation. This requires digging activity to be concentrated at the apex of the shell (Figure 4.7) and is considered apomorphic.

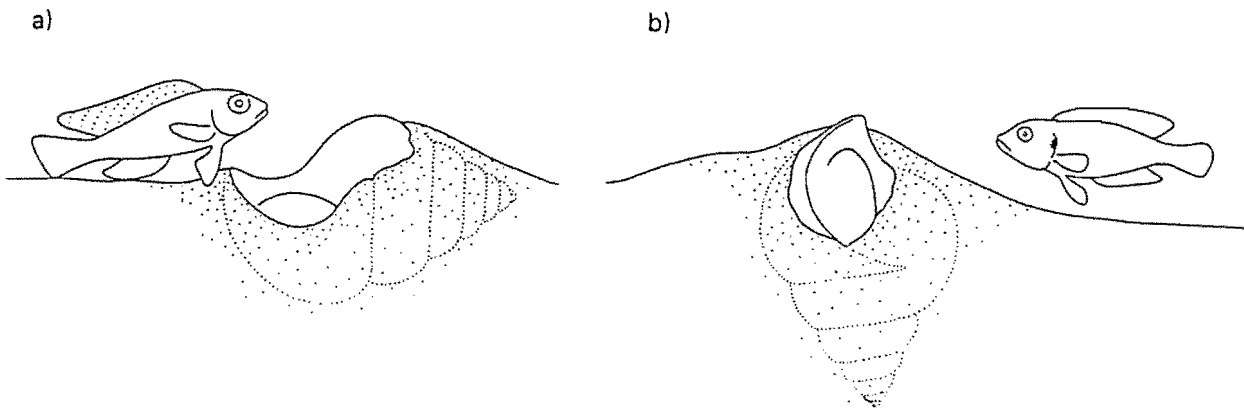


Figure 5.2 Shells buried a) horizontally (e.g. *L. ornatipinnis*) and b) vertically (e.g. *L. ocellatus*).

3. Hiding shells (hs).

All the *Lamprologus* 'buriers' also hide shells. Shell hiding is where a shell is buried, filled in and then covered with sand. Although hidden shells are not visible, sand mounds surrounded by radiating 'digging lines', indicate their locations (Figure 5.3). I consider that this behaviour has evolved to reduce competition for space by reducing available shell refuges (see Chapter 6). Within the *Lamprologus* 'buriers' this character is considered plesiomorphic.

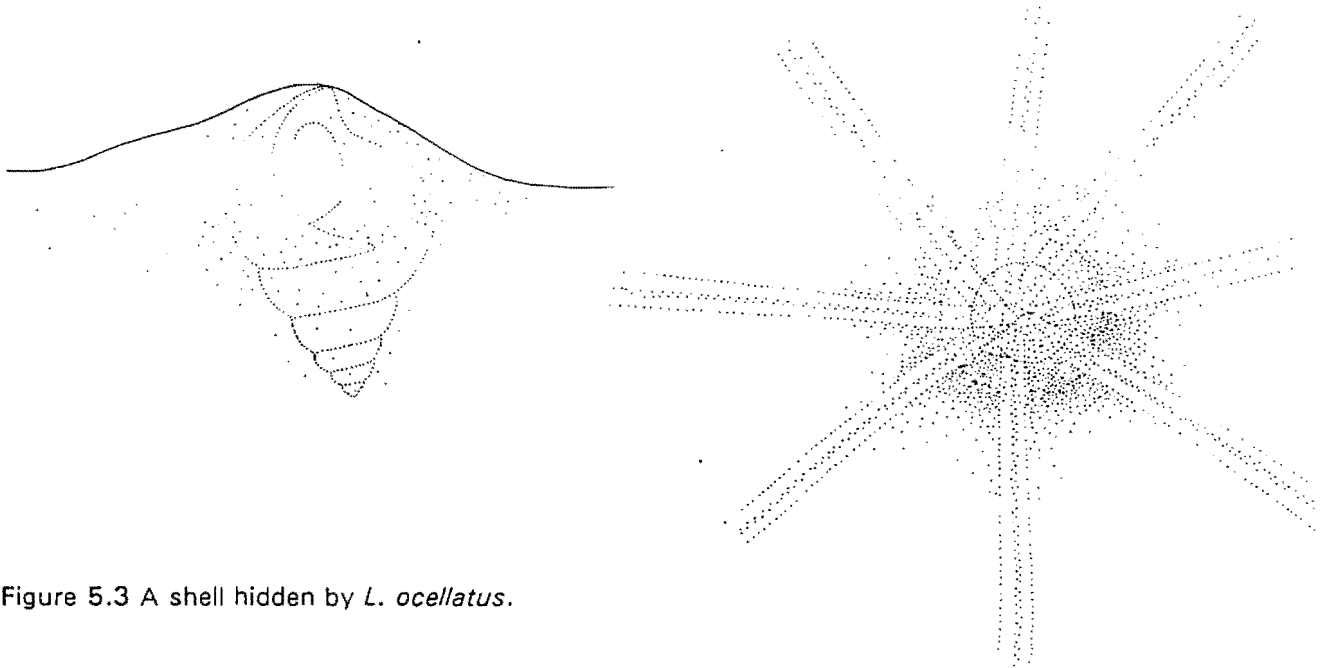


Figure 5.3 A shell hidden by *L. ocellatus*.

4. Moving shells (ms).

Only males of *L. ornatipinnis* and *L. callipterus* are known to move shells. Shells are grasped by the lip of the shell mouth and the fish then swim upwards in the desired direction. The behaviour is considered a synapomorphy. Whether this behaviour evolved once, indicating a close relationship between these two species, or independently is unknown.

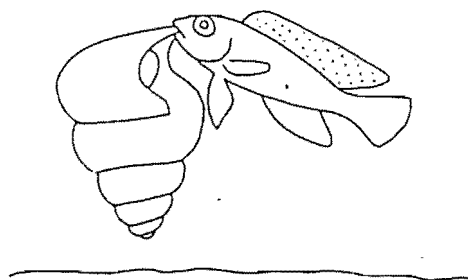


Figure 5.4 A male *L. ornatipinnis* moving a shell.

5. Hole digging (ho).

L. signatus and *L. laparogramma* are facultative shell/hole-dwellers and *L. kungweensis* an obligate hole-dweller. The direction of evolution for these hole/shell-dwellers could be argued either way. Changing water levels could have forced fish to move from mud substrates into shell-rich habitats. Alternatively, fish could have remained in the same location and winnowing currents could have exhumed shells in mud habitats. Under both circumstances mud-dwelling species could have progressively evolved from obligate hole-dwellers to facultative and latter obligate shell-dwellers. It is equally possible, although less parsimonious, to argue that shell-dwelling behaviour was progressively lost under conditions of reduced shell numbers.

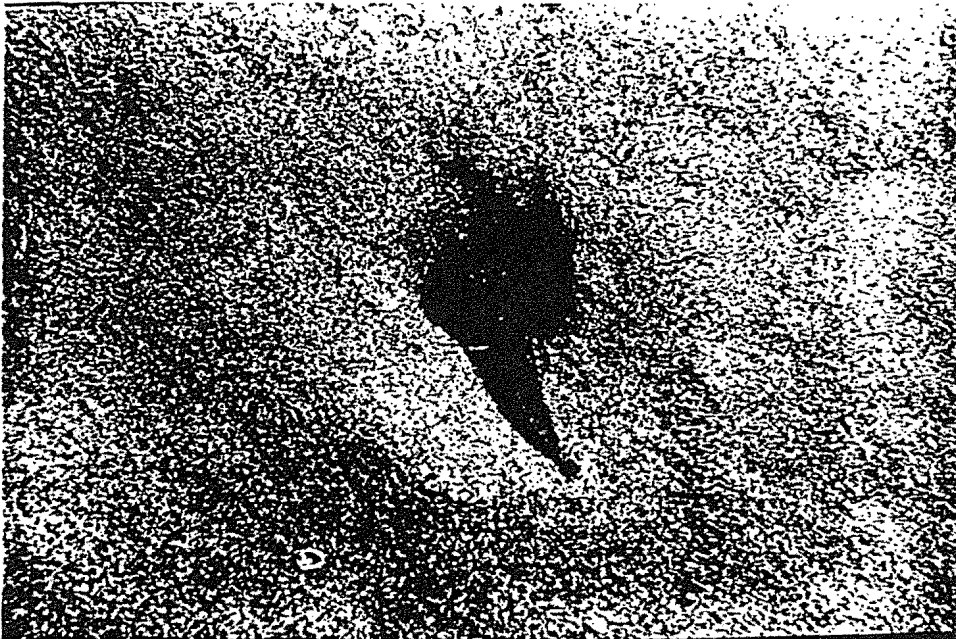


Figure 5.5 A male *L. laparogramma* resting at its principal refuge hole.

I have concentrated on the *Lamprologus* complex as the core of my work has examined species of this genus. No information was available for *Lamprologus finalimus* or *L. stappersi* and so these are not included. Two outgroup species, *Nepholamprologus hecqui* and *N. brevis*, are considered. The seven species and their behaviour patterns are given in Table 5.1.

Table 5.1 Shell using behaviours in seven lamprologine shell-dwellers.

	digging around shells	shell orientation	hides shells	moves shells	digs holes
<i>L. ocellatus</i>	B	V	+	-	-
<i>L. ornatipinnis</i>	B	H	+	+	-
<i>L. laparogramma</i>	B	H	+	-	+
<i>L. signatus</i>	B	H	+	-	+
<i>L. kungweensis</i>	-	-	?	-	+
<i>L. lemairii</i>	E	H	-	-	-
<i>L. callipterus</i>	-	H	-	+	-
<i>N. hecqui</i>	E	H	-	-	-
<i>N. brevis</i>	B	H	?	-	-

B = buries shells, E = excavates depressions around shells, H = orientates shells horizontally, V = orientates shells vertically, ? behaviour unknown, + = exhibits the trait, - = does not exhibit the trait.

MATERIAL AND METHODS

Behaviour patterns are based on the results of observations reported in Chapter 2 and experiments in Chapters 3 and 4.

Colour patterns were determined from preserved specimens (RUSI collection), colour photographs (Konings 1988, personal collection) and observations of live specimens.

Morphological and meristic features were extracted from species descriptions (Poll 1956, Bills Appendix 1).

Scale patterns were examined on enzyme-cleared specimens which were stained with alcian blue and alizarin red. These specimens are in the RUSI collection.

Specimens used for analysis. *Lamprologus kungweensis* 42616 & 42614; *L. ocellatus* 38839 & 49313; *L. ornatipinnis* 49311 & 38822; *L. laparogramma* 49261 & 43553; *L. signatus* 43551 & 43577; *L. lemairii* 42436; *L. callipterus* 38834; *Neolamprologus brevis* 49855 & 38862; *N. hecqui* 49291 & 38812.

The five behavioural characters being examined were not used in the construction of the phylogenetic tree. These were superimposed onto the tree later to determine their phylogenetic distribution.

The lamprologine character matrix (Table 5.2) consists of 28 characters: (9) behaviour patterns; (11) morphological features; (8) colour patterns and colouration. These were used in the construction of the phylogeny and were mainly generated from my own studies. The characters, their states and polarities are listed below. The coding of states is: plesiomorphic (0); apomorphic (1 or more).

CHARACTERS, CHARACTER STATES AND CHARACTER STATE POLARITIES

Behaviour

1. Adult shell use (asu): 0) none; 1) facultative; 2) obligate.

As the majority of lamprologines and other fish are not shell-dwellers, this is considered the plesiomorphic state. The shell-dwelling species exhibit a range of behaviour relating to shell utilisation. Obligate shell-dwellers are considered the most derived. The two outgroup species are both obligate shell dwellers.

2. Juvenile refuge use (jru): 0) refuges not used; 1) facultative; 2) obligate.

After juveniles leave parental territories some do not use shells or holes but wander through a variety of habitats e.g. *N. brevis*. I consider this behaviour the most primitive state. Juveniles of other species use shells as refuges if available (facultative, e.g. *L. lemairii*). A few species use shells exclusively throughout their life histories (obligate, e.g. *L. ocellatus* & *N. hecqui*).

3. Larval refuge use (lru): 0) same shell or hole as adult; 1) additional holes or shells used.

Within the lamprologines, larvae are usually cared for in a central territory and use the same refuge as that used by the parent. This is the case with *N. brevis*, one of the outgroup species, and is considered the plesiomorphic state. In many of the shell and hole-dwellers larvae spread out among all the available refuges within a territory. In some instances, e.g. *L. ornatipinnis* and *L. ocellatus*, this may

mean that some juveniles receive reduced parental protection. This adaptation to dispersed refugia may have evolved to reduce sibling feeding competition (see Chapter 6).

4. Refuge function (rf): 0) refuge only; 1) breeding only; 2) both.

Presumably shell-dweller ancestors were non shell-dwellers. The two outgroup species and the majority of *Lamprologus* species use shells or holes as refuges and as breeding sites. Within the shell-dwelling complex the use of shells as both breeding sites and refugia appears to be synapomorphic. One species uses shells as refuges only (*L. lemairii*, Figure 1.6) and one species uses shells for breeding sites only (*Lepidolamprologus attenuatus*, Figure 1.7).

5. Mating strategy (ms): 0) monogamous; 1) polygamous.

The majority of lamprologines (including the two outgroup species) are monogamous egg guarders. In the polygamous shell-dwellers males control female access to shell refuges, either directly or by altering shell abundance (Sato 1989a, Walter & Trillmich 1994, Chapters 3 & 4).

6. Position of egg laying in the shell (eg): 0) 1st whorl; 1) 2nd or 3rd whorl.

Two egg laying sites, within the shell, were recognised (Figure 2.7). One whorl around from the mouth was the most common site used and this is considered plesiomorphic. Only *N. brevis* lays its eggs in the 2nd-3rd whorl of the shell. *N. brevis* is unusual because both adults share a single shell (see character 7.). Female *N. brevis* are smaller than males and always enter the shell first. To allow the male to fit into the shell completely the female must move deep inside the shell. Thus laying of eggs in the 2nd-3rd whorl is considered an adaptation to shell sharing and the apomorphic state. The laying sites for eggs of obligate and facultative hole dwellers were not observed.

7. Number of refuges used: 0) male and female share one shell; 1) male and female use one shell or hole each; 2) female uses one shell and male uses two shells; 3) female uses one shell & male uses three or more shells.

The number of refuges used within the shell-dwelling group varies considerably between species. *N. brevis* adults share the use of a single shell while male and female *N. hecqui* each use single shells. *L. ocellatus* and *L. ornatipinnis* males use 2-3 shells while females normally use one shell. *L. callipterus*

males construct nests of over fifty shells while females use single shells within a nest. The hole-dwellers use single holes within joint territories. I consider the use of single shells primitive and the use of higher numbers derived. The number of shells used is not related to body size.

8. Habitat use (hb): 0) eurytopic; 1) stenotopic.

Eurytopic species are found in two habitat types e.g. the two outgroup species *N. hecqui* and *N. brevis* both occur in shell bed and scattered shell habitats. Most of the *Lamprologus* shell-dwellers are exclusively found in certain habitat types, e.g. the hole-dwellers are only found on mud substrates.

9. Feeding behaviour (fe): 0) feeds from above the substrate; 1) feeds from a resting position on the substrate.

The majority of lamprologines (including the outgroup species) and other Tanganyikan cichlids feed from above the substrate. This is therefore considered the plesiomorphic state. Feeding from a resting position on the substrate is unusual and is considered an adaptation to living in close association with the substrate.

Colouration and colour patterns

10. Opercular spot (os): 0) present; 1) absent.

Opercular spots occur in many genera of fish within Lake Tanganyika (lamprologines, limnochromines, perissodines and ectodines: Poll 1985). The two outgroup species have opercular spots.

11. Vertical 'chain' bars on body (cb): 0) absent; 1) present.

Vertical 'chain' bars (see Appendix, Figure 8a) are an unusual colour pattern in Lake Tanganyika. Less than 10 species are known to exhibit this pattern in Lake Tanganyika and within the *Lamprologus* group only *L. signatus* and *L. laparogramma* exhibit this character. I consider this feature apomorphic.

12. Eye colour (ec): 0) uniform colour; 1) upper-anterior section coloured differently to rest of eye.

Several species of *Lamprologus* have the upper-anterior section of the eye coloured differently to the rest of the eye e.g. *L. signatus*. Eye colouration may be a key character in species recognition in dark

environments. Neither of the outgroup species exhibit this feature.

13. Sexual dichromatism (sd): 0) monochromatic; 1) slightly dichromatic; 2) grossly dichromatic.

Within the lamprologines the majority are sexually monochromatic and I consider that this is the primitive situation. However, the shell-dwellers are characterised by varying degrees of sexual dichromatism (see Chapter 6). A few species are monochromatic e.g. the outgroup species *N. hecqui*. Certain species exhibit slight sexual dichromatism with the intensity of colours varying between sexes e.g. *L. ocellatus* and *N. brevis*. Others show marked dichromatism with sexes showing differences in colour patterns e.g. *L. kungweensis* and *L. signatus*. I consider marked sexual dichromatism the most derived state.

14. Female dorsal fin spot (♀dfs): 0) absent; 1) present.

The presence of an ocellated dorsal fin spot in females is a rare characteristic amongst the Tanganyika cichlids. It is present in occasional specimens of *L. ornatipinnis* and in all *L. kungweensis* examined. I consider it a derived character.

15. Head spot (hs): 0) absent; 1) present.

The presence of rust-coloured spots on the occipital region of the head is exhibited by *N. brevis* and *N. calliurus*. This feature is considered apomorphic.

16. Dorsal fin lappet pattern (dfl): 0) double line; 1) single colour.

The single colour of dorsal lappets is the simpler feature than the double line and so initially I anticipated that this would be the plesiomorphic state. However, the two outgroup species exhibit dorsal fin lappets with double colour patterns. Dorsal lappet colouration is a dominant feature within the lamprologines and is also present in several other genera within Tanganyika (e.g. *Limnochromis* spp., *Simochromis* spp.) This character shows a great deal of variation in all these genera.

17. Hind dorsal fin pattern (hdf): 0) same as rest of fin; 1) different than the anterior dorsal fin.

In the majority of the lamprologines the pattern of the dorsal fin is uniform along its length. In certain species e.g. *L. signatus* and *N. brevis*, the posterior-dorsal section of the dorsal fin is patterned

differently to the rest of the fin. In *L. signatus* the black and gold lines are striking when the fin is held open in displays. Enhanced patterning of the hind dorsal fin is considered apomorphic.

Morphological and meristic characters

18. Rounded pelvic fins (rp): 0) filamentous; 1) rounded.

In most of the lamprologines, including the two outgroup species, the 2nd and 3rd rays of the pelvic fin are elongated. This is the plesiomorphic state. In the majority of the *Lamprologus* species pelvic fins are rounded. This character is considered apomorphic and related to facilitating the use of these fins as props when resting on the substrate.

19. Gill rakers (gr): 0) eight or more; 1) less than eight.

The two outgroup species, together with the majority of lamprologines, have gill raker counts of more than eight. This is considered the plesiomorphic state. The reduction of gill rakers may be associated with specialised benthic feeding.

20. Dorsal spines (ds): 0) 18 or more; 1) less than 18.

The two outgroup species have high dorsal spine counts. These two species have periods where juveniles and sub-adults are not associated with shell refuges. The reduction of dorsal spines in the smaller *Lamprologus* species may be an adaptation to the permanent use of refuges. I consider a low dorsal spine the apomorphic state.

21. Anal spines (as): 0) seven or more; 1) less than seven.

As in character 21 above both the outgroup species exhibit high spine counts. This feature is considered to be related to anti-predation and so is affected by the relative use of shell or holes as refuges. The loss of spines in the species which use shells for their entire lives is considered an apomorphy.

Squamation

22. Scales on the occipital region of the head (soc): 0) few or no scales; 1) fully covered with scales. The two outgroup species and most of the *Lamprologus* species have reduced numbers of scales anterior of the dorsal fin and between the eyes.

23. Scales between the lateral line and the 1st dorsal spine (sld): 0) partially covered; 1) fully covered with scales.

The majority of *Lamprologus*, *N. brevis* and *N. hecqui* have reduced scale cover between the lateral line and first dorsal spine (Figure 3, Appendix 1).

24. Scales at the base of the pectoral fins (spc): 0) present; 1) absent.

One of the outgroup species (*N. brevis*) and just over half of the *Lamprologus* species have scales at their pelvic fin bases. These scales are smaller and more deeply imbedded in the skin than the surrounding flank scales.

25. Scales on the anal and dorsal fins (sfi): 0) absent; 1) present.

Most lamprologines examined lacked scales on the dorsal and anal fins and this is considered the plesiomorphic state. In two species, *L. ocellatus* and an undescribed *Altolamprologus*, scales occurred between the rays on both anal and dorsal fins. This is unusual, and while their function is unknown, their occurrence is considered apomorphic.

26. Scales in front of the pelvic fins (s>p): 0) present; 1) absent.

N. brevis, *L. lemairii* and *L. ocellatus* have scales anterior of the pelvic fins. Reduced, small and deeply embedded scales may be an adaptation to being in contact with the substrate for prolonged periods.

27. Preopercular scales (pos): 0) 10 or more; 1) less than 10.

One of the outgroup species (*N. hecqui*) has more than ten scales on the preoperculum. The majority of the *Lamprologus* genus has very few scales and this may be an adaptation to benthic habits.

28. Scales on the operculum (sop): 0) 10 or more; 1) less than 10.

The two outgroup species have scale counts greater than 10 on the operculum as do all the other lamprologines examined except for the three hole-dwellers.

CHARACTER ROOTING

The outgroup species. Character rooting was determined by outgroup comparison (Maddison et al. 1984). The phylogenetic tree of the lamprologines is not fully resolved (Poll 1985, Colombe & Allgayer 1985). Consequently the sister group for the genus *Lamprologus* is unknown. The two outgroup species used in this study were chosen because they occurred within study sites in Zambia and so were available for study.

