FEEDING ECOLOGY OF *BATHYCLARIAS NYASENSIS* (SILUROIDEI: CLARIIDAE) FROM LAKE MALAWI

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By

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To my family

ABSTRACT

In Malawi, fish contribute about 60-80% to the country's animal protein supply. The greater proportion (> 50%) comes from Lake Malawi. *Bathyclarias nyasensis* and other clariid catfish contribute up to > 20% of the total catches. Catches of *Bathyclarias nyasensis* in the inshore area of the south-east arm of Lake Malawi are declining and a management plan for the fishery is essentially lacking. There is paucity of biological data that precludes the use of any option to manage the species.

The principal aim of the thesis was to define the ecological role *B. nyasensis*, the most abundant and common of the *Bathyclarias* species. By examining life history characteristics within a food web context, it was hypothesized that the study would provide an insight into the interrelationships between species, and, hence form the basis for the development of a rational exploitation strategy for the species. The study was undertaken in the south-east arm of Lake Malawi (9^0 30'S, 14^0 30'S). The principal objectives of the study were to investigate the feeding ecology of *B. nyasensis* by examining morphological characters and structures associated with feeding, diet of *B. nyasensis,* food assimilated in the species using carbon ($\partial^{13}C$) isotope analysis, daily food consumption rate for *B. nyasensis*; and to relate the feeding ecology to life history traits such as age, growth, and some aspects of the reproductive biology of *B. nyasensis*.

The suitability of sectioned pectoral spines and sagittal otoliths to age *B. nyasensis* was assessed. Due to reabsorption of growth zones with increasing spine lumen diameter with fish size, and the relatively low number of spines that could be aged reliably, only otoliths were used. The maximum age for *B. nyasensis* was estimated at 14 years. Growth was best was described by the four parameter Schnute mc $l_t=\{42+(81^{1.8}-42^{1.8})x\frac{1-e^{-0.05(t-1)}}{1-e^{-(-0.05)(11)}}\}^{1/1.8}$

for female, and $l_t=\{41+(98^{1.2}-41^{1.2})x\frac{1-e^{-0.02(t-1)}}{1-e^{-(-0.02)(13)}}\}^{1/1.2}$ for male fish. Age-at-50% maturity for females and males were estimated at 7 years and 4 years, respectively. Typically, fish grew rapidly in the first year, but slower during subsequent years. Smaller fish were found inshore while larger fish were found in offshore regions. It was hypothesised that the rapid growth in the first year and slower growth later is a consequence of change in diet from high quality and abundant food source to a more dilute food and that this may be associated with a shift in habitat.

Morphological characters associated with feeding were used to predict the food and feeding behaviour of *B. nyasensis*. The size of premaxillary, vomerine, pharyngeal dental and palatine teeth and premaxillary and vomerine tooth plates suggested the capability of *B. nyasensis* to handle both large and small prey, with a propensity towards smaller prey in composition to *C. gariepinus*. The molariform teeth on the vomerine tooth plate suggested that molluscs form part of the diet. The relative gut length (1.27±0.24) suggested omnivory, with an ability to switch between planktivory and piscivory. Buccal cavity volume and filtering area changed with fish size at 500–600 mm TL upon which it was hypothesised that the fish diet changed to planktivory at this size.

Detailed diet analysis provided information upon which the above hypotheses could be accepted. Percent Index of Relative Importance (%IRI) and a multi-way contingency table analysis based on log-linear models were used to analyse diet data. Results showed that *B. nyasensis* is omnivorous, but with a distinct ontogenetic dietary shift from piscivory to zooplanktivory at 500 - 600 mm TL. The increased buccal cavity volume at the same fish size therefore, suggests that *B. nyasensis* is well adapted to filter the dilute zooplankton resource. Increased foraging costs of feeding on zooplankton explained the

slower growth of larger fish. The dietary shift was finally corroborated by results of the $\partial^{13}C$ isotope analysis. A polynomial equation described the change in carbon ratios with fish size: $\partial^{13}C = -33.188 + 0.4997L - 0.0045 (\text{total length})^2$ ($r^2 = 0.598$, n = 12, p=0.022).

The ontogenetic shift in diet was synchronised with a habitat shift postulated in life history studies. In the inshore region, *B. nyasensis* were predominantly piscivorous (apex predators), and were zooplanktivorous in the offshore region, thereby forming part of the pelagic food web in the latter region.

After examining "bottom-up" and trophic cascade theories, it was postulated that perturbations of the *B. nyasensis* stock would be discernible both at the top and lower trophic levels. As a piscivore and therefore apex predator, effects of overfishing *B. nyasensis* in the inshore region could cascade to unpredictable ecological changes in inshore areas and, due to the ontogenetic habitat shift, in the offshore regions. Examples of trophic cascade phenomena are provided.

On the basis of the feeding study, it was possible to reconstruct the pelagic food web of Lake Malawi. Apart from the lakefly *Chaoborus edulis*, *B. nyasensis* is the other predator that preys heavily on zooplankton in the pelagic zone. Perturbations of the *B. nyasensis* stock could affect size composition of zooplankton which in turn, could affect production of *C. edulis,* a resource for the top predators in the food web.

The findings of the present study contributed to the ongoing debate of introducing a zooplanktivore into the pelagic zone of Lake Malawi. Proponents for the introductions have argued that zooplankton predation by fish is inferior to that of *C. edulis*. Introduction of a clupeid zooplankton was proposed as a strategy to boost fish production

in the lake. The zooplanktivore would either out-compete or prey on *C. edulis* to extinction. Opponents to this view argued that zooplankton biomass in the pelagic region was too low to support introductions and that the fish biomass in the pelagic region may have been underestimated. Results from the present study suggest that planktivorous fish (including *B. nyasensis*) might not be inferior to *C. edulis* in utilising the zooplankton resource; *B. nyasensis* is well adapted to utilise the dilute zooplankton resource, and by omitting B. nyasensis from previous studies, overall zooplankton predation by fish may have been underestimated by between 7 – 33%.

On the basis of the theoretical migratory life history cycle of *B. nyasensis*, it is recommended that the current interest in increasing fishing effort in offshore areas should proceed with caution. Ecological changes that may have occurred in the inshore areas due to overfishing have probably not been noticed, as the offshore zone has never been fished. The latter zone may have acted as a stock refuge area. Higher fishing intensity in the offshore areas could lead to serious ecological imbalances and instability. The study has shown that life history characteristics studied in the context of the food web, and in the absence of other fisheries information and/or data, strongly advocates the precautionary principle to managing changes in exploitation patterns.

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CHAPTER 1

Introduction

Fishes of the family Clariidae belong to the suborder Siluroidei (commonly known as the catfishes), of the order Siluriformes (Burgess 1989, Teugels 1996). Siluroids are comprised of 33 families with 416 genera and 2,584 species and are recognised from North, Central and South America, Africa, Eurasia, South-East Asia, Japan and Australasia. Except for two marine families (Ariidae and Plotosidae), catfishes are generally freshwater fishes (Teugels 1996). The Siluriformes are thought to have evolved in fresh water in the South American and African tropics (Greenwood *et al.* 1966), although Roberts (1973) suggested that they arose independently in Africa, Asia and South America.

Great variation exists in the external morphology of catfishes, but in general, the body is naked, although in some families (*e.g.,* Callichthyiadae and Loricariidae) it is covered with bony plates. Up to four pairs of circumoral barbels may be present; one nasal pair, one (or two) maxillary pair(s) and two mandibular or mental pairs. In some families one or more pairs are missing. The barbels are equipped with numerous taste-buds and are used in detecting food. The mouth is generally non-protractile and the eyes are relatively small. The dorsal and pectoral fins are often provided with a leading spine. An adipose fin is often present. The pelvic fins have an abdominal position. Important variations are also noted in maximum body size. The smallest catfish are found in the genus *Scoloplax* (Scoloplacidae) with a maximum size of 14 mm total length (TL), while the largest the *Silurus glanis* (Siluridae) may exceed 5 m and 330 kg (Bruton 1996, Teugels 1996).

The ecomorphologies and life-history patterns of the catfishes are diverse (Bruton 1996) and this has enabled them to exist and evolve in different ecosystems. Their predominant mode of feeding is suction or gulping feeding, which is made possible by their large bucco-phyrangeal volume and wide mouth. They usually have small and villiform teeth in bands on the premaxillary, vomerine, mandibular and pharyngeal jaw bones, which are used to retain the prey in the mouth rather than to bite or lacerate it.

The group also has a wide array of breeding guilds ranging from non-guarders (Schilbeidae and Clariidae) through guarders that protect their young such as *Ictalurus nebulosus* to mouth brooders (Ariidae) which are reproductively the most specialised (Bruton 1996). These breeding guilds place catfishes on different levels of the altricial/precocial continuum. Altricial fishes produce small incompletely developed young, with a long larval stage. They are generalists capable of surviving in unstable, uncrowded environments and are mainly subject to density-independent mortality. Precocial fishes produce large eggs and well-developed young with an abbreviated larval stage or no larval stage (direct development); typically they are specialists, able to survive in a stable, crowded environment in which they are mainly subject to density-dependent mortality (Balon 1981, Bruton 1989, 1996).