The lamprologine character matrix (Table 5.2) was analysed to produce putative phylogenies using the computer program HENNIG86 (Farris 1989). This program resolves character conflicts on the basis of parsimony (Hennig 1966).

Character independence: There is a concern that certain characters may show a correlation and this will result in increased weighting for these characters. Where two characters in a category showed the same states for each species one was removed. All the remaining characters show variation between species so that I am satisfied that the characters are independent.

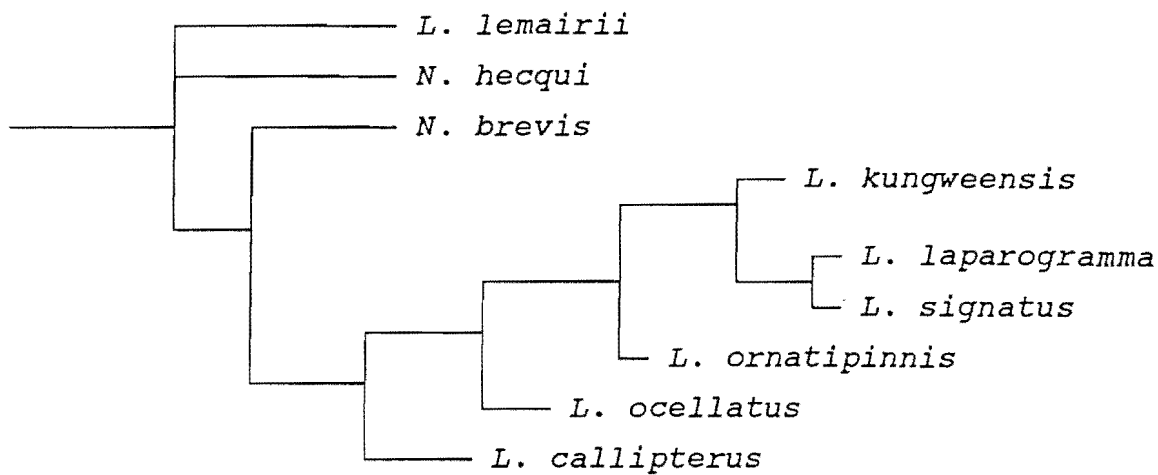
Character polarity: Where possible I have attempted to categorise characters into two states. Polarity is automatic for binary characters. Where characters have multiple states I have used knowledge of outgroups and non-shell-dwelling lamprologines to predict the evolutionary sequence. In the instance of meristic counts for example, I consider that gill raker numbers increased or decreased gradually through an intermediate stage (low GR's => medium GR's => high GR's) rather than immediately from a high to a low number (low GR's => high GR's).

PHYLOGENETIC ANALYSIS AND DISCUSSION

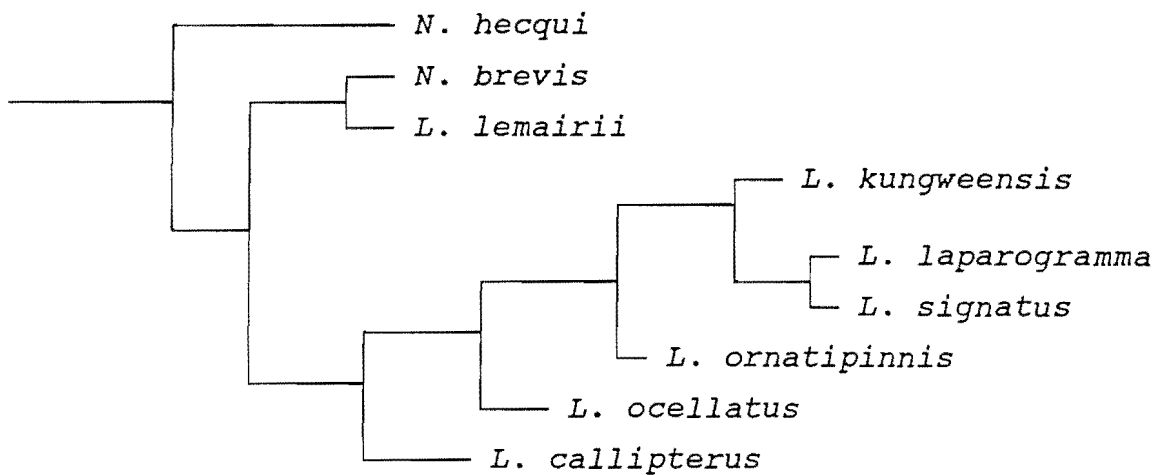
The HENNIG86 (Farris 1988) analysis of unweighted data in Table 5.2 produced two trees each with a length of 290 steps, ci = 58, and ri = 60. A branch swapping procedure ('bb' option) applied to the same data produced an additional tree. These three trees are shown in Figure 5.6. Refinement of this data by a successive weighting procedure ('xs' option, Farris 1988), to the point of stability, produced a single tree with a length of 179, ci = 87, ri = 92 (Figure 5.7). This procedure was carried out using

Characters /	kun	oce	orn	lap	sig	lem	cal	bre	hec
Behaviour patterns									
1. aru	0	2	2	1	1	0	2	2	2
2. jru	0	2	2	0	0	1	0	0	2
3. lru	1	1	1	1	1	0	0	0	1
4. rf	2	2	2	2	2	0	1	2	2
5. ms	0	1	1	0	0	0	1	0	0
6. eg	-	0	0	?	?	-	0	1	0
7. ns	1	2	2	1	1	-	3	0	1
8. hb	1	1	1	1	1	0	0	0	0
9. fe	1	0	1	1	1	1	1	0	0
Colouration and colour patterns									
10. os	1	0	1	1	1	0	0	0	0
11. cb	0	0	0	1	1	0	0	0	0
12. ec	1	0	1	1	1	0	0	0	0
13. sd	2	1	1	2	2	0	1	1	0
14. ♀fs	1	0	1	0	0	0	0	0	0
15. hs	0	0	0	0	0	0	0	1	0
16. dfl	1	1	1	0	0	0	1	0	0
17. hdp	0	1	0	1	1	0	1	1	0
Morphological and meristic characters									
18. rp	1	1	1	1	1	0	0	0	0
19. gr	1	1	1	1	1	0	0	0	0
20. ds	1	1	1	1	1	0	0	0	0
21. as	1	0	1	1	1	0	1	0	0
Scale patterns									
22. soc	1	1	0	1	1	1	0	1	1
23. sld	1	0	1	1	1	1	0	1	1
24. spc	1	0	0	1	1	0	0	0	1
25. sfi	0	1	0	0	0	0	0	0	0
26. s>p	1	0	1	1	1	0	1	0	1
27. pos	1	0	1	1	1	1	0	1	0
28. sop	1	0	0	1	1	0	0	0	0

Species abbreviations are as follows: kun - *L. kungweensis*; oce - *L. ocellatus*; orn - *L. ornatipinnis*; lap - *L. laparogramma*; sig - *L. signatus*; lem - *L. lemairii*; cal - *L. callipterus*; bre - *N. brevis*; hec - *N. hecqui*. Character state unknown (?) or not exhibited by the species (-). For character abbreviations see text.



Tree 2



Tree 3

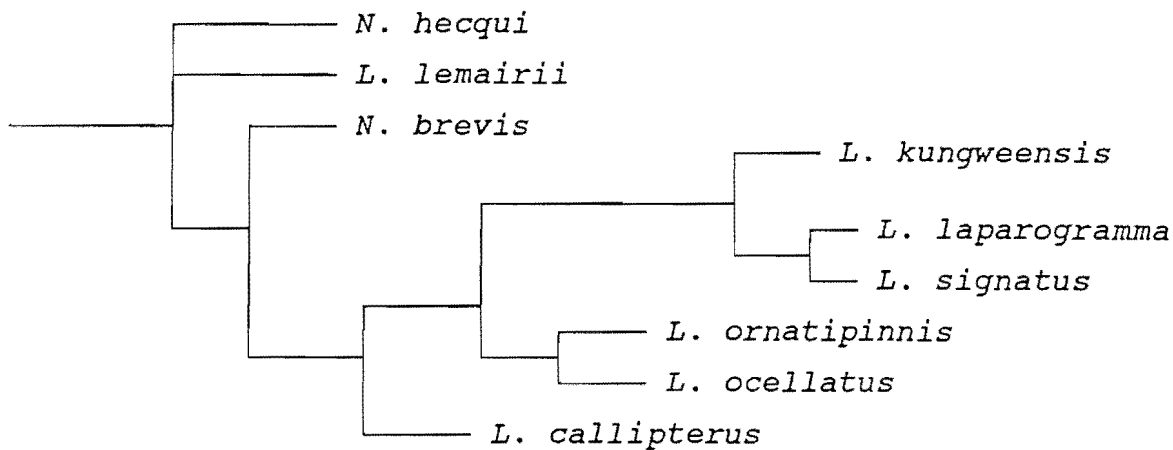
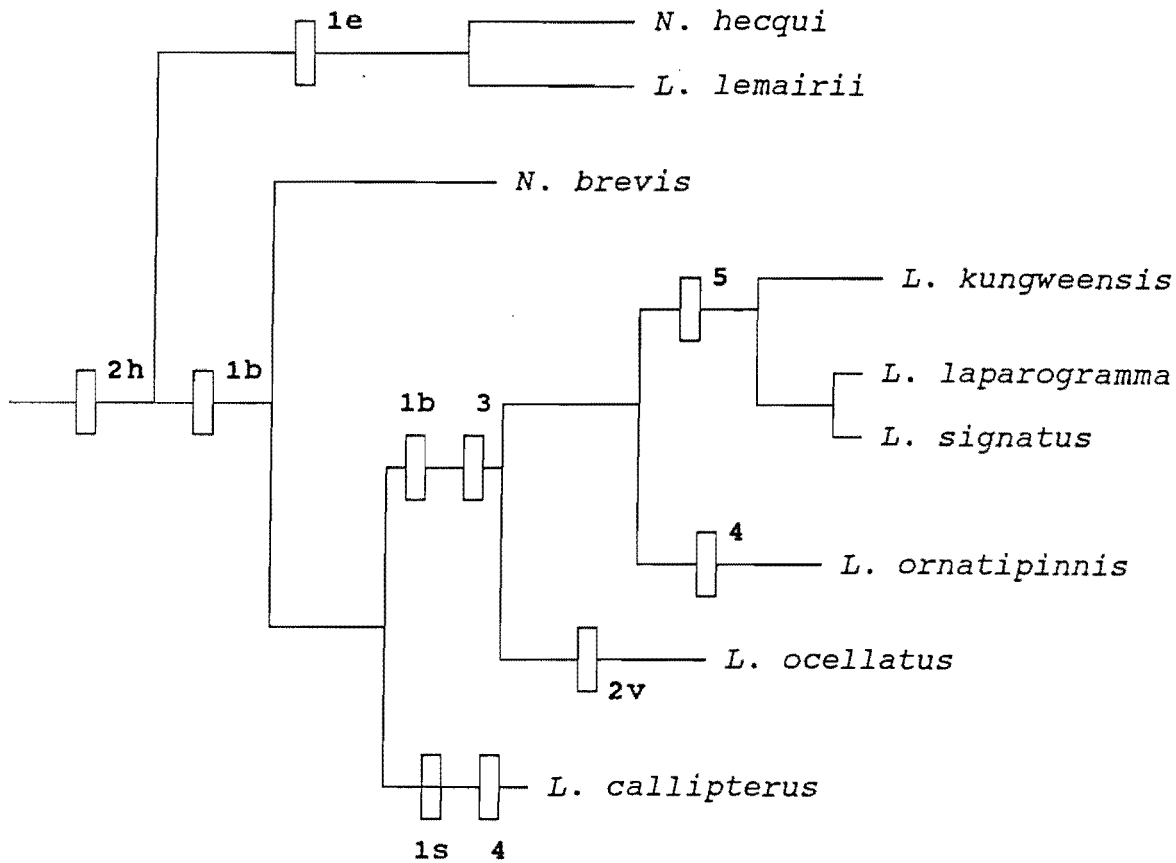


Figure 5.6 Phylogenetic hypotheses of relationships of the genus *Lamprologus* based on data in Table 5.1 (HENNIG86, outgroup = *N. hecqui*, length = 65, ci = 60, ri = 59).



Character 1: 1s = Uses shells on surface; 1e = excavates depressions around shells; and 1b = buries shells.

Character 2: 2h = horizontal shell burial; and 2v = vertical shell burial.

Character 3: 3 = hides shells

Character 4: 4 = moves shells

Character 5: 5 = digs holes

Figure 5.7 Phylogenetic hypothesis of relationships of the genus *Lamprologus* based on data in Table 5.1 (HENNIG86, data was iteratively reweighted (post hoc) to stability, length = 179, ci = 87, ri = 92). The five behaviour patterns are superimposed onto this tree.

both *N. hecqui* and *N. brevis* as the outgroup species. The only effect of changing outgroups was to change the outgroup positioning while the order and branching of the genus *Lamprologus* was unaffected. All of these trees are equivalently resolved with regard to the shell-burying and hole-dwelling *Lamprologus* species examined in this study. I am therefore confident that the *Lamprologus* phylogenetic sequence (Figures 5.6 and 5.7) is robust.

The genus *Lamprologus* is not a monophyletic group and *L. lemairii* does not seem correctly placed within the genus (sensu Poll 1985). However, the lower end of the tree is not well resolved as with different treatments of the data the two outgroup species and *L. lemairii* changed positions. The five behaviour patterns were fitted to the phylogenetic tree in Figure 5.7. The following conclusions can be made (Figure 5.8).

- > excavates a depression around shell
1. surface
shell user
- =====> buries shell
2. horizontal shell burial —————> vertical shell burial
3. not —————> hides shells
4. not =====> moves shells
5. not —————> hole digging

Figure 5.8 Rooted polarity diagrams of the five behaviour patterns.

Indicates trait has arisen once —————> or twice =====>

1. Digging around the shell - excavation or burial (eb).

In the introduction I hypothesised that the evolution of excavating and burying could have followed two routes:

- a) use shells on the surface => excavate depression around shell
=> bury shell; or
- b) use shells on the surface => excavate shells, and separately
use shells on the surface => bury shells.

It seems that the latter has occurred with excavators and buriers evolving in different lineages (Figure 5.8, 1).

Shell burying behaviour seems to have evolved twice: in the *Lamprologus* species; and in *N. brevis*. In each of the trees these two groups were separated by the surface shell user *L. callipterus*. While a reversal in *L. callipterus* could also account for this I do not favour this possibility as there are several morphological features which place these fish in different genera (Poll 1985). To resolve this problem the entire shell-dwelling group needs to be examined. If this is done I anticipate that *N. brevis* will become further removed from the *Lamprologus* clade.

The hypothesis that *L. lemairii* is incorrectly placed within *Lamprologus* is supported by the behaviour of excavating depressions around shells. Other species also excavate depressions around shells. This behaviour may indicate a close phylogenetic relationship and could be grounds for identifying a new taxon with the following species: *Lepidolamprologus attenuatus*, *Neolamprologus meeli*, *N. Boulengeri*, *N. hecqui* and *N. pleuromaculatus*. Other characteristics which would support such a grouping include elongated bodies, high lateral line scale counts, predatory feeding behaviour, and several colour patterns.

2. Shell orientation (or).

The hypothesis that horizontal shell orientation is plesiomorphic (see Introduction) is confirmed. All the species, with the exception of *L. ocellatus*, whether 'excavators' or 'buriers' orientate shells horizontally (Figure 5.8, 2).

Why has vertical shell burying evolved? It is my hypothesis that burying a shell vertically, in some way, deters other species from using that shell. In particular this has evolved in the presence of *L. ornatipinnis* which is *L. ocellatus*' most common shell competitor. *L. ornatipinnis* orientates shells horizontally and moves shells. A shell vertically positioned is deeper in the substrate than one horizontally buried and may therefore be more difficult to move. A vertically positioned shell may also have its lower end filled with sand and thus be heavier to move. This is discussed further in Chapter 6.

Burying shells vertically requires more work than horizontal shell burial. Presumably the additional costs of shell burial in *L. ocellatus* must be balanced with benefits accrued from this behaviour.

3. Hiding shells (hs). (Figure 5.8, 3).

All the *Lamprologus* 'buriers' hide shells. It is unknown if *N. brevis* does this. However, I suspect that it does not as this species only uses one shell and does not defend a large territory. This is probably because *N. brevis* is a planktivore feeding 30-50cm above the substrate. In contrast the *Lamprologus* species feed from the substrate and thus food resources are defendable. One method of protecting resources is to prevent access to potential refuges within the territory i.e. hide all unused shells. I was unable to observe *L. kungweensis* for long periods and am unsure if it hides shells. However, I suspect that *L. kungweensis* does hide shells because: a) it also feeds primarily from the substrate; and b) its close relatives, *L. signatus* and *L. laparogramma*, hide shells even when they are using holes. This is

discussed further in Chapter 6.

4. Moving shells (ms).

Shell movement is carried out by two species - *L. callipterus* and *L. ornatipinnis*. These species occur in different habitats and yet the movement of shells appears to fulfil the same function i.e. giving additional refuges to attract mates and protect young. Both species steal shells from their neighbours (Sato 1994, Chapters 3 & 4). However, *L. callipterus* has gone a stage further as stolen shells often contain females (Sato 1994). Thus in *L. callipterus* shell theft is also a method of acquiring mates.

From the trees (Figures 5.6 & 5.7) the two species appear to be closely related. Consequently shell moving behaviour may have evolved in two ways:

- a) arisen once and was subsequently lost in *L. ocellatus* and in the hole-dwellers; or
- b) arisen independently on two occasions in *L. callipterus* and *L. ornatipinnis*.

I favour option b) as it is more likely that such a beneficial trait will have arisen twice rather than been lost twice (Figure 5.8, 4). However, more detailed observations of this behaviour pattern in future may indicate which of these possibilities is correct.

5. Hole digging (ho). (Figure 5.8, 5).

The trees confirm that hole-dwelling species have evolved from shell-dwelling ancestors closely related to *L. ornatipinnis*. Interestingly *L. kungweensis* appears to have split away from the facultative shell dwellers rather than developing from them. The development of obligate hole-dwelling direct from obligate shell-dwelling may be explained in two ways.

a) It is possible that there are undiscovered taxa that will fill the gap between *L. ornatipinnis* and *L. kungweensis*.

b) I observed *L. kungweensis* in Zaire and Burundi where shell abundance was low. Obligate hole use by *L. kungweensis* in these areas may simply be a product of low shell availability. In contrast

the southern basin, where *L. laparogramma* and *L. signatus* occur, is rich in surface shells deposits.

Further analysis is required to expand this phylogeny to include all the other shell-dwelling lamprologines. A greater number of characters will be required to ensure good resolution of the entire group. Techniques such as DNA finger-printing and karyology could enhance the character matrix significantly.

CHAPTER 6

GENERAL DISCUSSION

INTRODUCTION

Aspects of the physical environment of natural habitats and the ecology and behaviour of shell-dwelling fish were recorded in Chapter 2. The shell-dwelling communities in soft substrate habitats were identified as being of particular interest due to their manipulation of shell resources and complex behaviour patterns relating to shell use. These behaviour patterns are complex, requiring numerous discrete acts which may be alternated many times before a final response is achieved.

A series of experiments was conducted in Chapter 3 to examine the purpose of shell-burial in *L. ocellatus* and *L. ornatipinnis*. Field experiments and field observations indicate that shell burial may be a method of reducing competition for shell refuges by preventing intruders from gathering information about shell quality and size.

During the course of initial observations and experiments interspecies differences in behaviour patterns and shells used were noted. These were investigated in Chapter 4. Results confirmed several interspecific differences in behaviour patterns and shell resource use. Shell orientation and shell movement have a direct effect upon other shell-dwellers e.g. shells buried vertically inhibit shell use by *L. ornatipinnis*. There is also a hierarchy of fish using shells, with the smallest shells being used by *L. ocellatus* females and the largest by *N. hecqui* males (Table 4.2). Resource partitioning and certain behaviour patterns therefore seem to enhance individuals ability to defend shell resources and hence territories.

In Chapter 5 a phylogenetic tree was used to examine the distribution of five behaviour patterns. Shell burying and hiding behaviour are ancestral to the *Lamprologus* 'burying group' (five or more species). Vertical shell orientation and shell movement are probably unique behaviours (autapomorphies). Hole-digging behaviour is common to three species (synapomorphic) and has evolved

from shell-dwelling ancestors.

In all of the experiments, individuals varied in their responses to shells. For example new shells placed into *L. ornatipinnis* territories were:

- a) ignored;
- b) picked up and discarded outside the territory;
- c) relocated within the territory;
- d) buried where it was found; or
- e) hidden where it was found.

Clearly the process of responding to shells is complex. An individual's response to shells may be affected by a host of factors which can result in one of several responses. The process of shell inspection and acquisition is similar in many ways to that in marine hermit crabs. Models (Elwood & Neil 1986 & 1992) concerning the response process are taken from hermit crab research and applied to these shell-dwelling cichlids. In this chapter observations and results from Chapters 2, 3 and 4 are explained and discussed in the light of these behavioural models.

RESPONSE POINTS

Shell assessment behaviour in *L. ocellatus*, *L. ornatipinnis* and marine hermit crabs (reviewed in Elwood & Neil 1992) is similar. Jackson (1988, cited in Elwood & Neil 1992) split the shell assessment process in the hermit crab *Pagurus bernhardus* into a series of simple 'decision points'. Applying this method to the Tanganyikan shell-dwellers may help understand how the burial behaviour process works. The word 'decision' implies a weighing of factors or judgement. I consider that these cichlids respond to a variety of factors in a simple stimulus-response reaction which is correlated with levels of motivation. I therefore have replaced the term 'decision' with response. A single 'response point' (Figure 6.1) comprises the following.

- a) The initial stimulus. Usually the sighting of an empty unburied shell within an individuals territory is the major stimulus to initiating responses.