Clariids occur in Africa, northward to Syria and southern Turkey, and in south-east Asia. Fourteen genera are recognized (Teugels 1996) of which only *Clarias* is common to both continents. Clariids have a suprabranchial organ (reduced or virtually absent in some genera), formed by arborescent structures originating from the second and fourth epibranchials, enabling them to utilise atmospheric air. Some clariids are able to leave water and cross land for several hundred meters, using their pectoral spines and sinuous body movements (Teugels 1996).

Information on the phylogenetic relationships within the family Clariidae is limited. Reagan (1911) suggested that the Clariidae are closely related to the Schilbeidae. Roberts (1970) suggested that the Clariidae (together with the Heteropneustidae) represent a separate evolutionary line relative, to other catfishes that have encapsulated air bladders. In an arrangement of families from primitive to most derived, Roberts (1970) placed the Clariidae in the central array together with the Pimelodontidae and the Ariidae. In this arrangement, the Diplomystidae are recognised as the most primitive while the most advanced families are the Trichomycteridae, Callichthyidae, Loricariidae and the Astroblepidae. Based on the degree of fusion of the anterior vertebrae and nature of swimbladder, a cladogram constructed by Howes (1983) places the Clariidae in a similar position.

Clariid species can be arranged in a series of increasingly eel-like forms (Boulenger 1907). The genus *Heterobranchus* stands at one end (presumably primitive end) (Alexander 1965) of the series. These fish have a well-developed adipose fin, and their body shape and the arrangement of the fins suggest that they are unspecialised (Alexander 1965). The genus *Channallabes* at the other end of the series (presumably most advanced) also has an eel-like body, is small, has no adipose fin or paired fins, and the dorsal, caudal and anal fins have coalesced to form a single fin with about 300 rays. The genus *Clarias* stands between these extremes. *Clarias* and *Heterobranchus* have well-developed aerial respiratory organs, and the dorsal surface of the head is almost entirely covered by dermal bone. *Dinotopterus* species have poorly developed aerial respiratory organs and much less dermal bone in the skull (Alexander 1965). The genus *Bathyclarias* are intermediate between *Clarias* and *Dinotopterus*, with species having a diversity of aerial respiratory organs ranging from a mere stub (as in *Dinotopterus*) to well-developed organs, (as in *Clarias*).

The issue of whether *Bathyclarias* and *Dinotopterus* are separate genera has been a taxonomic debate for decades (see Anseaume & Teugels 1999). Boulenger (1906) described the genus *Dinotopterus* as endemic to Lake Tanganyika, with *D. cunningtoni* as the only representative. Jackson (1959) erected the genus *Bathyclarias* recognising 11 species endemic to Lake Malawi. Species in the genera *Dinotopterus* and *Bathyclarias* are characterised by an incompletely ossified cranium, laterally placed eyes, and an extremely high gillraker number (first arch). However, *Dinotopterus* species have a noticeable adipose fin while in *Bathyclarias* species the adipose fin is reduced or absent. Furthermore, in *Dinotopterus* the arborescent organ is consistently reduced, while in *Bathyclarias* the organs vary from a stub or reduced type to a well-developed, branched organ similar to that found in *Clarias* (Greenwood 1961).

Using osteological examination of the neural spines posterior to the caudal fin, Greenwood (1961) synonymised the genera *Dinotopterus* and *Bathyclarias,* where *Bathyclarias* became the junior synonym. Greenwood (1961) described one additional species from Lake Malawi raising the number of species in the genus *Dinotopterus* to 13 (including one from Lake Tanganyika). Recently, using morphological, osteological and zoogeographical evidence, Anseaume & Teugels (1999) reinstated the genus *Bathyclarias* for species found in Lake Malawi as valid. Among the differences they found (Anseaume & Teugels *op cit.*) were that fish in the genus *Dinotopterus* have a larger head, a greater distance between the dorsal and caudal fins, and between the occipital process and the dorsal fin, while the length of the rayed dorsal fin and the pectoral spines are shorter than in *Bathyclarias* (other differences are detailed in Anseaume & Teugels 1999).

Based on the length of the gill rakers the *Bathyclarias* species in Lake Malawi can be divided into two groups; those with relatively long gill rakers (70-100% of gill filament

length) and those with short gill rakers (30-60% of gill filament length). Four species (*B. nyasensis*, *B. jacksoni*, *B. loweae*, and *B. ilesi*) have long gill rakers, while the rest (*B. filicibarbis*, *B. foveolatus*, *B. euryodon*, *B. longibarbis*, *B. rotundifrons*, *B. worthingtoni*, *B. gigas* and *B. artribranchus*) have short gill rakers (Greenwood 1961). *B. nyasensis* (Worthington 1933), locally known as *Sapuwa*, (see description by Jackson 1959) is the most common and abundant of the *Bathyclarias* species (Jackson 1959; Jackson *et al.* 1963), and, hence, was chosen for this study.

The *Bathyclarias* fishery in Lake Malawi

In Malawi, fish contribute about 60-80% to the country's animal protein supply (ICLARM 1991); food fish are predominantly obtained from capture fisheries, with aquaculture contributing less than one percent to the total supply (Kaunda 1994). Between 1979 and 1996, fish from Lake Malawi accounted for some 53% of the country's total annual fisheries production (Bulirani *et al.* 1999); the remainder originated from Lake Malombe (14%), Lake Chilwa (20%), Shire River (10%) and Lake Chiuta (3%). The greatest proportion of fish caught from Lake Malawi (>80%) are taken by the small-scale (artisanal) sector while the remainder are taken by the industrial sector.

The exact contribution of the *Bathyclarias* catch to the overall fisheries production of Lake Malawi is not adequately quantified. However, *Bathyclarias* species are important in both the artisanal and the industrial fisheries sectors (Jackson 1959, Thompson *et al.* 1996). In some localised areas (e.g., the long-line fishery of Chembe village) and where artisanal fishermen target large catfishes, *Bathyclarias* species and *Bagrus meriodinalis* form a substantial part of the catches (Smith 1993) (Table 1.1).

Table 1.1. Total catch estimates (kgs) over a six-month period for Chembe long-line fishery, January to June 1993 (compiled from Smith, 1993). The fishery had 11 longlines with an average of 414 hooks per longline.

Month	Other cichlids non-cichlid fishes	*Clarias gariepinus*	*Bagrus meridionalis*	*Bathyclarias* species
January	90.6	63.6	1,295.3	1,041.6
February	2.2	22.5	441.7	116.2
March	8.6	13.6	336.3	242.5
April	3.5	5.51	251.5	315.1
May	15.9	3.6	200.7	106.5
June	9.8	13.2	259.7	185.2
Total	**130.6**	**122.01**	**2,785.2**	**2,007.1**
% of Total	**2.6**	**2.42**	**55.2**	**39.8**

In a survey of the demersal trawl (at depths <101m) in the southern part of Lake Malawi (Banda *et al.* 1995), *Bathyclarias* species and other catfishes (*Bagrus meridionalis* and *Synodontis njassae*) contributed 20% of the catch by weight. In the same area *Bathyclarias* species formed approximately 20% of total catch (by weight)(Tweddle & Makwinja 1995). In a gill-net fishing survey, *Bathyclarias* and other clariids comprised 8% of the catches in the south-east arm of the lake (Tweddle *et al.*, 1994). In an overall catch assessment, Tweddle *et al.* (1994) noted that the catches of the two catfishes *Bathyclarias* spp and *Bagrus meridionalis* in shallow waters were significantly lower in heavily fished areas. This suggests that the artisanal sector that predominantly exploits the shallow waters (ICLARM, 1991; Smith, 1993) is overfishing the stock.

While the stocks of the *Bathyclarias* and other large catfishes are said to be declining (Tweddle & Makwinja 1995) no attempt has been made to manage them. Their large size subjects them to overexploitation, a feature common to many multispecies, multigear fisheries (Thompson *et al.* 1996). The lack of a management policy for these fishes can is evidenced in a report by the Department of Fisheries (Tweddle *et al.* 1994): "a catfish

fishery would involve the use of much larger mesh sizes than employed at present with a minimum of <100 mm. However, if the fisheries were managed to optimise catfish yield, the extra tonnage achieved would not exceed a few hundred tonnes and would in no way compensate for the loss of the several thousands tonnes of cichlids taken in trawl fishery". While management of a fishery is partly a political decision, Thompson *et al.* (1996) noted that knowledge of the population biology of *Bathyclarias* spp., is lacking, although it is vital to any effort to conserve them.

It is generally accepted that successful management of a fisheries can be undertaken once the ecological role of the species has been established (Nagelkerke 1997). Feeding studies contribute importantly to management of multispecies fisheries, as there is a growing consensus among fisheries scientists and managers that the traditional single-species approaches should be replaced by methods that account for the highly interactive nature of the species and the fisheries. One of these methods is the ECOPATH approach (Polovina 1984), which was recently employed to model the pelagic food web of Lake Malawi (Allison *et al.* 1995). ECOPATH requires estimates of production, ecotrophic efficiency, and relative food consumption and diet composition at all levels of the ecosystem as well as an indication of fish yield (Moreau *et al.* 1997). Given that *Bathyclarias* species may be important component of the pelagic zone (Thompson *et al.* 1995), it is unfortunate that only 27 specimens were captured during the two-year ECOPATH study, and were therefore omitted from the analysis (Allison *et al.* 1995). A study of the feeding ecology of *B. nyasensis* could provide the necessary information upon which to reconstruct the food-web model of the lake's pelagic ecosystem. This would provide an integrated and complete understanding of the trophic system within the lake. In cognizance of the fact that a prerequisite to the development of a fisheries management plan of *Bathyclarias* species is necessarily a fuller understanding of the

biology of the species, it was further decided to investigate aspects of its growth and reproductive biology.