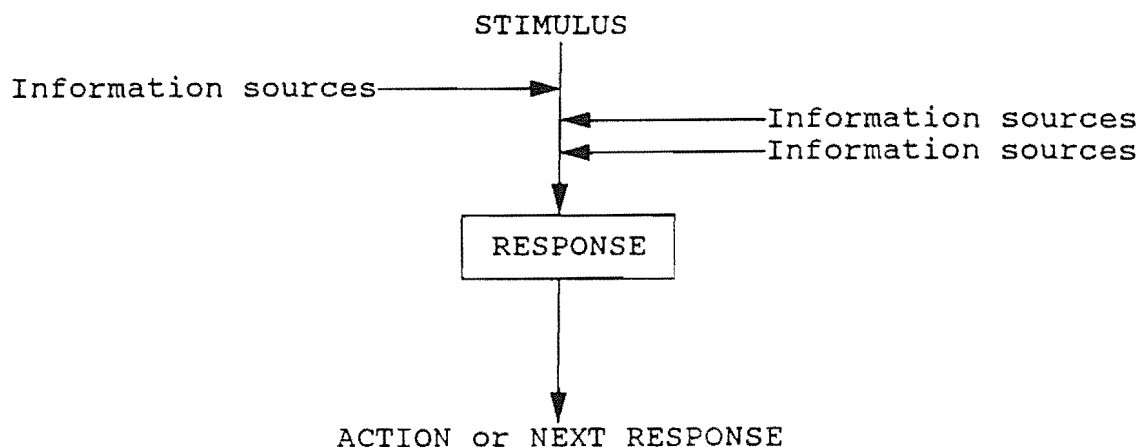


Figure 6.1 A diagram showing a single stimulus-response in *L. ocellatus* and *L. ornatipinnis*.

b) Other information sources. Other stimuli both from within the territory (e.g. the quality, size and number of other shells in the residents territory) and from outside the territory (e.g. neighbouring shell resources, neighbour sizes) affect responses to shells.

b) A response. This is a non-random change in behaviour such as 'move to and inspect a shell' or 'commence digging'. A response occurs when causal factors cross a threshold level (Figure 6.2). No judgement by the individual is implied.

c) An action or move to the next response point. The result of a response may be an observable act e.g. 'move to and inspect a shell' or 'commence digging'. However, a response may also result in no discrete response e.g. 'do not approach the shell'.

MOTIVATION

The motivation model (Elwood & Neil 1992, Figure 6.2) can be used to explain how a response is made. An individual may start off with a certain motivational level and as it gathers information this level will change. If causal factors take the motivational level above or below certain thresholds the animal will respond by a change in activity - referred to here as a 'response'.

Where a shell-dwelling fish possesses a single poor quality shell its motivation to accept a new shell will be high (a. Figure 6.2). Under such circumstances the stimulus of a new intact shell should result in causal factors rapidly rising above the threshold levels of 'accept and start to bury shell' (line 1, Figure 6.2). If a new shell is of poor quality the time taken to reject the shell should be longer (line 2, Figure 6.2). Note that the speed with which the fish 'moves' towards the response point, i.e. accepting or rejecting the shell, varies.

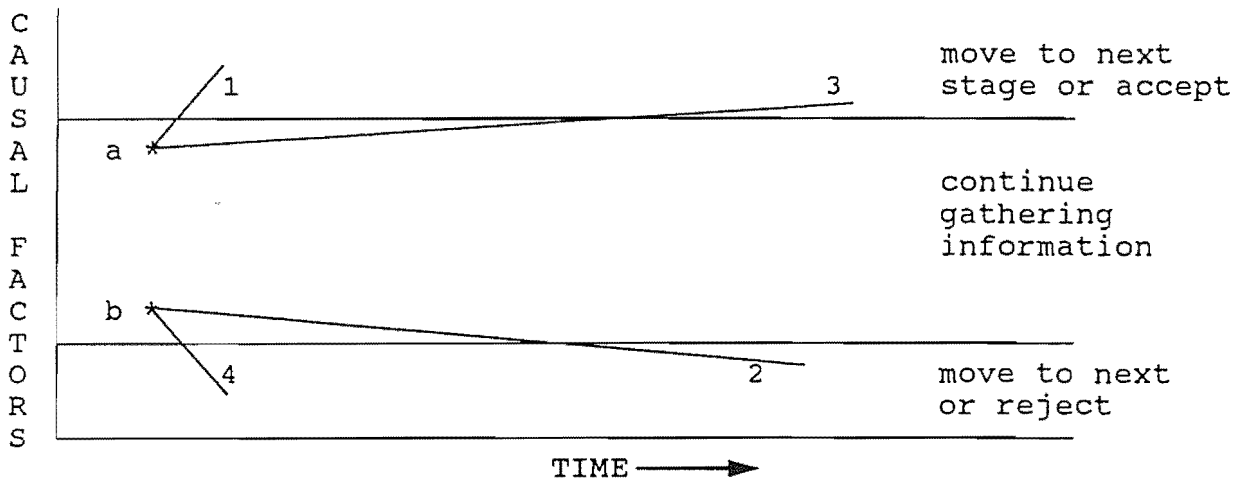


Figure 6.2 A motivational model (Elwood & Neil 1992) showing the possible response to accept or reject a shell (see text for explanation of the model). a = high initial motivation, b = low initial motivation.

Conversely a fish with a good quality shell will have a low motivation to accept a new shell (b, Figure 6.2). In this situation a fish given a new intact shell it will take longer to inspect and move to accepting a shell (line 3, Figure 6.2). If given a poor quality shell rejection should be very quick (line 4, Figure 6.2). Again note the different line slopes indicating differences in speed of acceptance or rejection of shells.

The above examples are simplified and in reality there appear to be numerous causal factors such as quality, size and distribution of old and new shells, the presence and size of juveniles, mates and neighbours and the size of the resident. Other factors, such as food abundance and predation

levels, may also affect the economic defendability of shells. These factors contribute to a single output in causal factor space. At different response points in the shell burial process the weighting of individual factors may vary.

RESPONSE POINTS IN SHELL ASSESSMENT AND USE

I consider that the shell acceptance and burial process consists of a series of simple response points linked together. This could account for the flexibility in responses exhibited by shell-dwelling fish.

Where a shell is of acceptable quality and size I predict that in *L. ocellatus* there are a minimum of six response points (Figure 6.3). This compares with five response points in hermit crabs (Elwood & Neil 1992). The major difference between these cichlid fish and hermit crabs is not in assessment but in the final responses concerning how the shells are dealt with. In hermit crabs the shell assessment process is a comparative one. The shell presently in use is compared with a new one. The result is that the better shell is occupied and the poorer one rejected and left. In most cases other hermit crabs will then inspect and use the rejected shell. Few shells remain unused in marine habitats.

L. ocellatus and *L. ornatipinnis* differ from hermit crabs in that they defend territories. Consequently if a resident fish ignores a new shell it risks intruders inhabiting the shell and in turn losing part of its territory. I propose that this is why all shells within certain size and quality ranges are responded to in some way. If there is only one shell in a territory, a new shell will be buried and used. If there are already many shells in a territory the new one may be carried away and discarded by *L. ornatipinnis* or hidden by either species.

Of course in both hermit crabs and cichlids there can be more than five or six possible responses points. Hermit crabs may compare original and new shells several times resulting in shell swapping and reinvestigations. However, once a crab rejects a shell another crab is then able to use it (McLean 1983, Vance 1972, McClintock 1985, and others). Thus the process usually ends, for the individual, with 'shell rejection'. This is not the case in the cichlids and there seem to be additional influences upon responses and final options resulting in a more complex behaviour patterns. By

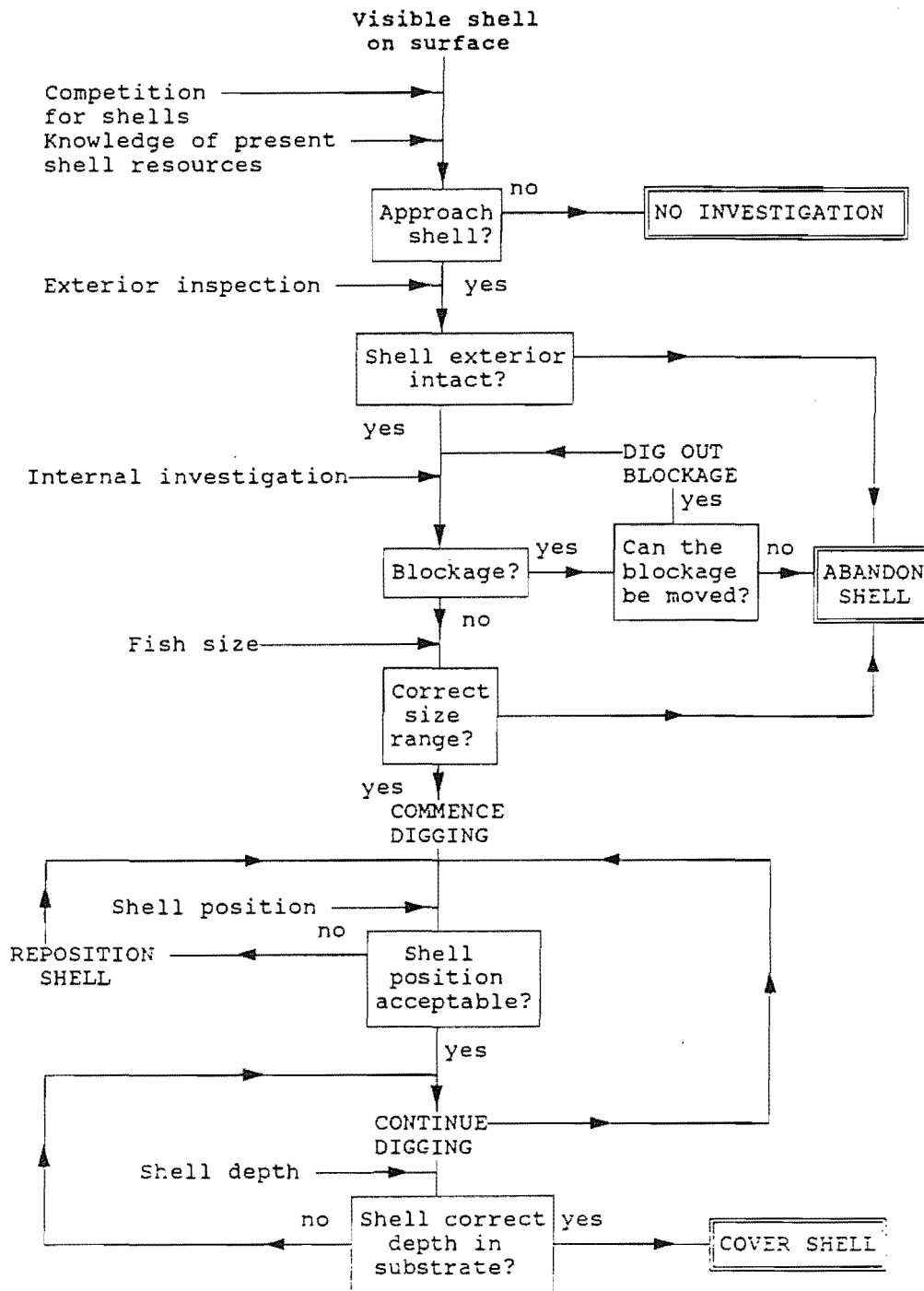


Figure 6.3 Possible response points during shell assessment and burial in *L. ocellatus*.

External investigation (lower case) = information source, = response point,

COMMENCE DIGGING (CAPITALS) = result, = end result.

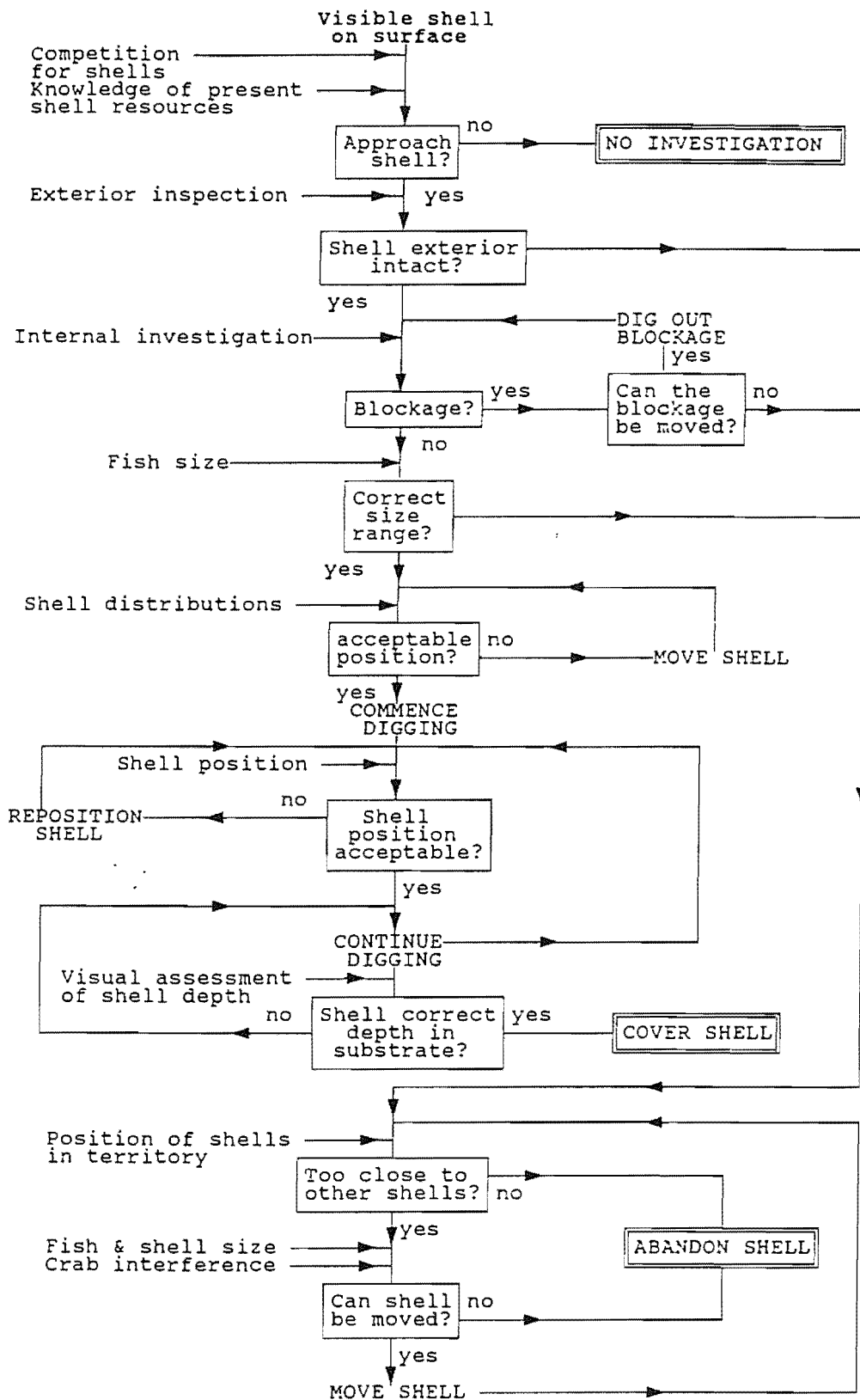


Figure 6.4 Possible response points during shell assessment and burial in *L. ornatipinnis*.

External investigation (lower case) = information source, [] = response point,

COMMENCE DIGGING (CAPITALS) = result, [] = end result.

defending territories and shell resources there are possibilities for later reassessment and use of shells. The cichlids do reassess conditions and alter which shells are used and hidden and *L. ornatipinnis* is able to change shell distributions within its territories.

INTERSPECIFIC DIFFERENCES IN RESPONSES TO SHELLS

In most situations during experiments *L. ornatipinnis* took longer to respond to shells and responded to fewer shells than *L. ocellatus*. This may be explained in two ways: a) differences in motivation; and b) the different number of response points between the two species (due to movement of shells by *L. ornatipinnis*).

a) Motivation.

L. ornatipinnis attains a larger size than *L. ocellatus* and so should be more capable of defending territories from other shell-dwelling competitors. If this assumption is correct and shell burial is related to competition for shell resources *L. ornatipinnis* may be less motivated than the smaller *L. ocellatus*. This would explain why responses to situations and actions being carried out by *L. ornatipinnis* takes considerably longer than in *L. ocellatus*.

This could be tested under controlled conditions in a series of tank experiments. Fish of varying sizes and with principal shells of the same size and quality would be given new shells of varying quality. Times taken to accept or reject additional shells could be predicted from fish sizes and additional shell quality and size. The null hypothesis is that there would be no difference between the response times of different fish. The alternative hypothesis is that larger fish would take longer to respond to shells than smaller fish.

b) Shell movement by *L. ornatipinnis*.

The ability of *L. ornatipinnis* males to move shells adds a degree of complexity to the response making process (Figure 6.4). A greater number of final responses are possible when an individual can move

shells. The moving of shells may affect other behaviours relating to shell burial. For example *L. ornatipinnis* can remove excess shells of good quality from a territory in a few seconds rather than spending one to two hours burying them. Where two shells are close together one can be moved and then buried. The value of more evenly distributed shells may be greater than clumped resources (see below). In both instances *L. ocellatus* must bury shells where they are located or leave them on the substrate surface and risk their use by other competitors.

A further consequence of shell movement may be that shells are more thoroughly inspected before a response is made. It would be a waste of energy to start digging prior to completing an inspection only to then move the shell. Thus *L. ornatipinnis* may conduct a more thorough examination of shells prior to progressing to the next response point. This may be an alternative explanation why *L. ornatipinnis* responds to shells more slowly than *L. ocellatus*.

WHY WERE SOME BLOCKED SHELLS BURIED OR HIDDEN?

Two types of blocked shells were added to fish territories:

- a) those blocked with silicone glue; and
- b) those blocked with freshwater crabs (*Platythelphusa maculata*).

The latter are natural competitors for shell refuges in soft substrate habitats in Lake Tanganyika. Fish responses to the two types of blocked shell varied and I propose the following explanations.

Artificially blocked shells.

In the experiment where blocked shells were added to fish territories 5% of *L. ornatipinnis* and 55% of *L. ocellatus* initiated shell burial and only later did they abandon shells. This can be explained this in two ways. Firstly the response process in Figures 6.3 and 6.4 indicate an orderly stepwise process. I propose that information is feeding into various 'response points' in an unordered way resulting in certain response points progressing faster than others. This may be further affected by motivational levels which may have unequal effects upon the 'progress' of different response points. Thus in individuals highly motivated to accept shells, the response to 'accept the shell and initiate digging' (line

1, Figure 6.5) is reached before the response to 'reject the shell' (line 2, Figure 6.5). The time difference (x, Figure 6.5) between initiating digging and stopping digging will be dependant on the individuals initial motivation and the external quality of the blocked shell.

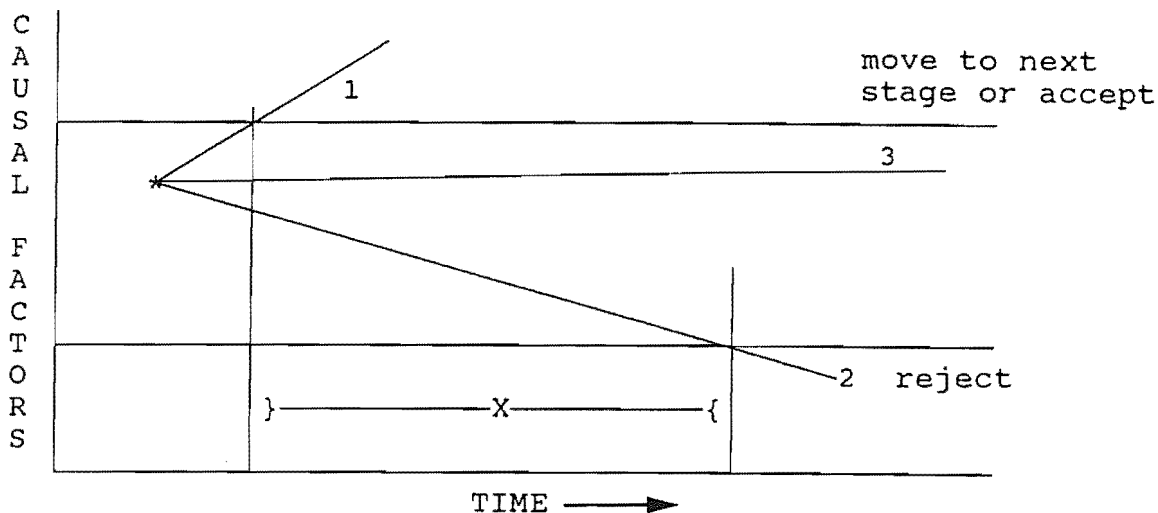


Figure 6.5 A model explaining the onset of burying and subsequent cessation by individuals provided with blocked shells.

Shells occupied by crabs - surface shells.

Most shells inhabited by crabs and lying on the substrate surface were left unburied by fish. As with silicone blocked shells the presence of crabs prevents internal inspection of shells. However, crabs also seem to inhibit the initiation of shell burial and shell movement. When crabs in shells were approached they extended their chela (the larger chela was always outermost) into the shell mouth. This antagonistic behaviour by the crab can only go so far as if the crab comes too far out of the shell it risks removal by the fish. However, this antagonistic behaviour may increase the fishes initial inspection time (line 3, Figure 6.5). This means that the response 'reject the shell due to blockage' will occur before digging is initiated.

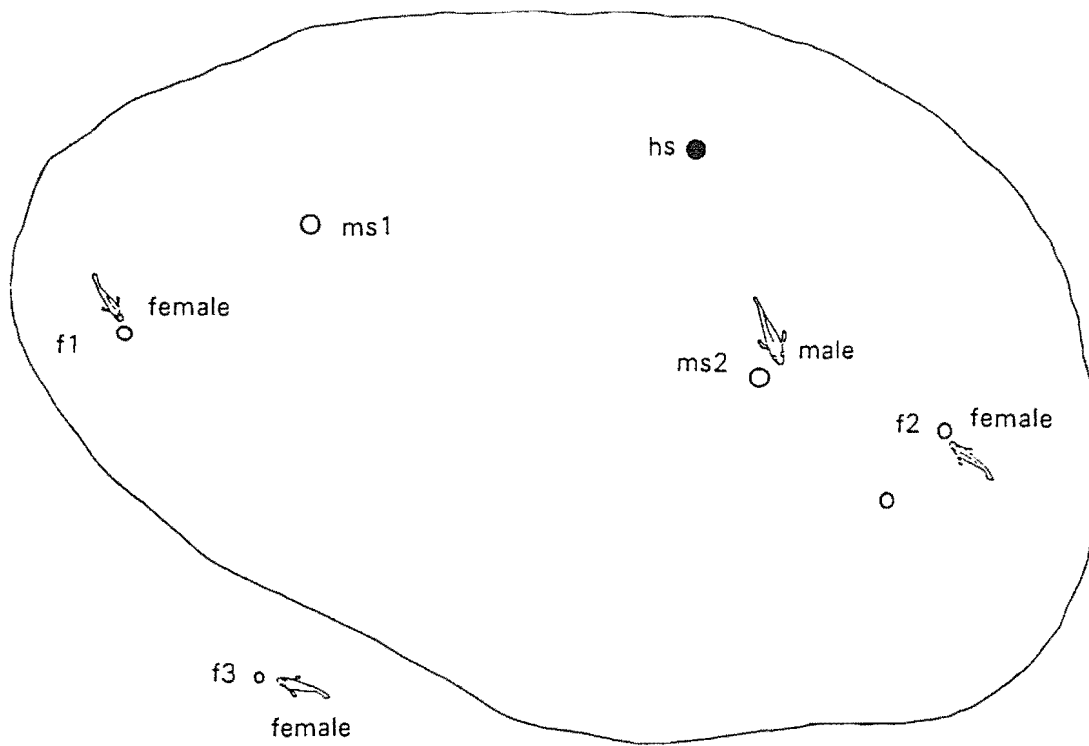
- buried shells.

During the course of experiments many hidden shells were found to contain crabs. As surface shells with crabs are not buried, these hidden shells must have been buried as open shells by the fish, occupied by crabs and then hidden. The hypothesis that shells were being hidden in order to evict crabs is not supported by observations. Crabs remain in hidden shells for several days and, when no shells are available, will bury themselves into the substrate for refuge. In contrast to shell burying, shell hiding is not inhibited by the presence of crabs. This may be because crabs are not affected by shell hiding and therefore do not attempt to disrupt this activity. Alternatively the activity of hiding the shell by 'horizontal digging' (Hausknecht & Kuenzer 1990) is conducted 1-2cm away from the shell, and the crab may therefore not be able to disturb this activity without exposing itself to being removed from the shell.

Observations indicate that shells (with and without crabs) are being hidden to prevent other fish from gaining entry to shells. Shell-hiding seems to be elicited by the absence of a mate rather than the presence of a crab. This was confirmed by laboratory studies (Walter & Trillmich 1994). In natural habitats the number of shells usually used by males is two and females 1-2. Excess numbers of shells within territories are usually hidden.

CONTROL OF MATE DISTRIBUTION

Lamprologus ocellatus and *L. ornatipinnis* bury greater numbers of shells than are required for use. Large male *L. ornatipinnis* are also capable of picking up and moving shells which enables them to: a) relocate shells within their own territories; b) to steal shells from neighbours; and c) to remove unwanted shells from territories. In the majority of cases males (both species) maintained two open shells and females one shell. Where males were removed from territories the remaining females often did not respond to vacated shells. In the reverse situation remaining males hid and moved shells. Males therefore seem to play a dominant role in controlling access to shell resources and this affects mate immigration and distribution.



2.

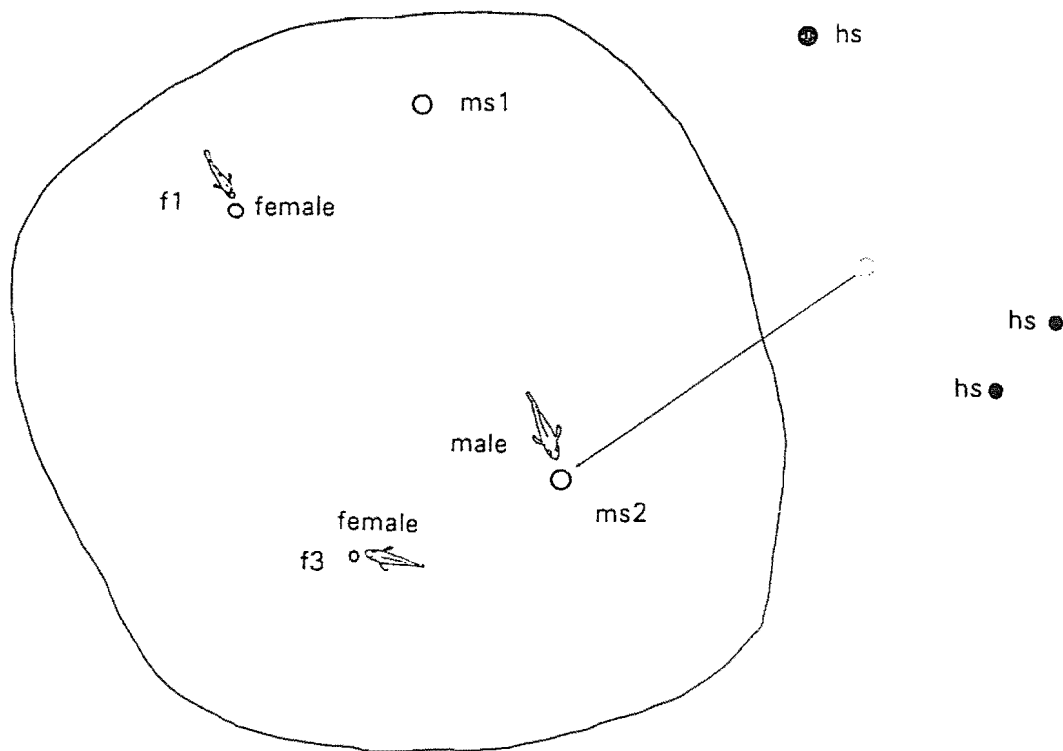


Figure 6.6 An *L. ornatipinnis* territory (one male and two females) showing the redistribution of shells with changing mate distribution.

1. The solid line indicates the territory boundary, f1 = the first female at its principal shell, f2 = the second female, f3 = 3rd female, ms1 = males' principal shell, ms2 = males' secondary shell, hs = hidden shells.
2. When the second female (f2) is either preyed upon or leaves the territory, its shell is hidden by the male, and a new territory boundary may be established. This is achieved by moving the 'ms2' shell closer to the new female (f3) so altering the distribution of open shells.

In laboratory conditions Walter and Trillmich (1994) showed that *L. ocellatus* males open hidden shells for females. They also noted, in polygynous territories, aggression between females and male intervention in conflicts. One of their conclusions was that females must remain close together so that males can ensure paternity over broods. Male 'peace-keeping' between females was considered a regular event. In natural conditions this does not appear to be the case. In polygynous territories females were usually separated by 0.5-1m (Table 2.6). Thus males seem to reduce female-female aggression by either spreading shell resources (by shell relocation) and/or regulating access to certain shells (by hiding and opening shells).

The accumulation of shell-rich territories, where several shells are hidden, thus gives male territory holders a great deal of flexibility with regard to shell usage. Females occupying shells close to the territory may be enticed into it by the male moving shells or opening hidden shells closer to the female. As *L. ocellatus* is unable to move shells it is tied to a specific area if it wishes to retain all its shells. However, *L. ornatipinnis* may move shell and shift its territorial boundaries without losing resources (Figure 6.6).

MATE CHOICE

There are presently 59 species of lamprologines (substrate spawners) described which comprise 34% of the cichlids of Lake Tanganyika (Poll 1985). Typically the lamprologines are sexually monochromatic (Poll 1956, Konings 1988, Table 6.1). However, most of the shell-dwelling species show sexual dichromatism. The shell-dwellers differ from other dichromatic species (e.g. the maternal mouth-brooders) in having brightly coloured females. In the genus *Lamprologus* the extent of the dichromatism varies with the trend reaching its extreme in *L. kungweensis* where females are more brightly coloured than males (Figure 17, Appendix 1). A similar trend appears in the West African genera *Nanochromis*, *Teleogramma* and *Pelvicachromis* (Richter 1989, Stewart & Roberts 1984).

Instances of reversed sexual dichromatism are rare amongst fishes and no other such cichlids are known from Lake Tanganyika. Common features shared by these species are:

1. female presentation behaviour (Richter 1989, pers. obs.);

2. early parental care (up to free swimming stage) mostly or completely by the female;
3. males are larger and carry out most of the territorial defense and later parental care; and
4. males may control female access to certain resources such as nest sites and refuges.

The control of essential resources (e.g. shell refuges) and mate choice by males may be significant factors influencing the evolution of sexual dichromatism within the shell-dweller group. Detailed phylogenetic studies may prove valuable in determining factors important in the selection and evolution of colour patterns in cichlids.

Table 6.1 Sexual dichromatism in the lamprologines (Poll 1985, Konings 1988, pers. obs.).

Genus	Number of species (Poll)	Dichromatic (%)
<i>Altolamprologus</i>	2	0
<i>Chalinochromis</i>	1	0
<i>Julidochromis</i>	5	0
<i>Lamprologus</i>	8	63*
<i>Lepidolamprologus</i>	6	17
<i>Neolamprologus</i>	32	3
<i>Telmatochromis</i>	5	20

(* 25% unknown: *L. stappersi* & *L. finalimus*)

CONCLUSIONS

Gastropod shells are the only refuges and oviposition sites within *L. ocellatus* and *L. ornatipinnis* territories and so they are integral resources. These species manipulate shells in several unusual ways and the variety of responses to new shells is impressive. New shells may be ignored, moved, buried (and used) or hidden (not used). How shells are utilised seems to be dependant on factors such as the size and quality of the new shell and the number already in the territory. Shell use may also be affected by neighbour species, sex and size, predation levels and a host of other factors.

New empty shells appear to be a common feature of the lakes' soft substrate habitats. If shells

are not responded to by the residents they risk other shell-dwellers using them and thus losing part of their territory. Shell burial is a considerable investment which may take several hours and hundreds of acts to complete. Numerous cues or information sources are involved in stimulating the various responses which result in shells being buried. Many of these cues are actively sought by the fish by means of external and internal investigations.

Shell burial appears to be a method of reducing the information gathering ability of potential shell-dwelling competitors. By burying shells the resident prevents intruders from inspecting (externally) shells and thus assessing their value. Consequently, an intruder's motivation to contest the possession of a buried shell should be less than for a unburied shell. As winning contests is often decided on a combination of individual size and motivation, successful intruders will have to be bigger than residents. Shell burial can therefore be regarded as an investment process which enhances the residents ability to defend its resources.

Behavioural differences between *L. ocellatus* and *L. ornatipinnis* in shell-burying methods result in species characteristic final shell orientations. These may be involved in reducing the motivation of intruders further as shell reorientation requires more work than simple burial. Behavioural differences may also be involved in specific mate recognition.

Shell burying has gone a stage further. Where the number of shells in a territory is higher than required, shells are hidden (filled in and covered). Hidden shells are reopened as required and large males thus control the structure of their territories (i.e. the distribution of open shells). In doing this they also control the number and distribution of their mates. Male mate choice may be a factor in the selection of distinctive colouration and colour patterns in females which is a feature of the lamprologine shell-dwellers.

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DESCRIPTION OF *Lamprologus laparogramma* sp. nov., AND REDESCRIPTIONS OF *Lamprologus*

signatus POLL 1952 AND *Lamprologus kungweensis* POLL 1952, WITH NOTES ON THEIR ECOLOGY

AND BEHAVIOUR (TELEOSTEI:CICHILDAE).

INTRODUCTION

Lamprologus kungweensis and *Lamprologus signatus* were described by Poll in 1952 from specimens collected during the Belgian Hydrobiological Expedition to Lake Tanganyika in 1946-47. *L. kungweensis* was collected in Kungwe Bay, Tanzania at approximately 10-20 m depth and was described from 6 specimens. *L. signatus* was collected at Moba, Zaire in 10-100 m depth and was described from 3 specimens. The capture sites for the two species were described as the deep (10-100m) sand floor and *Neothauma tanganyicense* shells were present in net catches together with *L. kungweensis*. Poll (1952) stated that the two species were closely related and further examination was necessary to determine their validity. Examination of the type material showed there to be only female *L. kungweensis* and only male *L. signatus* in the samples. This has caused some confusion among subsequent collectors.

Konings (1988), using SCUBA, observed wild populations of *L. kungweensis* near Kigoma, Tanzania and found that they were sexually dimorphic and dichromatic. Habitats were more accurately described as mud bottoms and the species found to dwell in holes. In some instances large males were reported to use *Neothauma tanganyicense* shells as refuges. Based on his observations Konings (1988) concluded that *L. kungweensis* and *L. signatus* were synonymous. Daget et al (1991), however, did not recognise this synonymy.

In 1988 collections of *L. signatus* were made by the author at Nundo Head, Zambia. These were exported to Europe and Puttberg (1990) has described their captive breeding behaviour. Collections of a new species similar to *L. signatus* were made by the author at Mpulungu, Zambia between 1989 and 1993. *L. kungweensis* were observed and collected in Burundi, Tanzania and Zaire from 1992 to 1993. All three species are sexually dimorphic and dichromatic and appear to have allopatric distributions within Lake Tanganyika.

The confusion over the identity of these *Lamprologus* species has therefore been partly due to limited descriptive material previously available and partly due to marked sexual dichromatism within the genus. The purpose of this paper is to describe the new species, to redescribe *L. signatus* and *L. kungweensis* based on both male and female specimens. As little is known of the biology of these species details of their distribution, behaviour and ecology are also reported.

METHODS AND MATERIAL

Collections and observations of the fish were made using SCUBA at depths of between 10-30 m. The fish were collected by chasing them into mosquito meshed standing nets (2m x 0.5m) and caught with hand nets. All specimens were fixed in 10% formalin and preserved in 70% propyl alcohol. Underwater observations were recorded on plastic paper. To determine the size and shape of *L. signatus* dwelling holes the fish were chased away from holes into which epoxy resin, premixed on the surface, was poured. The resin was allowed to harden over two days before removal from sediments. All underwater photographs were taken using an Olympus OM2 camera with an Ikelite housing and strobe system.

The taxonomic techniques employed for counts and measurements of fish follows Barel and Witte (1977). With the exception of gill-rakers all counts were taken from the left side of fish. Teeth counts are for one side of the jaw. Morphometric and meristic data were analysed by a stepwise discriminant programme at the Department of Mathematics, Rhodes University. Each specimen was radiographed (radiographs are held at the J.L.B. Smith Institute of Ichthyology, Grahamstown).

Material examined was from the following institutions; Musee royal de l'Afrique centrale, Tervuren, Belgium (MRAC); Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium (IRSNB); J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa (Rhodes University Smith Institute, RUSI); United States National Museum, Washington, USA (USNM); British Museum of Natural History, London, UK (BMNH).

RESULTS : DESCRIPTIONS

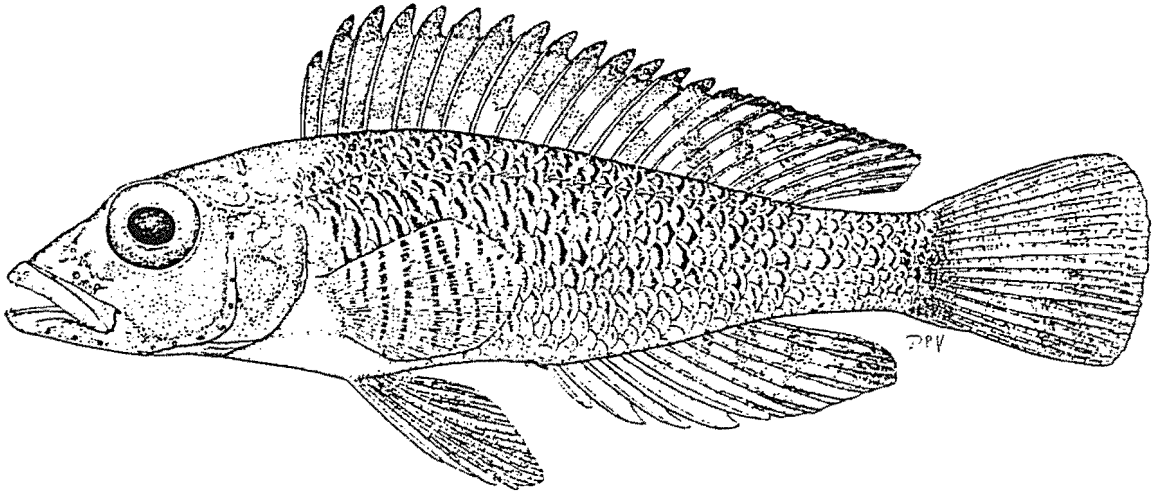
Lamprologus laparogramma new species.

Holotype. RUSI 43553 (Figure 1), male 34.7mm SL, Mpulungu, Zambia.

Paratypes. RUSI 38784 (Figure 2), 3, 26.2-29.6mm SL, Mpulungu, Zambia, 20/12/1990. RUSI 43558, 7, 24.4-36.8mm SL, Mpulungu, Zambia, 19/8/1990. RUSI 43555, 4, 26.7-40.1mm SL, Mpulungu, Zambia, 16/9/1990. RUSI 38800, 3, 23.3-26.6mm SL, Mpulungu, Zambia, 27/10/1990. RUSI 43556, 4, 28.2-35.2mm SL, Mpulungu, Zambia, 24/11/1990. BMNH 1994.1.5:1, male SL 33.9mm SL and BMNH 1994.1.5:2, female SL 27.0mm SL, Mbita Island, Mpulungu, Zambia, 27/10/90. MRAC 94-35-P-3-4, male 36.7mm SL and female 27.5mm SL, Mbita Island, Mpulungu, Zambia, 19/8/90. USNM 331639 male 39.9mm SL and female 29.2mm SL Mbita Island, Mpulungu, Zambia, 27/10/90.

Diagnosis. *Lamprologus laparogramma*, a sexually dichromatic species, closely resembles *L. signatus* and *L. kungweensis* and can be distinguished from them by the following colour patterns (live and

a



b

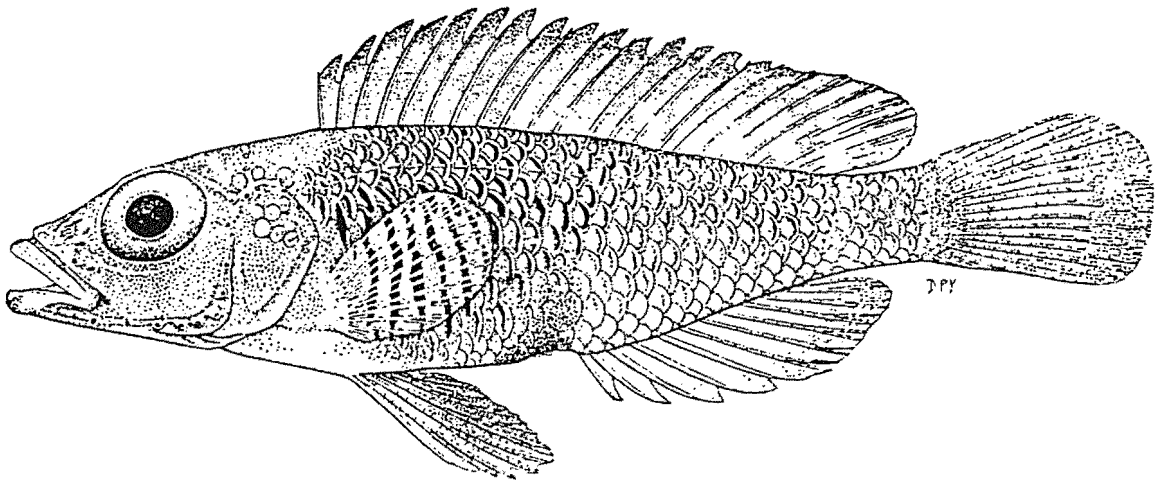


Figure 1 *Lamprologus laparogramma* from Mpulungu, Zambia: a) Holotype, RUSI 38784, 34.7mm SL (male); and b) paratype, RUSI 38784, 26.7mm SL (female).

preserved material);

Males; central portions of some scales are pigmented dark brown, and these link to form 5-9 vertical lines on the belly, and a variable number (0-8) of vertical braided bars on the posterior flank and caudal peduncle; there are 9-11 hyaline bands in the dorsal fin which usually do not extend forwards to the anterior section of the fin; 3-5 bands in the caudal fin.

Females; central portions of scales are pigmented dark brown which on the lower flank and belly link to form 5-9 vertical lines; some hyaline bands may be present in the posterior sections of the dorsal and anal fins; 2-3 bands are always present in the caudal fin.

Description. Measurements and counts are given in Table 1 and Figure 1 show body form, fin shapes and positions, and colour patterns.

The species is sexually dimorphic with mean male SL 35.6mm, (range 32.9-40.1mm, SD 2.8, number 12); mean female SL 27.8mm (range 26.2-29.6mm, SD 1.2, n 12). Body elongated and dorsal profile slightly arched. Greatest depth at the origin of the dorsal and pelvic fins. Depth of body 3.5-4.1 in SL with gravid females showing the largest range and depth. Head length 3.1-3.5 in SL. Preorbital depth, 7.9-18.5 in HL and 2.6-6.0 in eye length. Interorbital width 8.9-12.3 in HL and 2.9-4.3 in eye length. Snout length 2.9-4.4 in HL and 0.68-1.02 times its breadth. All four features show positive allometry with increasing SL. Eye is large 2.6-3.2 in HL, slightly elliptical (0.83-1.03 in depth) and is situated dorsally. Females have proportionately larger eyes. Cheek depth 4.5-6.2 in HL, showing slight positive allometry with SL. Caudal peduncle 5.7-7.3 in SL and 1.33-1.76 times longer than deep. Lower jaw length 2.0-2.6 in HL, showing positive allometry with SL, and 1.2-1.65 times longer than wide.