Aims and Objectives

The principal focus of the current study was to elucidate the trophic ecology of *B. nyasensis,* with the view that the study would provide basic data upon which fisheries management plans for the species can be based. With this in mind, the particular objectives of the study were to:

1. Describe age, growth, and aspects of the reproductive biology of *B. nyasensis*;
2. Examine the morphological characters associated with feeding;
3. Describe the diet of *B. nyasensis*;
4. Describe food assimilation in the species using carbon ($\partial^{13}C$) isotope analysis;
5. Estimate the food consumption rate for the species.

The work is structured in the following way: Chapter 2 is a synoptic review of the limnology of the study area, Lake Malawi, and provides physico-chemical and biological information that may explain findings on the trophic biology of *B. nyasensis.* Chapter 3 describes age, growth and aspects of the reproductive biology of *B. nyasensis*. Chapter 4 examines the morphological characters that are associated with feeding; the diet of *B. nyasensis* is described in Chapter 5. Chapter 6 describes food assimilation of *B. nyasensis* using carbon ($\partial^{13}C$) isotope analyses and estimates of food consumption are presented in Chapter 7. Finally, Chapter 8 summarises the life-history patterns and ecological role of *B. nyasensis* in Lake Malawi.

CHAPTER 2

A synoptic review of the limnology of Lake Malawi

Lake Malawi (9° 30' S, 14° 30' S; Figure 2.1), is the southernmost of the African Rift Valley lakes, with a surface area of 28 000 km^2, 8 400 km^3 volume, and average and maximum depths of 292m and 700m respectively (Patterson & Kachinjika, 1995).

Lake Malawi is meromictic or permanently stratified. The upper surface layer or epilimnion has an average temperature of approximately 27.2°C, and extends to about 40m depth. Below the epilimnion is a region of steep temperature decline, or thermocline, that extends to approximately 85m depth, followed by the cooler (23.5-22.8°C) metalimnion to about 230 m, and finally the anoxic hypolimnion (Fryer & Iles 1972, Eccles 1974, Beadle 1981, Ribbink *et al.* 1983, Patterson & Kachinjika 1995). The thermocline is formed due to high surface temperature (see Figure 2.2) while the relatively low in density of the epilimnion restricts vertical mixing with the lower, cooler (and therefore more dense) metalimnetic water.

A decrease in the temperature of the surface water will weaken the thermocline; further disruption of stratification may be caused by winds that create both turbulence and an increase in evaporative cooling of the epilimnion. Periods of relatively low air temperature (less than 25°C) occur in July to August (Figure 2.3) and coincide with periods of strong winds, dominated by the south-east trade winds (Figure 2.3); periods of low winds coincide with rains (Figure 2.3). Based on rain and temperature patterns, three seasons can be distinguished: warm-wet season (November - March), a warm-dry season (April - June), and a cold-dry season (July - October) (Figure 2.3).

In addition to disrupting stratification, winds will cause upwelling of water and internal waves (seiches), which in turn cause further upwelling of nutrient-rich waters from the