Gill rakers. There are 4-6 (usually 5) rakers on the ceratobranchial of the first gill arch. The rakers are short decreasing in length anteriorly, sometimes gradually and sometimes with the 4th and 5th abruptly reduced to slightly protruding elements, or even absent (Figure 2).

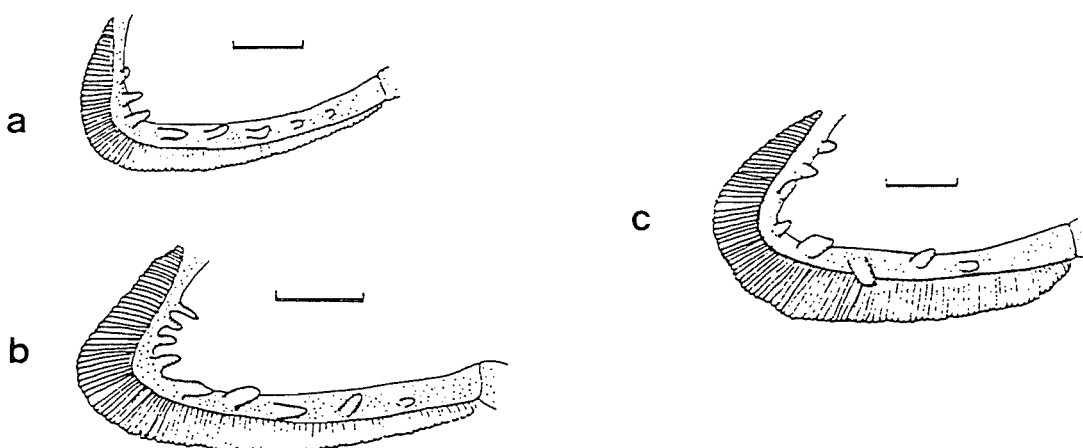


Figure 2 Gill rakers: a) *L. laparogramma*; b) *L. signatus*; and c) *L. kungweensis* (scale bar = 2mm).

Scales. Ctenoid scales on the body with the largest scales occurring on the mid flank and belly region. Scales are absent from the head and nape; the bare skin here extends backwards as a v-shaped strip to the 1st to 3rd dorsal spine (Figure 3). The cheeks and most of the operculum are devoid of scales; however the latter does have a small number (<10) of variably sized cycloid scales. There are no scales between the pectoral and pelvic fin bases. Lateral line series with 32-34 (usually 33) scales. The upper lateral line follows the dorsal body profile. The number of pored scales in the posterior upper lateral line and the entire lower lateral line are often variable and discontinuous. Scales between the lateral line and the origin of the dorsal fin vary between 1-4; usually a portion of this area is devoid of scales (see above). Scales on the caudal fin form a horizontal v-shape with the apex of the v at the fin base. These scales extend onto the fin 2.1-3.9 in caudal fin length.

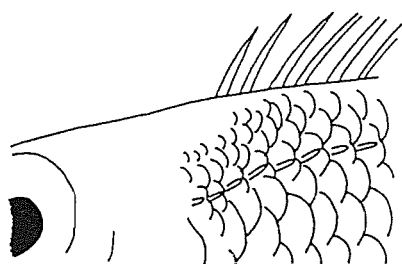


Figure 3 *L. laparogramma*, naked region of nape extending back to dorsal fin.

Fins. Dorsal fin with 14 or 15 spines (usually 15) and 8-10 (usually 9) branched rays. There are 5 or 6 (usually 5) anal spines and 6 or 7 branched rays. The 4th ray of the pectoral fin is the longest and shows slight positive allometry in specimens <32 mm SL; its length 1.5-1.8 in HL and 4.8-5.6 in SL. Pelvic fins are rounded; the second branched ray is longest and extends to the origin of the anal fin. Males have longer fins; mean male fin length 3.8 in SL (range 3.5-4.1 in SL); mean female fin length 4.0 in SL (range 3.7-4.3 in SL).

Vertebral column. Counts were obtained from radiographs of all 28 specimens. The total count is 30-32 (usually 31) and comprises 12 abdominal and 18-20 (usually 19) caudal vertebrae.

Jaw teeth. (A single specimen examined, 40mm SL) The shape of the dental arcade is rounded (Figure 4). Dentary has 5 or 6 irregular rows of teeth anteriorly, reducing to one row posteriorly. The total number of teeth in the outer row is 37-40 which can be divided into 3 distinct sections (Figure 4);

- 1) Anterior teeth are procumbent and consist of 4-5 large recurved canines increasing in size from the symphysis laterally and ending with a single massive, strongly recurved canine,
- 2) 19-23 middle row teeth are widely and regularly spaced and erect,
- 3) posterior section comprises a single row of 14-19 teeth with recumbent implantation.

Teeth in all rows are caniniform, sharply pointed and recurved to strongly recurved. The total number of teeth on the dentary is 115-120.

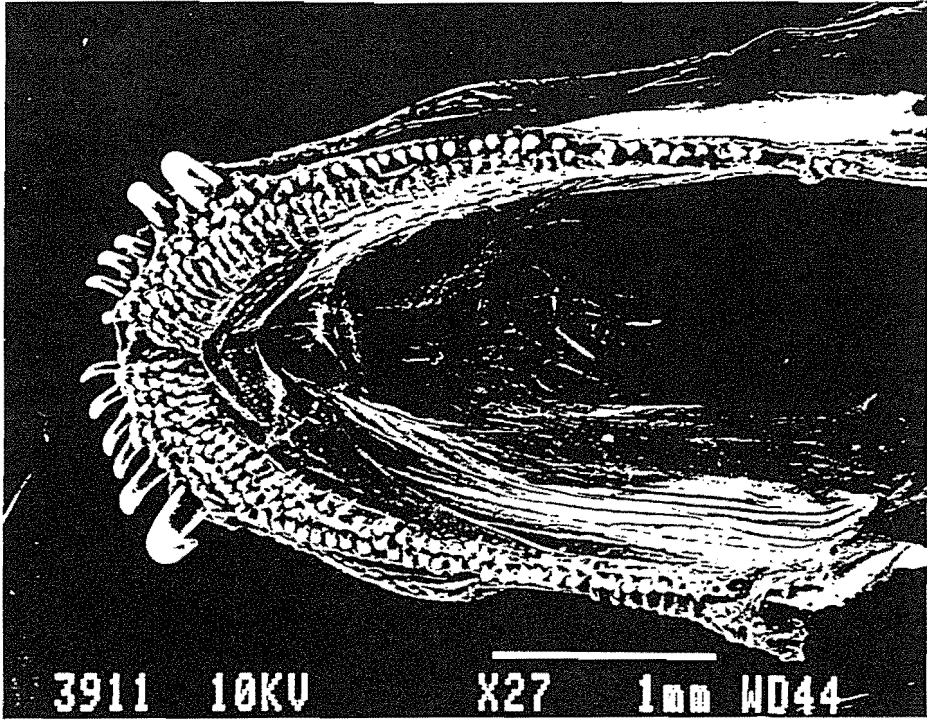


Figure 4 *L. laparogramma*, dentary.

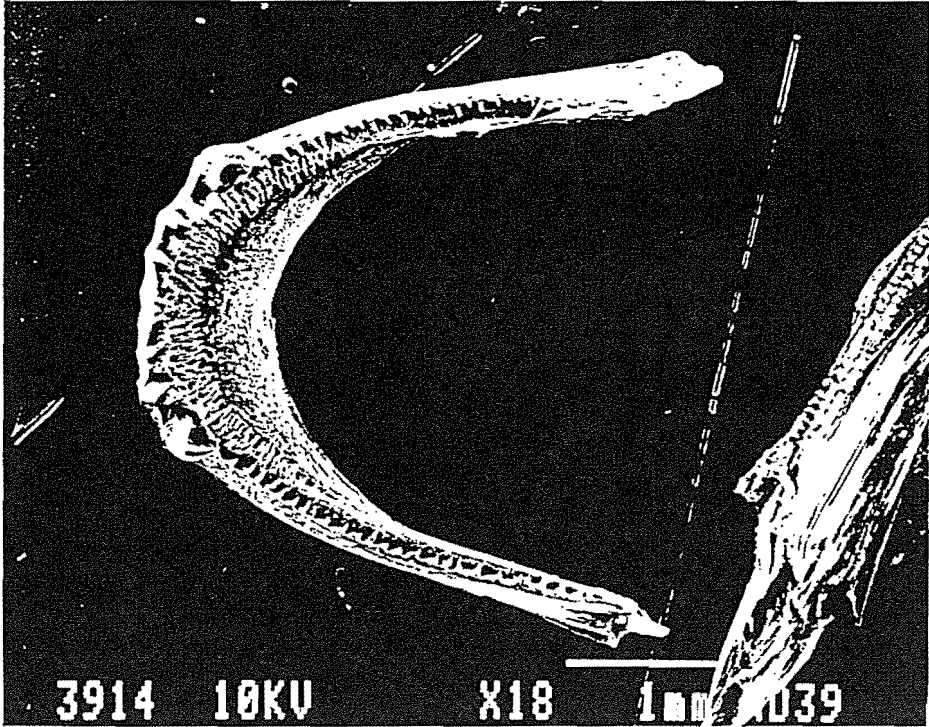


Figure 5 *L. laparogramma*, premaxilla.

Premaxillary teeth. Anteriorly there are 4 or 5 irregular rows of caniniform teeth reducing to a single row posteriorly (Figure 5). The total number of teeth in all rows is between 120 and 130. The anterior teeth of the outer row consist of 4 enlarged, recurved canines increasing in size from the symphysis laterally. Latero-posteriorly the outer row consists of 18-25 widely and irregularly spaced, recurved teeth.

Lower pharyngeal bone and teeth. The pharyngeal bone is equilateral, length of the dentigerous surface is 57% of the bone's total length and its width 77% of its total width (Figure 6). Six-seven teeth are on the midline of the bone and 30-35 along the entire posterior edge. The 3 or 4 median posterior teeth are molariform, surrounded by 10-12 enlarged bevelled teeth. These grade away from the central region of the bone into increasingly slender, bevelled teeth and anteriorly into a few unicuspid teeth.

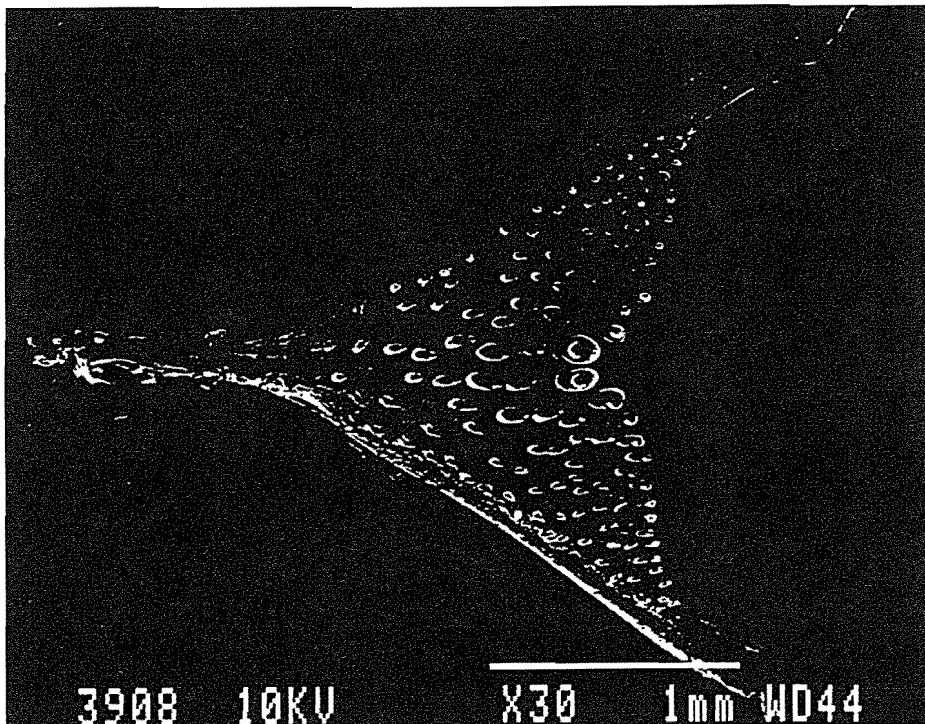


Figure 6 *L. laparogramma*, lower pharyngeal bone.

Coloration - live specimens. (Figures 7) In males the dorsum, flank, caudal peduncle and head are light brown grading towards a yellow belly. In females the body colour is similar except that the yellow belly is more brightly coloured. The scale centres over the whole body are dark brown and on the belly these link to form straight, vertical lines (usually 6-8) in both sexes. In addition, on the posterior flank and caudal peduncle of males there is a series of up to 8 vertical, braided bars. Overlying this general body coloration is an iridescent sheen which is found in most shell-dwelling *Lamprologus* species occupying similar habitats. The upper outer ring of the eye is blue in adults of both sexes. The ground colour of the dorsal fin in males and females is dark brown. In males, posterior of the 5th to 8th dorsal spines there are 9-11 vertical or slightly backward pointing hyaline bands; the lappets are dark brown to black

and below these is a horizontal gold-yellow line. These features become more distinct posteriorly as the black and yellow bands reach their greatest width in the branched ray section of the fin. In females there may or may not be a few hyaline bands on the posterior section of the dorsal fin.

The anal fin in males is light brown with a variable number (5-10) of hyaline bands, the higher numbers occurring in larger specimens. In females the fin is light brown and may or may not have a few (0-3) irregular hyaline bands on the posterior section. The caudal fin in males is brown with irregular vertical hyaline bands (3-4) with the dorsal posterior section dark brown to black. In females the caudal is predominantly brown with fewer (2-3) and thinner bands. The anterior 1-3 rays of the pelvic fin are white, the remainder dark grey in both sexes. Although coloration of pelvic fins is variable, females generally seem to be darker. The pectoral fin is hyaline in both sexes.

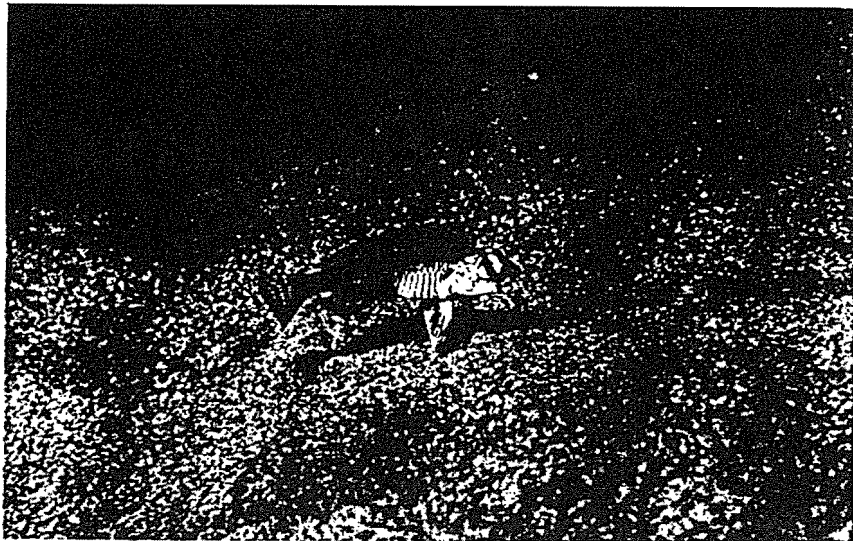
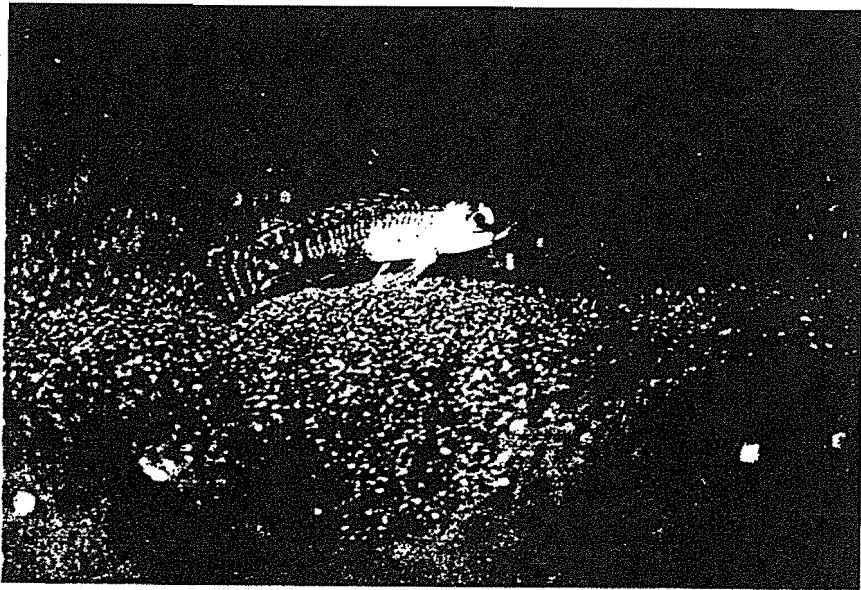


Figure 7 *L. laparogramma* live female coloration a) male and b) female.

Table 1 Morphometric and meristic data of *Lamprologus laparogramma*: H = holotype (male).

	H	mean	min-max	SD
Total length (mm)	43.7	37.8	(29.2-49.5)	5.81
Standard length (mm)	34.7	30.7	(23.3-40.1)	4.63
% of standard length				
Body depth	26.8	25.9	(24.2-28.6)	1.05
Pectoral fin length	20.5	19.4	(18.0-20.8)	0.68
Caudal peduncle length	16.7	15.6	(13.6-17.7)	0.95
Head length	30.8	31.2	(29.6-32.8)	0.94
Caudal fin length	25.1	22.8	(19.6-25.5)	1.22
Pelvic fin length	27.7	25.6	(23.1-28.4)	1.42
% of head length				
Snout length	27.1	26.9	(22.5-33.8)	2.68
Preorbital depth	8.4	8.9	(5.4-12.7)	1.64
Eye length	32.7	34.0	(30.9-39.1)	1.97
Cheek depth	21.5	19.9	(16.1-22.4)	1.34
Lower jaw length	44.9	44.4	(38.7-50.0)	2.36
Inter-orbital width	11.2	9.8	(8.1-11.2)	0.84
Ratios				
CPL/CPD	1.6	1.5	(1.3-1.8)	0.11
Snl/SnW	0.9	0.9	(0.7-1.0)	0.07
LaW/POW	1.2	1.2	(1.0-1.5)	0.12
ED/EL	0.9	0.9	(0.8-1.0)	0.04
CFS _c /CFL	0.4	0.4	(0.3-0.5)	0.05
LJL/LJW	1.5	1.5	(1.2-1.7)	0.14
Counts				
Scales : lateral line	34	33.3	(32-34)	0.65
: LL-dorsal fin	1	1.8	(1-4)	1.01
Dorsal fin rays: total	24	24.0	(23-25)	0.33
: branched	9	9.0	(8-10)	0.42
: spinous	15	15.0	(14-15)	0.19
Anal fin rays : total	12	11.8	(11-12)	0.43
: branched	7	6.7	(6-7)	0.47
: spinous	5	5.0	(5-6)	0.19
Vertebrae : total	31	30.2	(13-32)	3.35
: abdominal	2	12.0	(12-12)	0.00
: caudal	19	18.8	(18-20)	0.54
Gill rakers : total	5	4.8	(4-6)	0.51
: reduced	2	1.2	(0-2)	0.67

- preserved specimens. The body colour is yellow-brown and scale centres are brown with those of the upper belly and flanks darker. The nape and dorsal surface of the head are dark brown. In males the golden-yellow line on the posterior section of the dorsal fin becomes hyaline. Otherwise general fin and body markings remain as in life.

Etymology. Derived from the Greek *lapara*, meaning side or flank, and *gramma* meaning line and referring to the near vertical lines on the anterior flank and upper belly.

Lamprologus signatus Poll, 1952

Lamprologus signatus Poll, 1952: p.17, fig.7., (type locality Moba, Zaire)

Neolamprologus signatus Colombe & Allgayer, 1985

Holotype. MRAC RG 114259, 1 male 41.8mm SL, Moba, Zaire, 7/3/1947.

Paratypes. MRAC RG 114260, 1 male 41.7mm SL, Moba, Zaire, 30/12/1947. IRSNB I.G.20.661, 1 male 28.8mm SL, Moba, Zaire, 5/11/1947.

Comparative material. RUSI 38854, 1 female 26.3mm SL, Inangu Headland, Zambia, October, 1989. RUSI 42620, 1 female 28.3mm SL, Nundo Headland, Zambia, October, 1989. RUSI 43576, 5 males 32.6-36.3mm SL, Chimba, Zambia, 27/2/91. RUSI 43577 1 male 41.5mm SL, Chimba, near Nsumbu, Zambia, 27/2/91. Alizarin stained specimens: RUSI 43551, 3 males, Nundo Head, Zambia, 20/12/88. RUSI 43550, 1 female, Nundo Head, Zambia, 20/12/88. BMNH 1994.1.5.5-6, 1 male 35.0mm SL (Figure 8a), 1 female 26.8mm SL (Figure 8b), Chimba, near Nsumbu, Zambia, 27/2/91. MRAC 94-35-P-5-6, 1 male 34.9mm SL, 1 female 28.1mm SL, Chimba, near Nsumbu, Zambia, 27/2/91.

Diagnosis. *Lamprologus signatus* is sexually dichromatic and closely resembles *L. laparogramma* and *L. kungweensis*. It can be distinguished from these species by the following colour patterns (in live and preserved material);

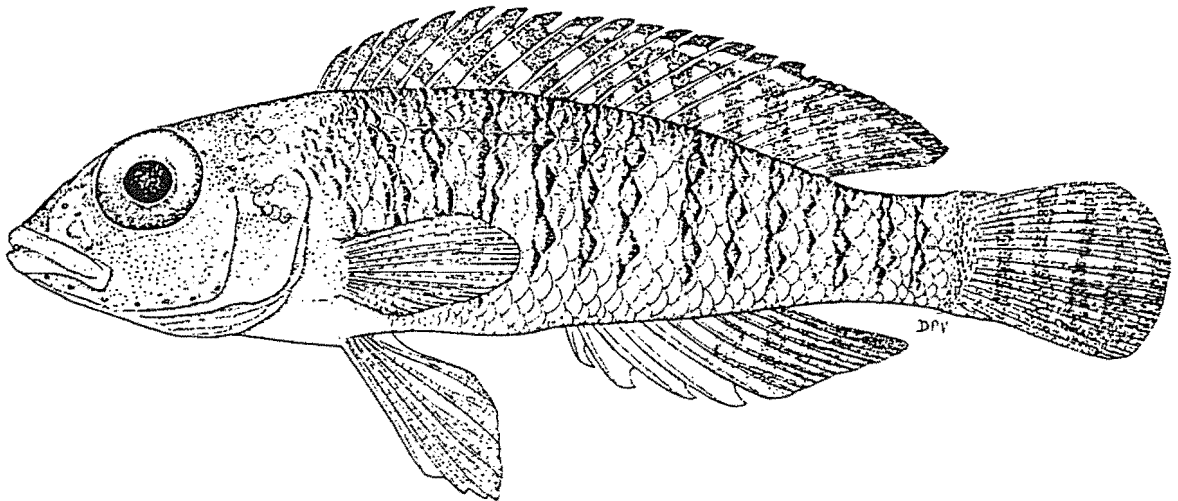
Males; central portions of many scales are pigmented dark brown forming 12-14 braided vertical bars on the flanks extending the whole length of the body; the lappets of the dorsal fin are black; there are 10-13 almost vertical hyaline bands on the dorsal fin extending forward to the 1st dorsal spine.

Females; central parts of scales are pigmented dark brown forming an irregular checkered pattern on the anterior flank and belly; no hyaline banding on the dorsal and caudal fins.

Description. Measurements and counts are given in Table 2 and Figure 8 show body form, fin shapes and positions and colour patterns of adult male and female fish respectively.

Sexually dimorphic; mean male SL 35.7 mm (range 28.8-41.9mm, SD 3.91, n 11); mean female SL 27.4 mm (range 26.3-28.3, SD 0.85, n 4). Depth of body 3.7-4.1 in SL with the region of greatest depth at the origin of the pelvic fin. Head length 3.1-3.3 in SL. Both body depth and HL show slight

a



b

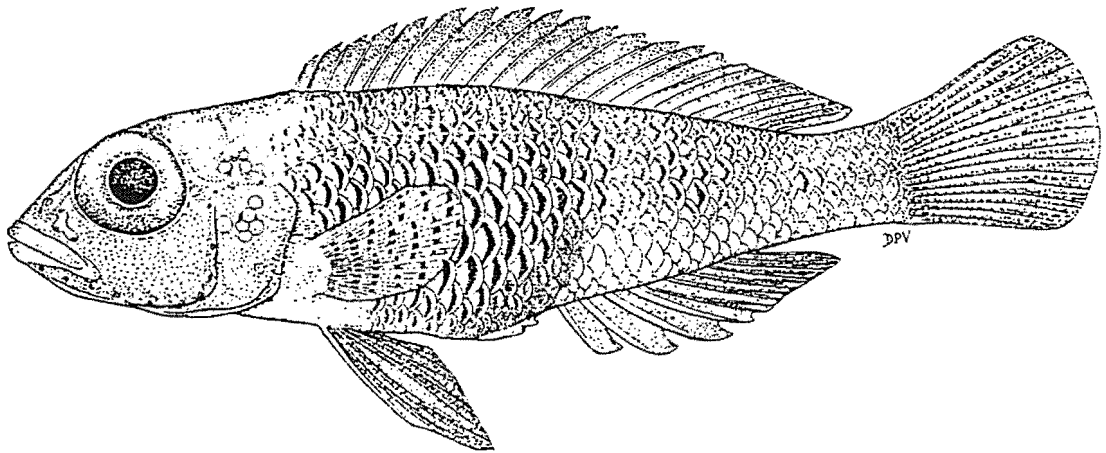


Figure 8 *Lamprologus signatus* from Sumbu Bay, Zambia: a) BMNH 1994.1.5.5-6, 35.0mm SL (male); and b) BMNH 1994.1.5.5-6, 28.6mm SL (female).

Table 2 Morphometrics and meristics of *Lamprologus signatus*: H = holotype (male).

	H	mean	(min-max)	SD
Total length (mm)	50.7	41.5	(31.6-51.8)	6.45
Standard length (mm)	41.8	33.8	(26.3-41.9)	5.15
% of standard length				
Body depth	25.1	25.7	(24.0 -27.2)	0.88
Pectoral fin length	21.5	19.9	(16.3-21.9)	1.50
Caudal peduncle length	15.6	15.5	(13.7-17.1)	1.14
Head length	32.3	31.5	(29.9-32.7)	0.83
Caudal fin length	23.0	22.2	(19.1-25.0)	1.50
Pelvic fin length	26.6	23.7	(18.5-28.1)	2.55
% of head length				
Snout length	26.7	27.4	(22.9-37.9)	3.47
Preorbital depth	11.9	10.1	(7.4-12.4)	1.49
Eye length	37.0	35.9	(32.7-40.1)	2.32
Cheek depth	19.3	20.4	(16.7-23.7)	2.18
Lower jaw length	40.7	43.3	(39.8-45.6)	1.59
Inter-orbital width	10.4	10.7	(7.8-12.3)	0.93
Ratios				
CPL/CPD	1.6	1.5	(1.3-1.8)	0.12
Snl/SnW	0.9	0.9	(0.7-1.2)	0.15
LaW/POW	1.1	1.2	(1.1-1.4)	0.09
ED/EL	0.9	0.9	(0.9-1.0)	0.03
CFS _c /CFL	0.4	0.4	(0.2-0.5)	0.07
LJL/LJW	1.3	1.4	(1.2-2.0)	0.21
Counts				
Scales : total	35	34.1	(33-35)	0.57
: LL-dorsal fin	1.5	2.5	(1-4)	0.80
Dorsl fin rays : total	24	23.7	(22-25)	0.67
: branched	9	8.9	(8-10)	0.50
: spinous	15	14.9	(14-15)	0.34
Anal fin rays : total	12	11.7	(11-12)	0.47
: branched	7	6.5	(6-7)	0.50
: spinous	5	5.0	(5-5)	0
Vertebrae : total	31	30.8	(30-31)	0.4
: abdominal	12	11.8	(11-12)	0.4
: caudal	19	19.0	(19-19)	0
Gill rakers : total	4	4.7	(4-5)	0.45
: reduced	1	1.1	(0-2)	0.74

positive allometry with SL. Preorbital depth small, 8.7-13.5 in HL and 2.8-5.0 in eye length. Interorbital space very small, 8.1-10.1 in HL. Snout length 2.6-4.4 in HL, showing strong positive allometry with SL, and the length 0.70-1.16 times its breadth. Eye large, its length 2.6-3.1 in HL, showing strong negative allometry with SL and females with proportionately larger eyes than males. Eye is elliptical, its length 0.87-0.96 times depth. Cheek depth 4.2-5.9 in HL. Caudal peduncle length 5.9-7.3 in SL, showing slight positive allometry with SL, and 1.33-1.65 times longer than broad. Lower jaw length 2.2-2.5 in HL and 1.2-1.58 times longer than broad.

Gill-rakers. Short rakers on ceratobranchial of first gill arch 4-5 (usually 5). They decrease in size anteriorly with the 5th often abruptly reduced or absent (Figure 2).

Scales. Body scales ctenoid, the largest scales on the mid flank, and a small number (<10) of irregularly sized cycloid scales on the upper and lower operculum. Scales absent from the head, nape, cheek and most of the operculum. A triangular strip of bare skin extends back from the nape to just past the origin of the dorsal fin. Scales in the lateral line series 33-35 (usually 34). The upper lateral line follows the dorsal body profile and ends close to the posterior rays of the dorsal fin. The number of pored scales in the posterior section of the upper lateral line and the entire lower lateral line are often variable. The number of scales between the lateral line and the 1st dorsal fin spine is from 1 to 4 and this area is usually partially devoid of scales. Scales on the caudal fin extend 24 to 47% of the caudal fin length.

Fins. Dorsal fin with 14 or 15 (usually 15) spines and 8 to 10 (usually 9) branched rays. Anal spines 5 or 6 (usually 5) and branched rays 6 or 7. Pectoral fin length 4.7-6.1 in SL, showing slight positive allometry with SL. Pelvic fins slightly longer in males; mean male fin length 3.9 in SL (range 3.5-4.2 in SL); mean female fin length 4.4 in SL (range 4.2-4.6 in SL).

Vertebral column. The total count 30-31 (usually 31) comprising 11-12 (usually 12) abdominal and 19 caudal elements.

Jaw teeth. The shape of the dental arcade is rounded (Figures 9 & 10). Anteriorly the dentary has 5-7 irregular rows of teeth that reduces to a single row posteriorly. The outer row comprises 42-46 teeth which can be divided into 3 distinct sections;

- 1) Anteriorly 5 large procumbent canines, increasing in size from the symphysis laterally and ending with a single massive, strongly recurved tooth.
- 2) a mid-section of 18 to 20 teeth with erect implantation.
- 3) posteriorly a single row of 15 to 20 teeth with recumbent implantation.

Teeth in all rows are caniniform, sharply pointed and recurved or strongly recurved and total 120 to 140.

Premaxillary teeth. Anteriorly there are 4 or 5 irregular rows reducing posteriorly to a single row (Figure 10). The anterior teeth of the outer row consist of 6 to 8 large canines, 3 or 4 on either side of the symphysis and increase in size outwards. All other teeth are caniniform and recurved, regular and widely spaced with erect to recumbent implantation. The outer row teeth count is 38-42 and the total teeth are 130-145.

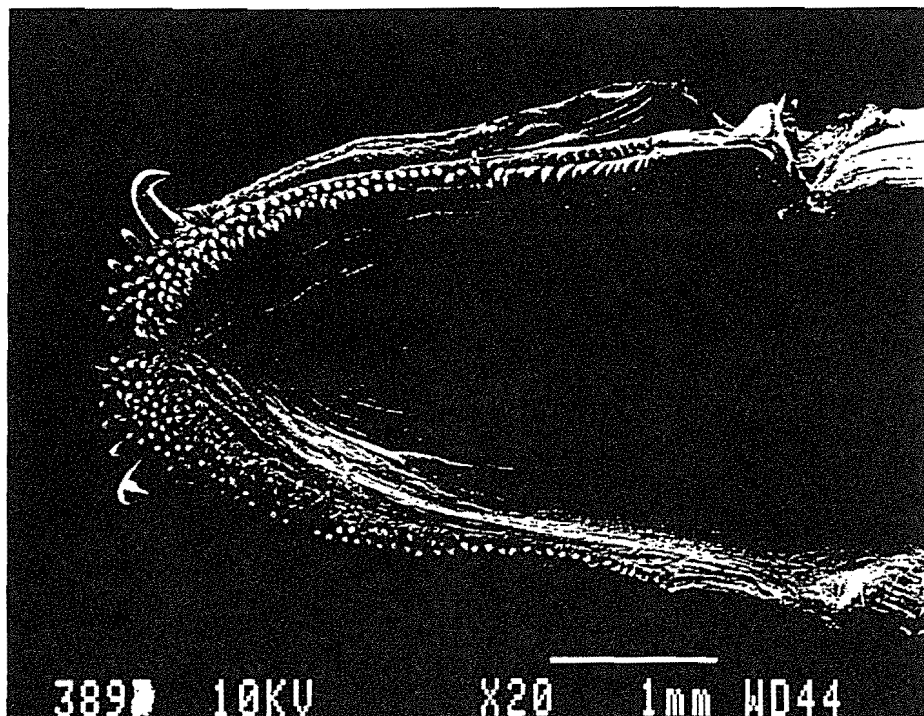


Figure 9 *L. signatus*, dentary.

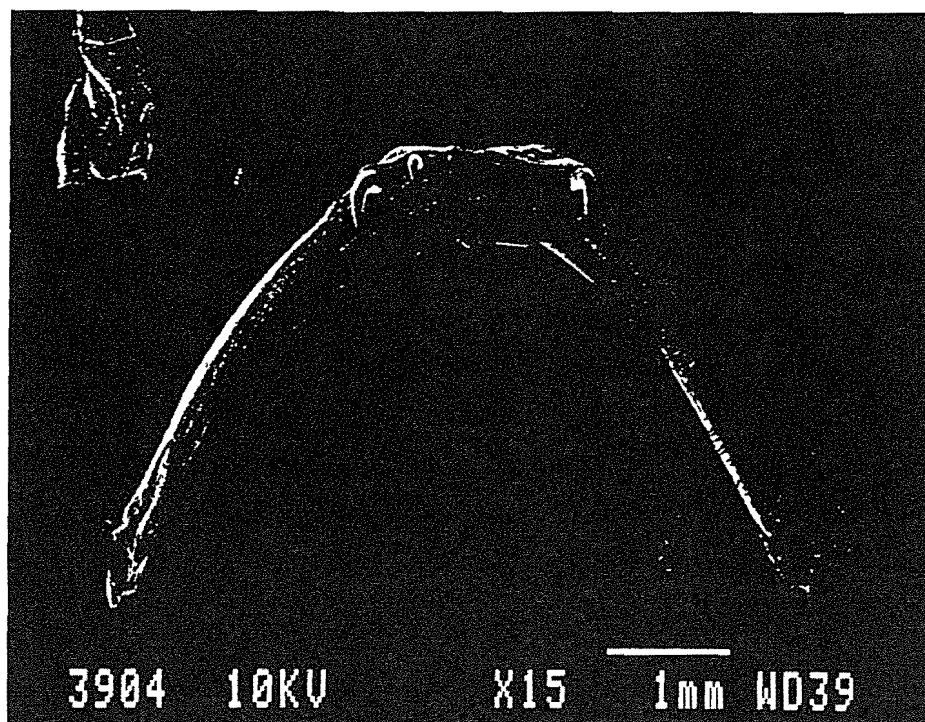


Figure 10 *L. signatus*, premaxilla.

Lower pharyngeal bone. The outer surface of the bone is equilateral, the length of the dentigerous surface is 56% of the total length of the bone and 73% of the dentigerous width (Figure 11). There are six or seven teeth on the mid-line of the bone and 30-32 along the posterior margin. The 4 or 5 median posterior teeth are large and molariform, and are surrounded by approximately 15 enlarged, bevelled teeth. Grading away from this central region teeth become more slender ending with a few unicuspid teeth anteriorly.

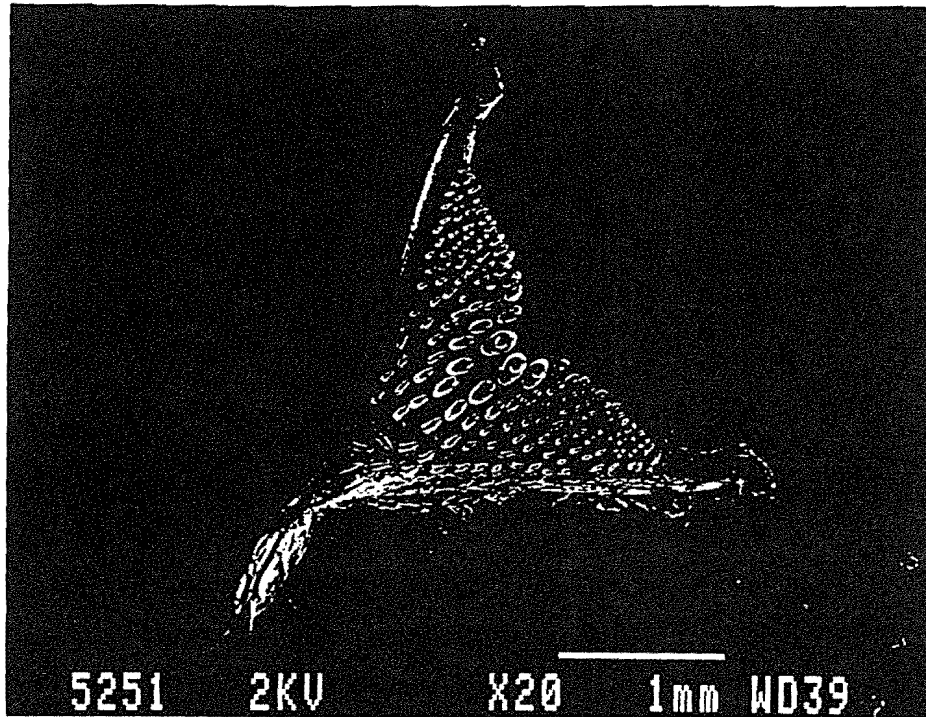


Figure 11 *L. signatus*, lower pharyngeal bone

Infra-orbital bones. In the four cleared and stained specimens examined no infra-orbitals posterior of the lachrymal bone were observed. However, the presence of a dermosphenotic bone cannot be ruled out due to its small size and possible loss resulting from long storage in formalin.

Coloration - live specimens. The flank is light brown grading ventrally into a white belly in males and a gold-yellow belly in females, overlying this is an iridescent sheen. The head and nape are dark brown. Males have 12-14 vertical braided bars or chains on the body starting immediately behind the operculum; 10-13 hyaline bands in the dorsal fin starting at the first dorsal spine; 5 hyaline bands in the caudal fin; and the posterior branched ray section of the dorsal fin has a yellow line directly under the black lappets. Females lack hyaline bands in the fins and the darkly pigmented scales on the abdominal flank-belly area form an irregular pattern. In males and females the upper anterior outer ring of the eye is blue.

- preserved specimens. The blue eye coloration is lost. The head becomes darker brown and the yellow line on the posterior dorsal fin of males becomes hyaline. The yellow belly of females becomes

light yellow-brown and in some specimens there is dark pigmentation around the anus. Otherwise body and fin markings are the same as in live specimens.

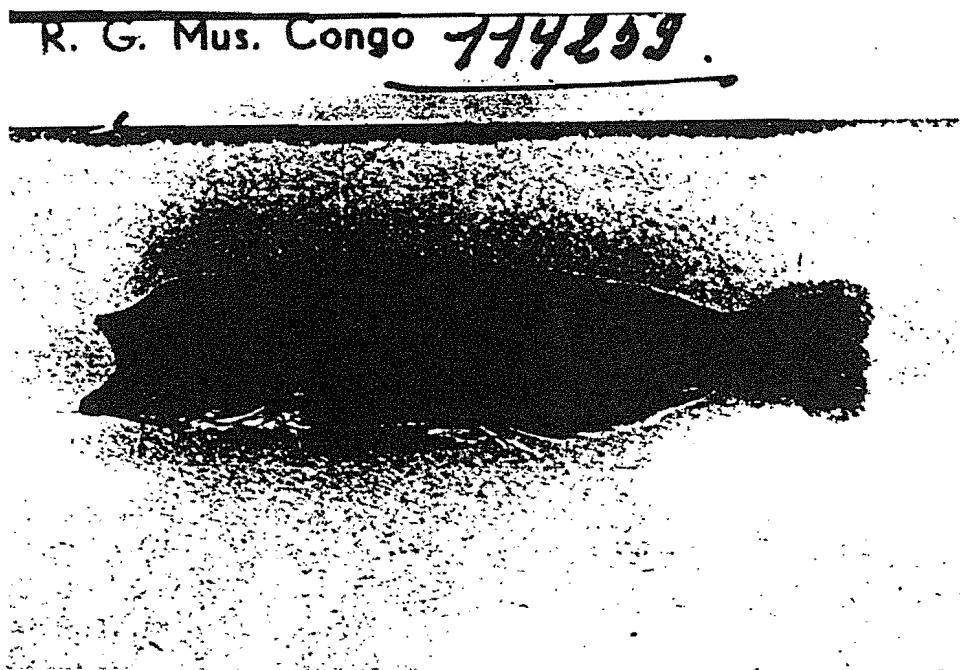


Figure 12 *L. signatus*, Type RG 117259, 41.8mm SL (male) from Moba, Zaire.

- Holotype RG 114259 (male, Figure 12). The body coloration has become very dark although markings are visible. The brown body is lighter ventrally, the head dark brown and the bony tissues (eg., jaws, branchyostegal rays and operculum) are grey-brown. Thirteen vertical braided bars on the body are barely visible while markings on the fins are not visible.

Lamprologus kungweensis Poll, 1956 (nom. nov. for *L. ocellatus* Poll, 1952.)

Lamprologus ocellatus Poll, 1952: p.15, fig.6, (type locality Kungwe Bay, Tanzania)

Neolamprologus kungweensis Colombe & Allgayer, 1985

Lamprologus signatus (non Poll) Konings, 1988

Holotype. MRAC 117258, 1 female 25.8mm SL (Figure 18), Kungwe Bay, Tanzania, 19/12/1946.

Paratypes. BMNH 1960.9.30.7952-7954, 3 females 22.4-25.7mm SL, Kungwe Bay, Tanzania

Comparative material. MRAC 114033-35, 3 females 26.1-28.3mm SL, Lagumba, Kalemie Bay (formerly Albertville), Zaire, 23/5/1947.

RUSI 42614, 6, 25.5-57.5mm SL, Luhanga, Zaire, 30/11/1992. RUSI 42612, 8, 33.7-47.8mm SL, Manga, Zaire, 4/12/1992. RUSI 42611, 6, 31.2-44.3mm SL, Manga, Zaire, 4/12/1992. RUSI 42617, 5, 25.8-47.5mm SL, North Gitaza, Burundi, 7/12/1992. RUSI 42614, 9, 28.8-48.1mm SL, Kigoma, Tanzania, 12/5/1993. RUSI 42613, 3, 26.9-43.9mm SL, Muguruka, Burundi, 12/6/1993. BMNH 1994.1.5.3-4, male 36.5mm SL and female 24.1mm SL, Kigoma Bay, Tanzania, 12/5/93. MRAC 94-35-P-1-2, male 36.6mm SL (Figure 13a) and female 24.8mm SL, Kigoma Bay, Tanzania, 12/5/93.

USNM 331638 male 35.3mm SL and female 24.5mm SL (Figure 13b), Kigoma Bay, Tanzania, 12/5/93.