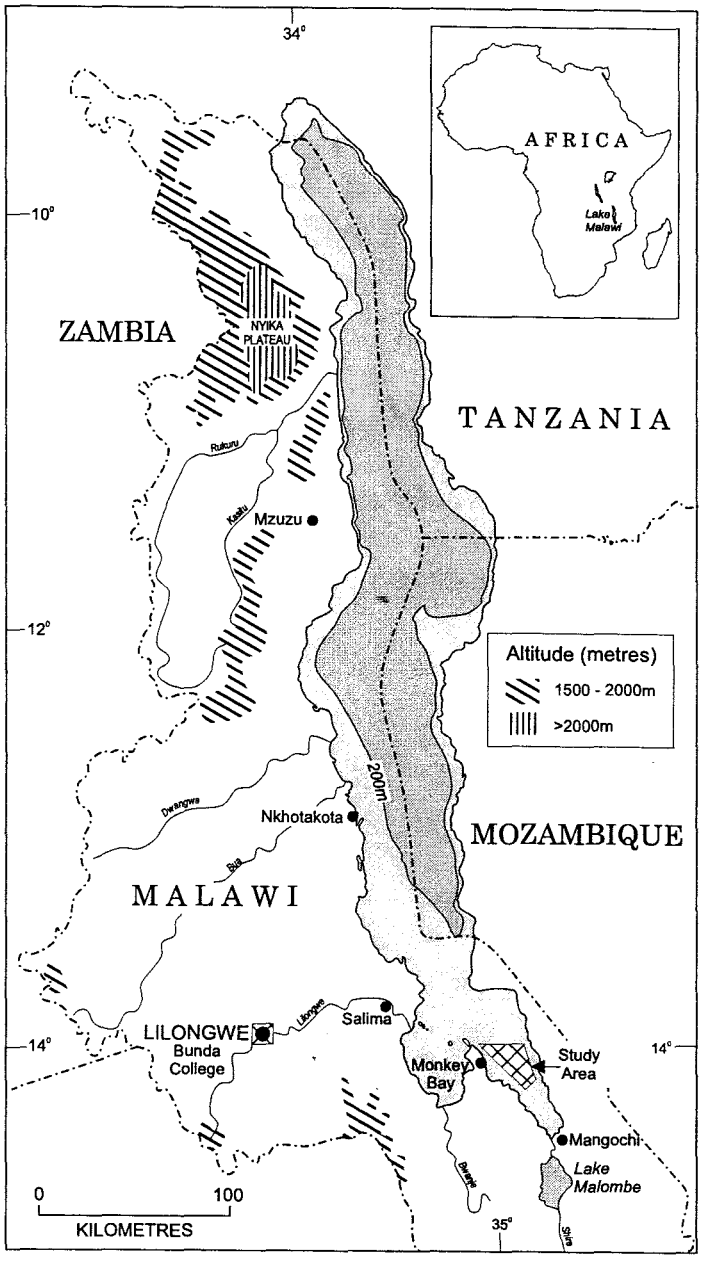


Figure 2.1. Lake Malawi and position of study area.

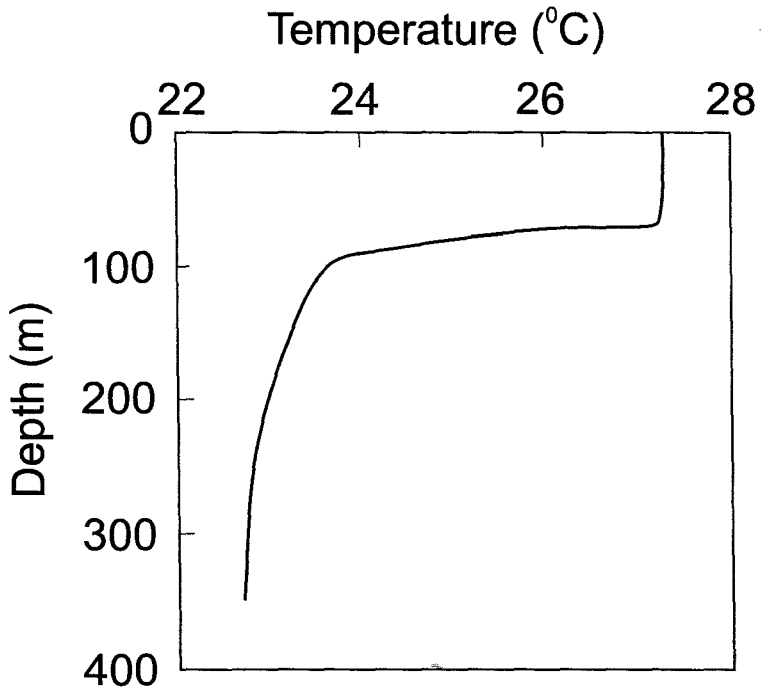


Figure 2. 2. Mean temperature with depth in Lake Malawi in May 1992 (adapted from Patterson & Kachinjika, 1995).

metalimnion to the epilimnion (Eccles 1974, Beadle 1981, Twombly 1983). The seasonality of the winds and upwelling events implies that nutrient availability and, therefore, the lake's overall productivity is also seasonal. Upwelling commonly occurs where the lake bed shelves, making the southern and northern parts of Lake Malawi more productive than the centre (Patterson & Kachinjika 1995).

Patterson and Kachinjika (1995) recorded a light extinction coefficient of approximately 0.1 (Figure 2.4); thus, on a sunny day, the light intensity at 100m depth would be 2.23 ln uWcm 2 s^{-1}, corresponding to a value of approximately 15 lux. Protasov (1964)

demonstrated a visual range for European anchovy (*Engraulis encrasicholus*) of 235cm at 10 lux and 175cm at 1 lux; A lower light concentration of about 1 lux in Lake Malawi occurs at around 120m depth. Mwanyama (1993) recorded secchi disk readings of 7.8m in shallow areas (maximum depth of 50m) and 12.5 m in deeper areas (90-20m) in the south east arm of the lake.

Oxygen concentration decreases steadily through the water column profile from about 7.4 mgl^{-1} in the epilimnion, to a value close to zero at the metalimnion-hypolimnion boundary (around 200 m depth), and remains at low levels for about 50 m below the boundary, below which the water becomes anoxic (Figure 2.5).

The distribution of pH values with depth follow a pattern similar to oxygen; pH decreases with depth, from about pH 8.6 near the water surface to around pH 7.2 at 240m (Figure 2.4). This seems to be due to biological factors. For example, photosynthesis dominates in waters close to the surface and utilises CO_2, which increases the pH, while in deeper waters respiration dominates in conjunction with the net production of CO_2, which lowers pH.

The major nutrients utilised by phytoplankton (nitrogen, phosphorus and silicon) increase with water depth (Figure 2.5). This is a common feature of stratified lakes and is particularly accentuated in meromictic lakes, where a continual loss of nutrients from the surface layers occurs due to the sinking of nutrient-rich detrital material.

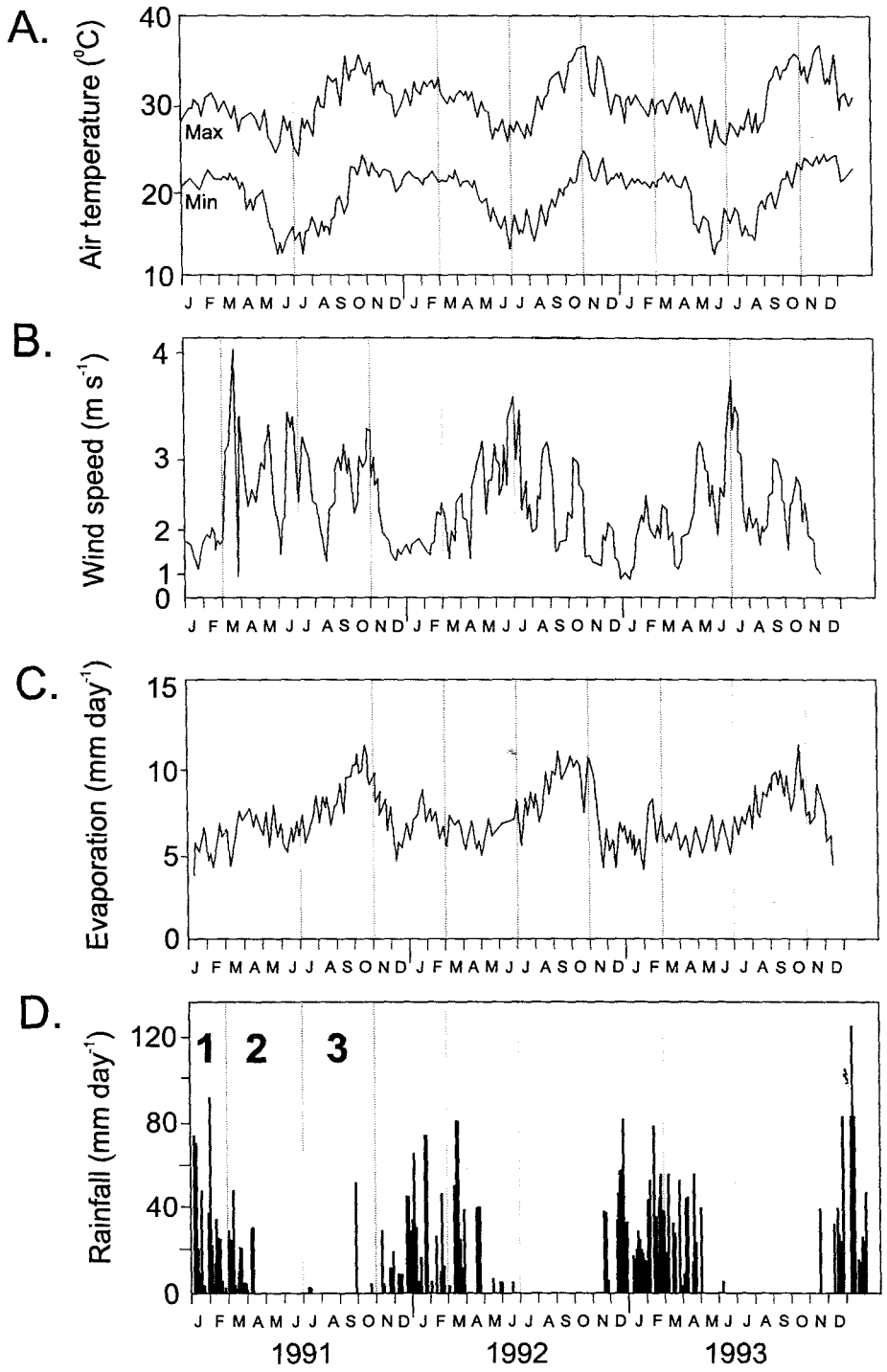


Figure 2.3. Meteorological data from the Salima meteorological station for 1 January 1991 to 31 January 1993. (A) Seven-day running average of mean daily maximum and minimum temperatures; (B) 21-day running average of mean daily wind speed (plotted on a square raw scale); (C) 7-day running average of evaporation; and (D) daily rainfall total. 1, 2, 3 are warm-wet, warm-dry and cold-dry seasons, respectively (adapted from Patterson & Kachinjika 1995).

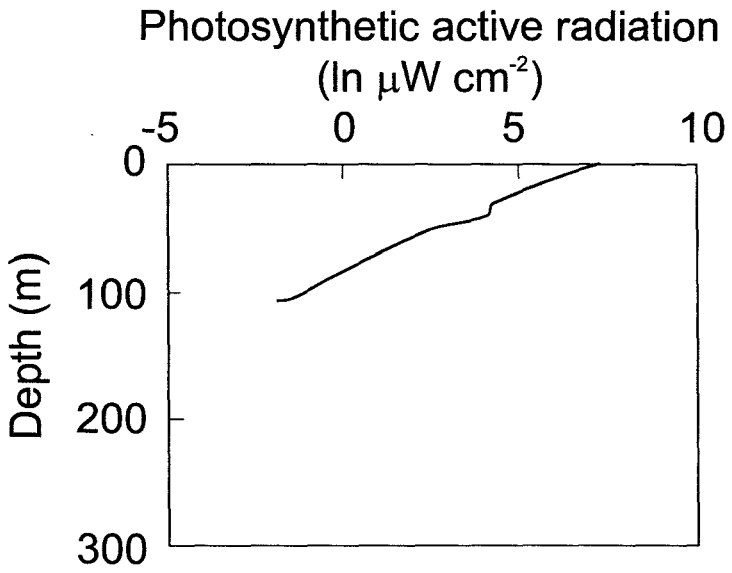


Figure 2.4. Depth distribution of light in Lake Malawi measured using a hydrographic probe in May 1992 (adapted from Patterson & Kachinjika 1995).

The oxidised form of nitrogen (NO_3-N) is the predominant form in the epilimnion and metalimnion, while the reduced form of ammonia ion (NH_4-N) predominates in the oxic-anoxic boundary layer (Figure 2.5).