Diagnosis. *Lamprologus kungweensis* is sexually dichromatic and the only species of *Lamprologus* in which females are more strikingly patterned than males. *Lamprologus kungweensis* resembles *L. laparogramma* and *L. signatus* in body form, however, it differs considerably in coloration;

Scale pigmentation is not pronounced resulting in a uniform grey-brown body. In life males and females have yellow lappets on the dorsal fin. In males the dorsal and anal fins grade from brown anteriorly to orange posteriorly. Females have an ocellated black spot extending between the 10th spine and 2nd branched ray of the dorsal fin, mature females have yellow belly-throat regions with a single peach-pink spot behind the pectoral fin.

Description. Measures and counts for type and new material are given in Table 3, and Figure 13 show body form, fin shape and positions and colour patterns. The holotype is shown in Figure 18.

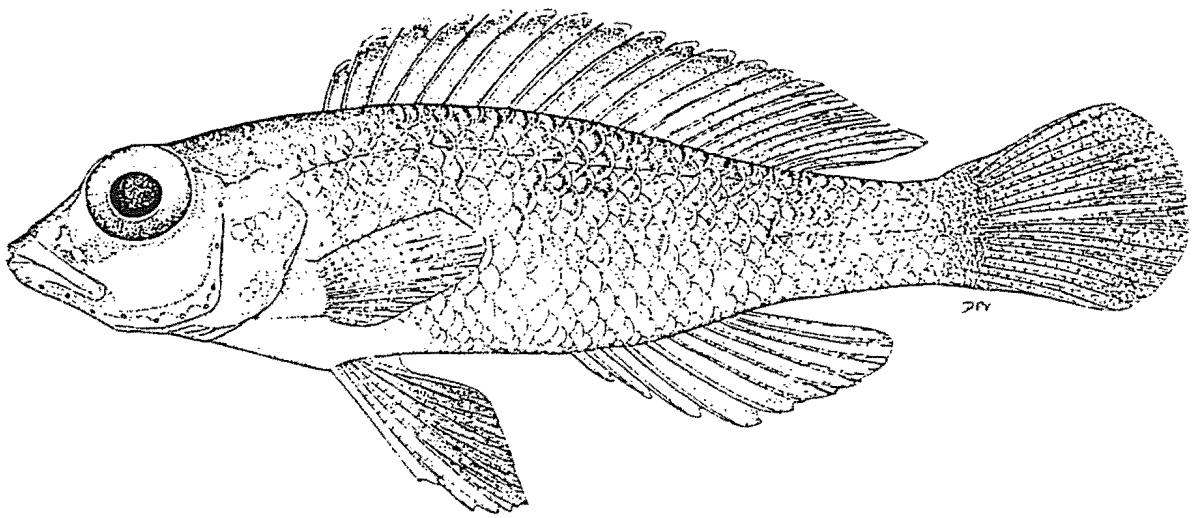
Sexually dimorphic; mean male SL 39.2mm (range 29.9-57.5mm, SD 6.44, n 19); mean female SL 26.4mm (range 22.4-30.9mm, SD 2.16, n 24). Body depth 3.5-4.5 in SL, head length 3.0-3.7 in SL. Both features show slight negative allometry with SL. Snout length 3.1-5.1 in HL showing negative allometry with SL, and 0.47-0.97 times longer than broad. Preorbital depth highly variable 6.7-19.0 in HL and 2.2-7.3 in eye length; interorbital width 7.9-12.7 in HL; cheek depth 3.7-6.1 in HL. All three features showing positive allometry with SL. Eye large 2.6-3.2 in HL, showing slight negative allometry with SL and slightly elliptical in outline, 0.7-0.96 times its depth. Caudal peduncle 5.6-7.4 in SL and 1.42-1.91 times longer than deep. Lower jaw length 2.0-2.6 in HL and 1.0-1.8 times longer than wide, this ratio showing slight negative allometry with SL.

Gill-rakers. Rakers are short and increase in size posteriorly, 3-5 (usually 4) in the outer series on the ceratobranchial of the first gill arch. Often 4th and 5th rakers absent or abruptly reduced (Figure 2).

Scales. Body scales are ctenoid. Scales are absent from the head and nape and a bare v shaped strip of skin extends back to the 1st to 3rd dorsal spine. Scales are also absent between the pectoral and pelvic fin bases, from the cheek, and over most of the operculum. There are a small number (<10) of irregularly sized cycloid scales on the operculum. The lateral line series has 31-35 scales (mode 33). The number of pored scales in the posterior section of the upper lateral line and the entire lower lateral line is variable (a feature noted by Poll, 1952).

Fins. The dorsal fin has 13-16 (usually 14 or 15) spines and 8-10 (rarely 10) branched rays; the anal with 5 or 6 (usually 5) spines and 5-7 (usually 6) branched rays. The 4th or 5th ray of the pectoral fin is the longest, 4.7-6.0 in SL. Pelvic fins are longer in males with the 2nd branched ray longest; mean male fin length 3.7 in SL (range 3.0-4.3mm); mean female fin length 4.1 in SL (range 3.6-4.7mm).

a



b

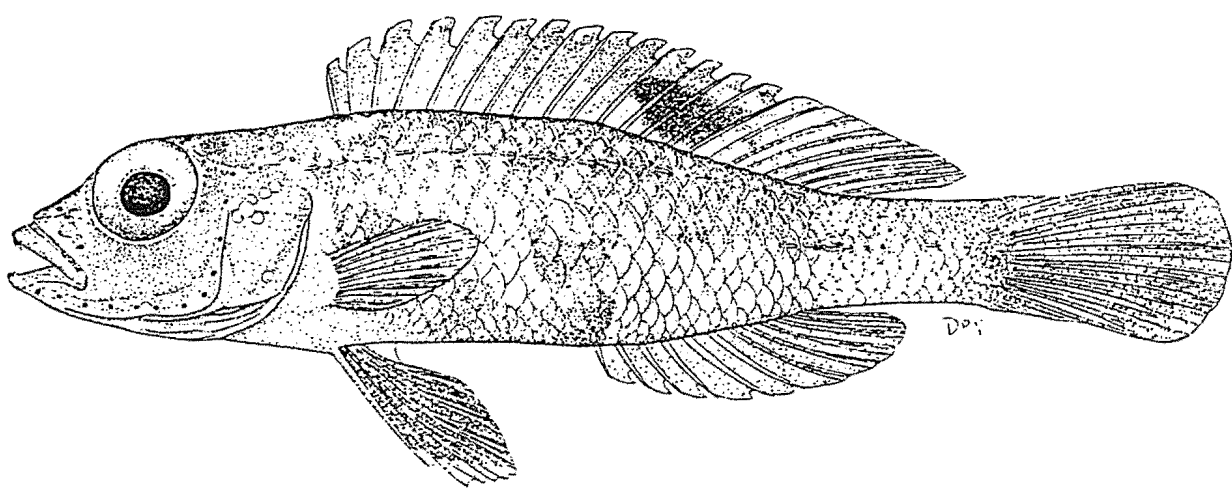


Figure 13 *Lamprologus kungweensis* from Kigoma, Tanzania: a) MRAC 94-35-P-1-2, 36.6mm SL (male); b) USNM 331638, 24.5mm SL (female).

Table 3 Morphometrics and meristics of *Lamprologus kungweensis*: H = holotype (female).

	H	mean	(min-max)	SD
Total length (mm)	31.3	38.2	(27.9-70.1)	9.11
Standard length (mm)	25.8	31.4	(22.4-57.5)	7.68
% of standard length				
Body depth	25.6	25.7	(22.3-28.5)	1.18
Pectoral fin length	17.4	19.2	(16.6-21.5)	1.13
Caudal peduncle length	14.3	15.9	(13.5-17.9)	0.99
Head length	31.4	31.2	(27.4-33.2)	1.00
Caudal fin length	21.7	22.3	(18.9-24.2)	1.05
Pelvic fin length	24.0	25.7	(21.3-32.8)	2.12
% of head length				
Snout length	8.1	22.7	(6.7-32.0)	6.73
Preorbital depth	9.9	9.1	(5.3-14.9)	2.01
Eye length	38.3	35.0	(31.3-40.7)	2.39
Cheek depth	19.8	20.8	(14.1-26.8)	2.82
Lower jaw length	-	41.2	(16.0-49.3)	9.20
Inter-orbital width	7.4	9.7	(6.3-12.7)	1.36
Ratios				
CPL/CPD	1.4	1.7	(1.4-1.9)	0.13
SnI/SnW	1.0	0.8	(0.5-1.0)	0.11
LaW/POW	1.1	1.2	(0.9-2.1)	0.17
ED/EL	0.8	0.9	(0.8-1.0)	0.03
LJL/LJW	-	1.5	(1.0-1.8)	0.20
CFS _c /CFL	0.3	0.4	(0.2-0.6)	0.08
Counts				
Scales: lateral line	33	33.1	(31-35)	0.77
: LL-dorsal fin	1	1.8	(1-4)	0.79
Dorsal fin rays: total	23	23.1	(22-24)	0.53
: branched	9	8.6	(8-10)	0.54
: spinous	14	14.6	(13-16)	0.61
Anal fin rays : total	11	11.1	(10-12)	0.53
: branched	6	6.0	(5-7)	0.43
: spinous	5	5.1	(5-7)	0.39
Vertebrae : total	30	29.9	(29-31)	0.39
: abdominal	12	11.8	(11-12)	0.37
: caudal	18	18.1	(17-19)	0.50
Gill rakers : total	4	4.2	(3-5)	0.44
: reduced	0	1.0	(0-2)	0.71

Vertebral column. The total vertebrae count is 29-31 (usually 30) and comprises 11 or 12 abdominal (usually 12) and 17-19 (mode 18) caudal elements.

Jaw teeth. The shape of the dental arcade is rounded (Figures 14 & 15). There are 5 or 6 irregular rows of teeth on the anterior portion of the dentary, posteriorly there is a single row. The dentary with 38-42 teeth in the outer row. These can be divided into 3 distinct sections;

1. Anterior procumbent teeth comprising 3-5 large canines which increase in size laterally from the symphysis and end with a single, massive strongly recurved canine,
2. middle teeth comprising 15-20 widely, regularly spaced erect teeth and,
3. posteriorly 17-20 recumbent teeth.

Total number of teeth in all rows is 110-125; all are caniniform, sharply pointed and varying from recurved to strongly recurved.

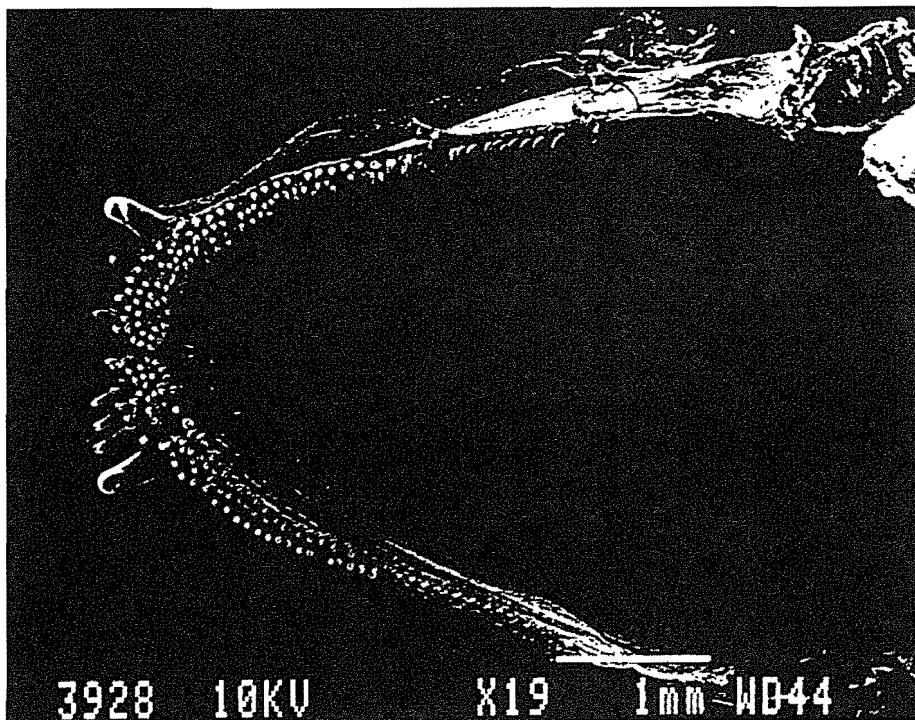


Figure 14 *L. kungweensis*, dentary.

Premaxillary teeth. Anteriorly 4 or 5 tooth rows, reducing posteriorly to a single row. The outer row comprises an anterior section of 4 or 5 large recurved canines increasing in size from the symphysis. Laterally and posteriorly in the outer row there are 32-35 caniniform, recurved to slightly recurved teeth.

Lower pharyngeal bone and teeth. (A single specimen examined) The outer surface of the pharyngeal bone is equilateral, the length of the dentigerous surface 63% of the bones total length and 79% of its dentigerous width (Figure 16). There are 6 or 7 teeth on the mid line of the bone and 30-34 along the entire posterior edge. The 7 or 8 median posterior teeth are molariform and are surrounded by 10-

15 enlarged, bevelled teeth. Grading from this central section the bevelled teeth gradually become more slender with a few anterior teeth being unicuspid.

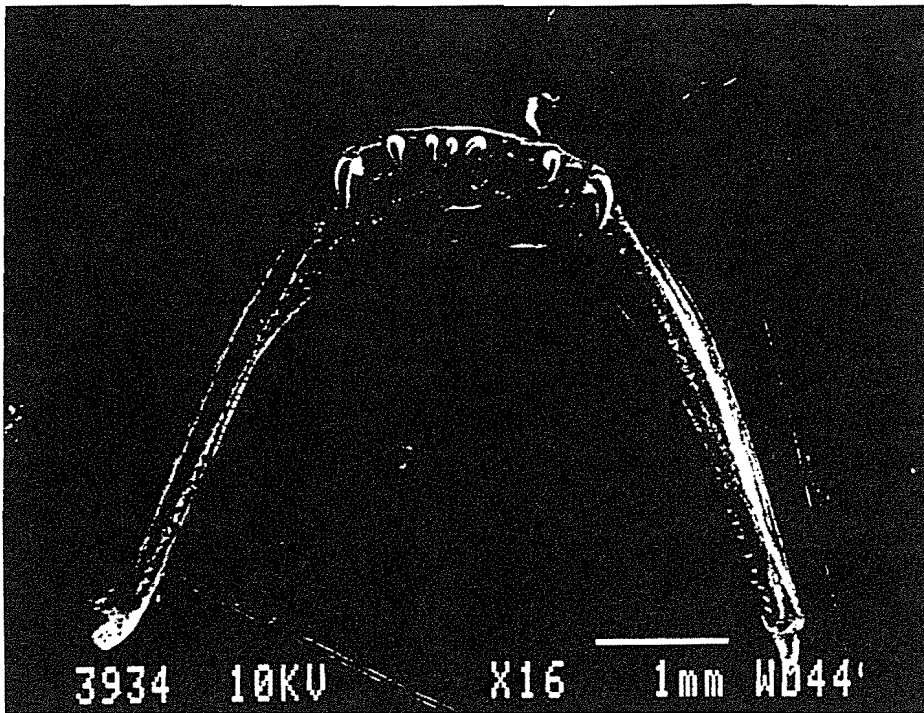


Figure 15 *L. kungweensis*, premaxilla.

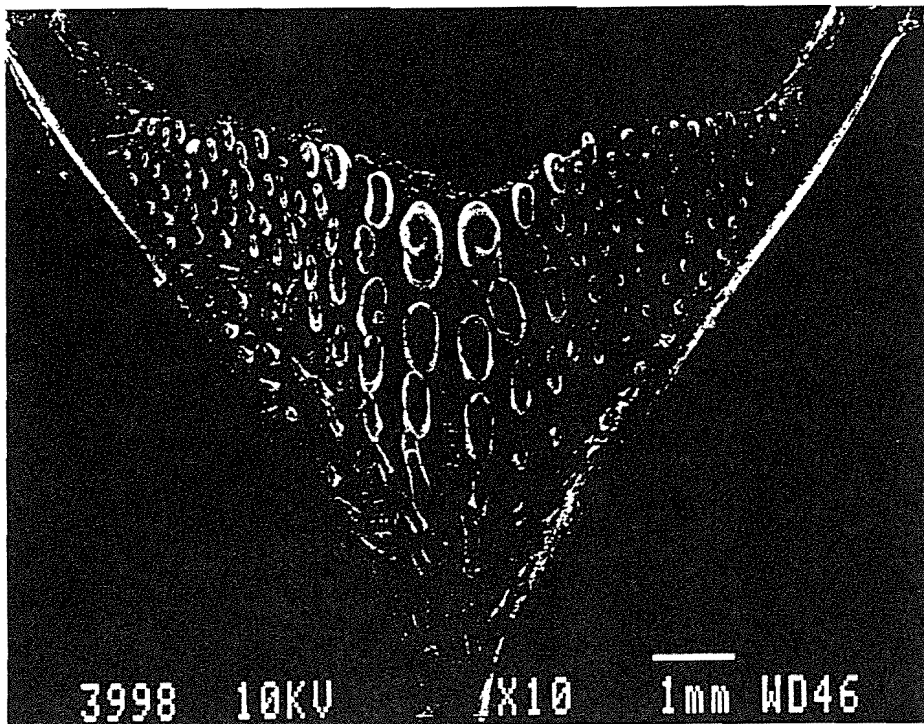


Figure 16 *L. kungweensis*, lower pharyngeal bone.

Coloration. - live specimens. (Figure 17) Dorsum, flank and caudal peduncle are light brown but darker dorsally, with the head and nape dark brown. The belly is white grading into yellow lower flank and operculum. The yellow belly of females is more brightly coloured and there is also a peach pink spot behind the pectoral fin. The occurrence and size of the spot is variable and may depend on sexual condition. The upper anterior outer ring of the eye is blue in both sexes. The dorsal fin has yellow lappets which are more pronounced in mature males. In males both the dorsal and anal fins grade posteriorly from brown to orange and have a series of 5-12 vertical or backward pointing hyaline bands. In females the dorsal fin is light brown becoming slightly darker dorsally with an ocellated black spot between the 10th spine and 2nd branched ray. There is often black pigmentation anterior and posterior to the white ocellus, giving a 2 or 3 spot effect in some specimens. Pelvic fins are white anteriorly (rays 1-3) grading to grey. Although a variable feature, females tend to have more darkly pigmented fins. Pectoral and caudal fins are hyaline.

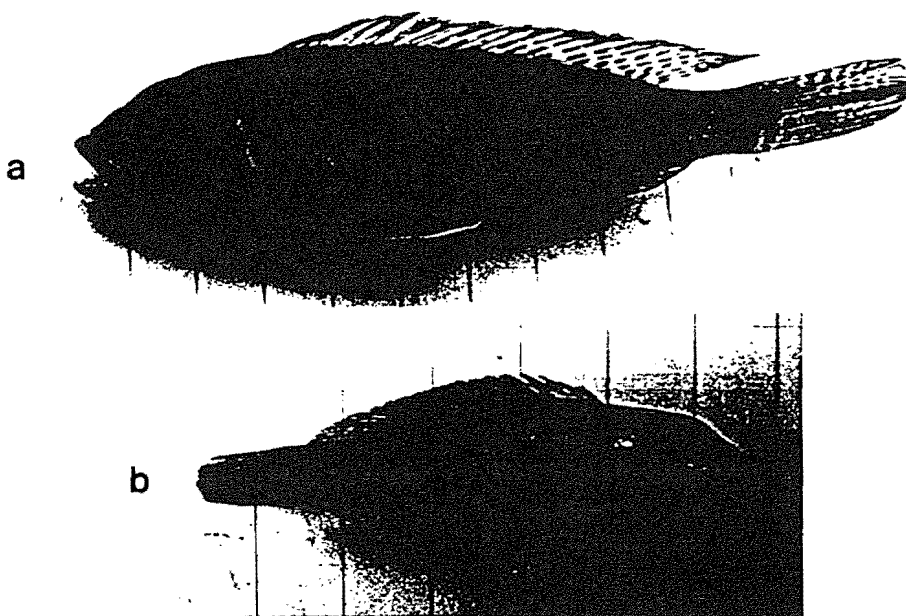


Figure 17 *L. kungweensis* from Luhanga (Zaire) showing live coloration in a) a male and b) a female.

- preserved specimens. Body colour is yellow brown with a double row of irregular brown patches following the upper and lower lateral lines. In females the abdominal region usually becomes dark brown-grey. Head and nape are dark brown-grey. The dorsal, caudal and anal fins are brown. The pelvic fins are white anteriorly and the remainder are dark grey.

- Holotype (RG 117258, female, Figure 18), Paratypes (BMNH 1960.9.30.7952-79543, 3 females). The specimens are discoloured being uniform brown over the body with slightly darker head and nape regions. The dorsal fin is dark brown with an ocellated black spot between the 10th spine to 2nd branched ray. The caudal and anal fins are brown with no other markings and the pectoral fin is hyaline. Pelvic fins are dark grey.



Figure 18 *L. kungweensis*, Type RG 117258, 25.8mm SL (female) from Kungwe Bay, Tanzania.

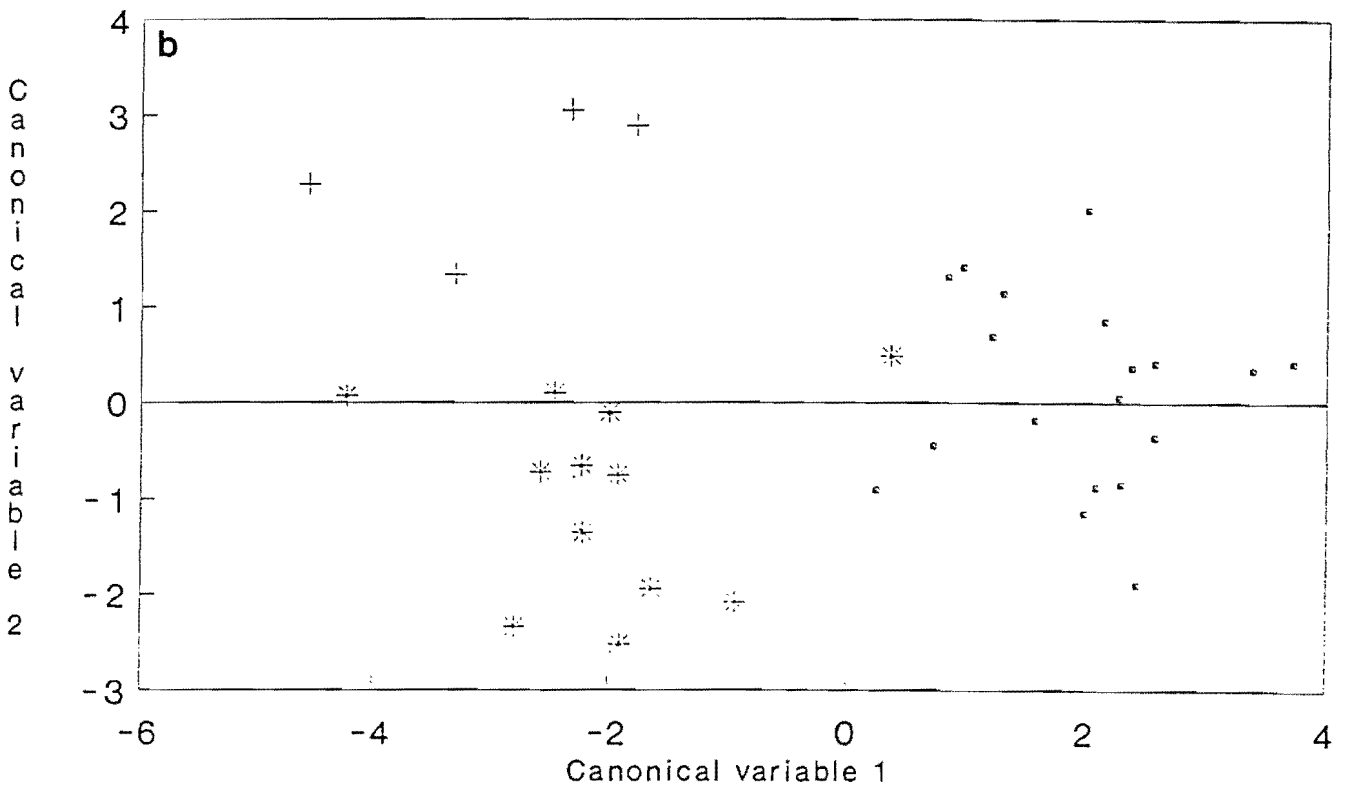
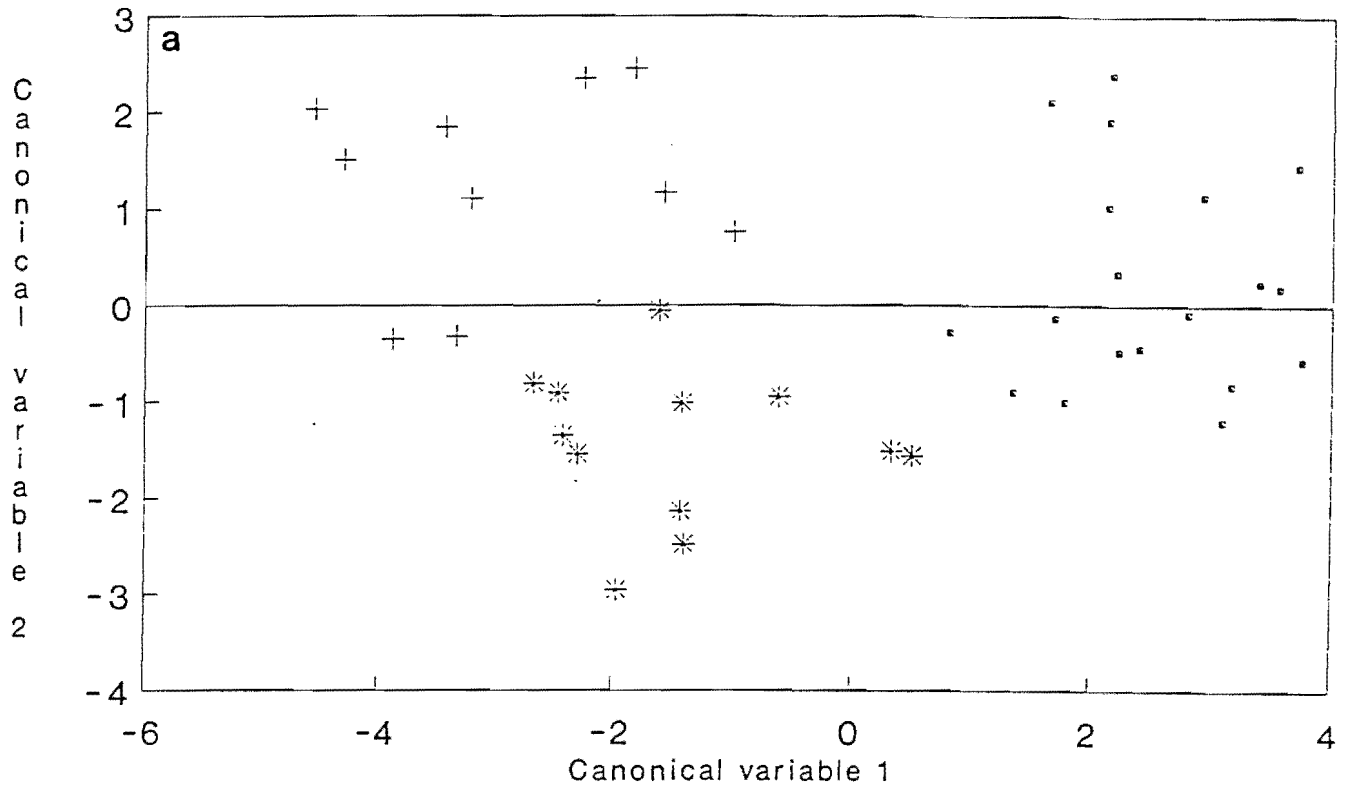
COMPARATIVE INTERSPECIFIC STUDIES

Discriminant analysis. Stepwise discriminant analysis was used to evaluate morphometric and meristic characters for recognizing *L. kungweensis*, *L. signatus* and *L. laparogramma*. Because of sexual dimorphism males and females were treated separately for this analysis (Figure 20). Features enabling the separation of species in rank order of importance are as follows;

males (7 steps); caudal vertebrae, pectoral fin length, pelvic fin length, cheek depth, total number of dorsal fin rays, lower jaw length and snout length.

females (5 steps); total number of vertebrae, the ratio of caudal peduncle length to caudal peduncle depth, total number of gill rakers, caudal fin length and lateral line scale counts.

Predictions for correct species identification, using the above features, were high: males = 100%, females = 97.1% (Table 4). One female *L. laparogramma* was misidentified as *L. kungweensis*.



• *L. kungweensis* + *L. signatus* * *L. laparogramma*

Figure 19 A discriminant function plot based on morphometric and meristic measures of *L. kungweensis*, *L. signatus* and *L. laparogramma* - a) males and b) females.

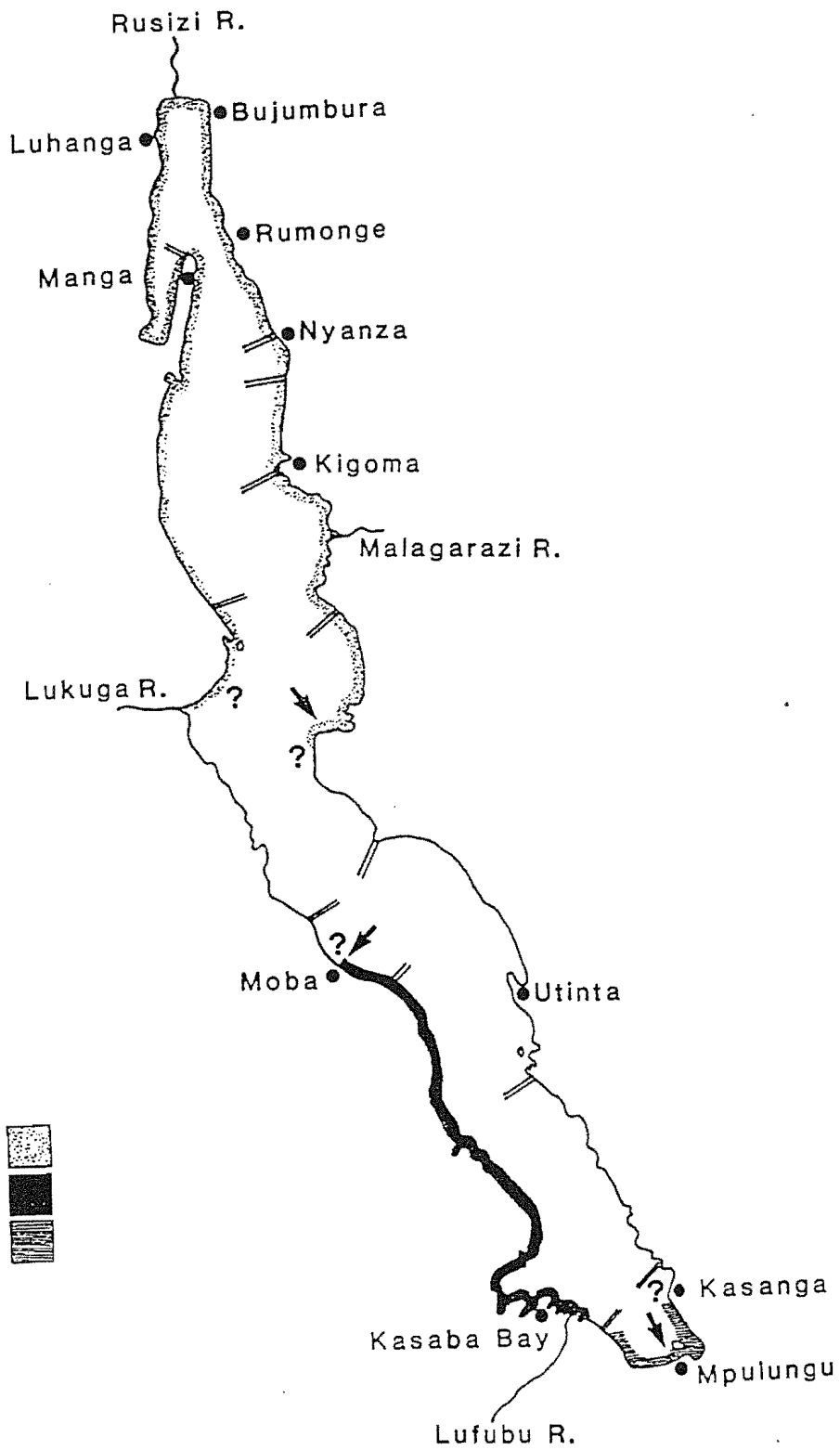


Figure 20 A map of Lake Tanganyika showing the distribution of *L. laparogramma*, *L. signatus* and *L. kungweensis*. Arrows point to type localities, double lines indicate step underwater slopes which may act as barriers to deep water benthic species.

Table 4 The results of discriminant analysis of morphometric and meristic characters for *L. kungweensis*, *L. laparogramma* and *L. signatus*, showing percentage of correct species identification (males and females were analysed separately).

Group	Percent correct	Predicted group		
		L. kung	L. sign	L. lapa
Males				
<i>L. kungweensis</i>	100	19	0	0
<i>L. signatus</i>	100	0	10	0
<i>L. laparogramma</i>	100	0	0	12
Total	100	19	10	12
Females				
<i>L. kungweensis</i>	100	19	0	0
<i>L. signatus</i>	100	0	4	0
<i>L. laparogramma</i>	91.7	1	0	11
Total	97.1	20	4	11

L. kungweensis = L. kung, *L. signatus* = L. sign and *L. laparogramma* = L. lapa

Distribution. The 3 species are endemic to Lake Tanganyika, Central Africa, however, their entire distributions within the lake are not well known (Figure 20).

1. *Lamprologus kungweensis* occurs from Kungwe Bay, Tanzania (the type locality) north to Bujumbura and then south to Lagumba River mouth, near Kalemie, Zaire.
2. *Lamprologus signatus* occurs at Moba, Zaire (the type locality) and extends south into Zambia with its southern limit being in the Lufubu River to Cape Kapembwa area.
3. The most north-westerly populations of *L. laparogramma* were found just north of Mwellia, Zambia and extend south and east to the Zambia-Tanzania border and presumably north of this point also. The type locality is at Mbita Island, Mpulungu, Zambia.

Habitat. *Lamprologus kungweensis*, *L. laparogramma* and *L. signatus* are all stenotopic, occurring exclusively on mud bottoms (Figure 7). This habitat is sub-littoral, ranging from 5m to more than 40m depth and is flat or of negligible gradient. At the collection sites in Zambia, Tanzania and Burundi a variety of shells, dominated by the gastropod *Neothauma tanganyicense*, were found scattered over the floor in low density (< 1 shell /square meter). At Luhanga, Zaire, *Neothauma* was absent and shells were dominated by a smaller gastropod species *Paramelania imperialis*.

Fish abundance. At Mpulungu fish abundance varied from 1-28/10m² in the mud habitat. The community was dominated by *L. laparogramma* (79.6% average of 10 transects). Other species present were: *L. ornatipinnis* (9.3%), *L. ocellatus* (7.9%), *Limnochromis auritus* (1.8%), *L. lemairii* (0.7%) and *N. tetracanthus* (0.7%). Fish abundance at Luhanga varied from 3-15/10m² in the mud habitat. The fish community was comprised of *L. kungweensis* (83.3% average of 2 transects) and *L. ocellatus* (16.7%).

Hole use. *Lamprologus kungweensis*, *L. laparogramma* and *L. signatus* dig holes in the lake floor which serve as refuges from predators, breeding sites and form the central parts of territories (Figure 7). Hole dimensions for *L. laparogramma* were found to vary with fish size; they were up to 12 cm long but rarely more than 1.6 cm wide (Figure 21). Holes used by *L. signatus* and *L. kungweensis* were observed but not measured although they appeared to be of similar dimensions. Larger holes are excavated by the parental fishes and are used by adults and juveniles. As with shell dwelling species there are distinct male and female holes. Smaller holes are excavated by the juveniles then individually inhabited and defended against siblings.

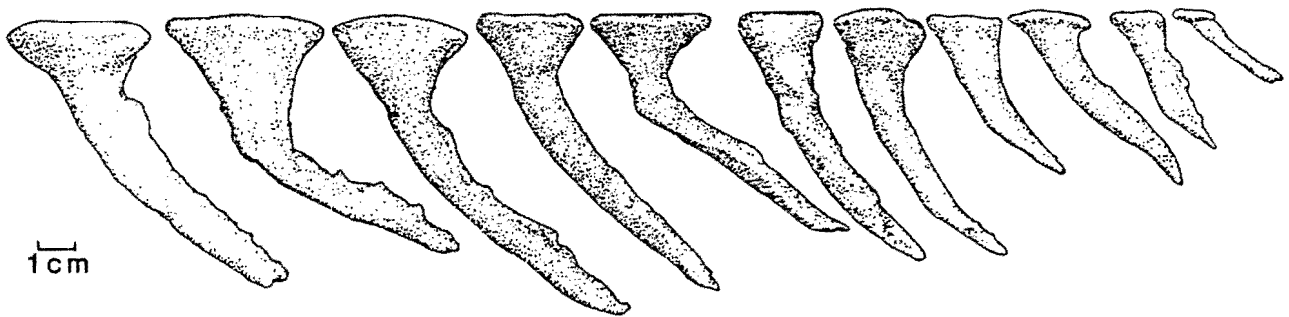


Figure 21 Lateral configuration of *L. laparogramma* holes determined by epoxy resin casts.

Shell use. *Lamprologus signatus* and *L. laparogramma* were also found to use shells of the gastropod *Neothauma tanganyicense* as refuges and breeding sites instead of holes. However, there appears to be competition for these with other shell dwellers mainly *L. ocellatus* and *L. ornatipinnis* and shell usage was observed to change with varying shell density (Table 5). *Lamprologus signatus* and *L. laparogramma* used shells at the edges of shell beds where the shells occurred in high densities. Moving away from the shell beds and onto the mud floor both shell density and shell use in *L. laparogramma* and *L. signatus* decreases.

Territory structure. *Lamprologus signatus*, *L. laparogramma* and *L. kungweensis* are monogamous. Joint male-female territories usually consist of separate male and female holes (and more rarely shells). The mean inter-hole distance for *L. laparogramma* was 45.4 cm (n = 14), ranging from 15-101 cm and

an estimated territory size varying between 1-3 square meters. When juveniles are present there may be up to 15 extra small holes within a territory.

Table 5 Shell use by *L. laparogramma* at Musende Rocks (2/4/1993.) on mud bottoms with varying shell densities.

shells / m ²	shell bed edge		20m depth		30m depth	
	17		0.35		0.15	
	holes	shells	holes	shells	holes	shells
males	1	27	55	17	23	7
females	1	30	35	16	24	6
juveniles	-	-	30	0	11	0
Total	2	57	120	33	58	13
% of shells used by adults	3	97	73	27	78	22

REMARKS

Generic placement. Colombe & Allgayer (1985) used reduced numbers or the absence of infra-orbital bones to define the genera *Variabilochromis*, *Paleolamprologus*, *Neolamprologus*, *Lamprologus* and *Lepidolamprologus*. According to their classification the three species under consideration would be placed in the genus *Neolamprologus* due to the absence of infra-orbital bones posterior to the lachrymal. However, I concur with Poll (1985) that the presence and number of infra-orbital bones is a highly variable character and thus not a sound basis for defining genera. This is particularly so in species with a small adult size. I therefore have followed Poll (1985) in placing the three species in the genus *Lamprologus*.

Of the several characters Poll (1985) indicates as defining the genus *Lamprologus* two are particularly evident in the three species examined;

1. Extreme reduction or absence of scales on the head, operculum, thoracic region and abdomen,
2. Rounded pelvic fins with the 2nd and 3rd soft rays being the longest.

Reduction in the squamation on the anterior body and head, rounded pelvic fins, low lateral line scale counts and elongated bodies are features shared with other species of the Zaire Basin and West Africa. Their resemblance to certain species of *Schwetzoichromis* (formerly *Orthochromis*, Greenwood & Kulander, 1994) in particular, with respect to both body form and coloration, is striking and all the more interesting when habitats are compared. Typically *Schwetzoichromis* are found in fast flowing

rivers and streams while the *Lamprologus* live in low current flow, sub-littoral regions of Lake Tanganyika. Thus these similarities would seem not to be a result of convergent evolution but may indicate a close phylogenetic relationship worthy of further investigation.

Distribution. The complete distributions for *L. signatus*, *L. laparogramma* and *L. kungweensis* are not known. However, despite being restricted to mud substrate habitats they have wide distributions within the lake. Mud habitats are extensive in deep waters (below 20m) and are subject to less fragmentation than littoral habitats. Affluent rivers would seem not to present a barrier to the movement of these species since the distribution of all three populations extends over river mouths, (eg. *L. kungweensis* occurs on either side of the Ruzizi and Malagarasi Rivers). In western Zambia the coast from Cape Kapembwa north to Cape Chaitika is very steep and drops below the 200m level within 2 km of the shore. The presence of suitable mud habitats in this area is unlikely and it is suspected that the nature of the coastline rather than the Lufubu River is the barrier between the ranges of *L. signatus* and *L. laparogramma*. Other underwater slopes which may form barriers to the movement of stenotopic species are identified in Figure 20.

CONCLUSIONS

Morphometric and meristic features show considerable overlap between the three species, indicating their close relations and behavioural and ecological information support this view. However, discriminant analysis of body parameters enables species separation with a high degree of accuracy. There appear to be behavioural differences between *L. kungweensis* and *L. signatus* and *L. laparogramma* with the latter two species using shells as refuges. The greatest differences in 'specific characters' are in coloration. All three species (live and preserved specimens) can be easily separated most readily on the basis of colour patterns and coloration. *Lamprologus signatus* and *L. laparogramma* seem to be more closely related if coloration, body morphometry and behaviour are the criteria used.

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Original resident standard length	Shell total height	Immigrant standard length	species
<i>♂ L. ocellatus</i>			
42.4	38.4	32.4	ocell (♂)
35.0	34.8	32.9	ocell (♂)
28.5	24.2	27.1	ocell (♂)
41.1	43.2	38.5	ocell (♂)
37.4	50.2	49.1	orn (♂)
41.2	42.8	37.5	hecqui (♀)
41.6	46.8	5.4	crab (♂)
38.4	37.1	-	-
37.4	35.6	-	-
40.5	-	-	-
<i>♀ L. ocellatus</i>			
27.6	34.1	33.5	ocell (♂)
25.0	23.9	28.3	ocell (♂)
25.1	26.1	24.5	ocell (♀)
24.8	15.8	21.9	ocell (♀)
24.4	17.5	22.4	ocell (♀)
23.6	21.8	25.7	ocell (♀)
26.2	34.3	-	-
19.8	17.1	-	-
28.4	36.3	-	-
27.1	-	-	-
<i>♂ L. ornatipinnis</i>			
50.9	46.3	47.0	orn (♂)
49.1	39.9	48.8	orn (♂)
45.0	46.1	46.9	orn (♂)
49.5	51.1	49.6	orn (♂)
46.0	49.3	44.1	orn (♂)
47.6	47.6	39.9	hecqui (♀)
48.4	48.5	46.3	hecqui (♂)
47.2	50.9	48.3	hecqui (♂)
48.2	45.9	-	-
47.6	46.1	-	-
<i>♀ L. ornatipinnis</i>			
32.9	47.9	-	-
30.4	47.1	-	-
32.9	41.5	-	-
35.1	38.5	-	-
31.7	45.9	-	-
31.2	45.2	-	-
29.0	38.2	-	-
32.8	44.3	56.8	orn (♂)
29.9	-	-	-