The nitrogen-phosphorus (N:P) ratio can provide insight into biological processes. Due to preferential uptake of phosphorus by phytoplankton (Reynolds 1984), the N:P ratio increased from 8:1 to 16:1 during the middle of the sample year (Figure 2.6). The level of the silicon, an important nutrient to diatom, decreased during the same period, indicating high utilisation of the silicon ion at the time (Paterson & Kachinjika 1995).

Phytoplankton production forms the main organic carbon input to the pelagic food web of the lake (Bootsma, 1993) and profoundly/ultimately influences production of the pelagic fish stocks (Patterson & Kachinjika 1995).

Patterson and Kachinjika (1995) identified the following phyla of phytoplankton: Cyanophyta (blue green algae), Bacillariophyta (diatoms), Chlorophyta (green algae) and Pyrrophyta (dinoflagellates). Phytoplankton production in the lake is estimated at 20-200 mg m^3 wet weight (Hecky & Kling 1987; Patterson & Kachinjika 1995). The Cyanophyta and Chlorophyta dominate the phytoplankton community during the period October to March while Bacillariophyta (diatoms) dominate during the remainder of the year - the cooler mixing period (Degnbol & Mapila 1982, Bootsma 1993). This may explain the lower levels of silicate (SiO_2) found during the cooler months.

Degnol and Mapila (1982) found chlorophyll-*a* values of 0.1 - 2.1 *u*g l^{-1} (mean 0.73 *u*g^{-1}) with evidence of a chlorophyll-*a* maximum at around 20-30m depth while Patterson and Kachinjika (1995) found chlorophyll-*a* values of 0.68 mg m^3, with maximum occurrence at depths of greater than 50m (Figure 2.7).

High peaks of chlorophyll-*a* were found during the month of July (Figure 2.8a) confirming that high nutrient loading during this period which resulted in higher biomass of phytoplankton. Subsidiary peaks occurred during the wet season and may indicate periods of external loading from rainfall or riverine input (Patterson & Kachinjika, 1995).

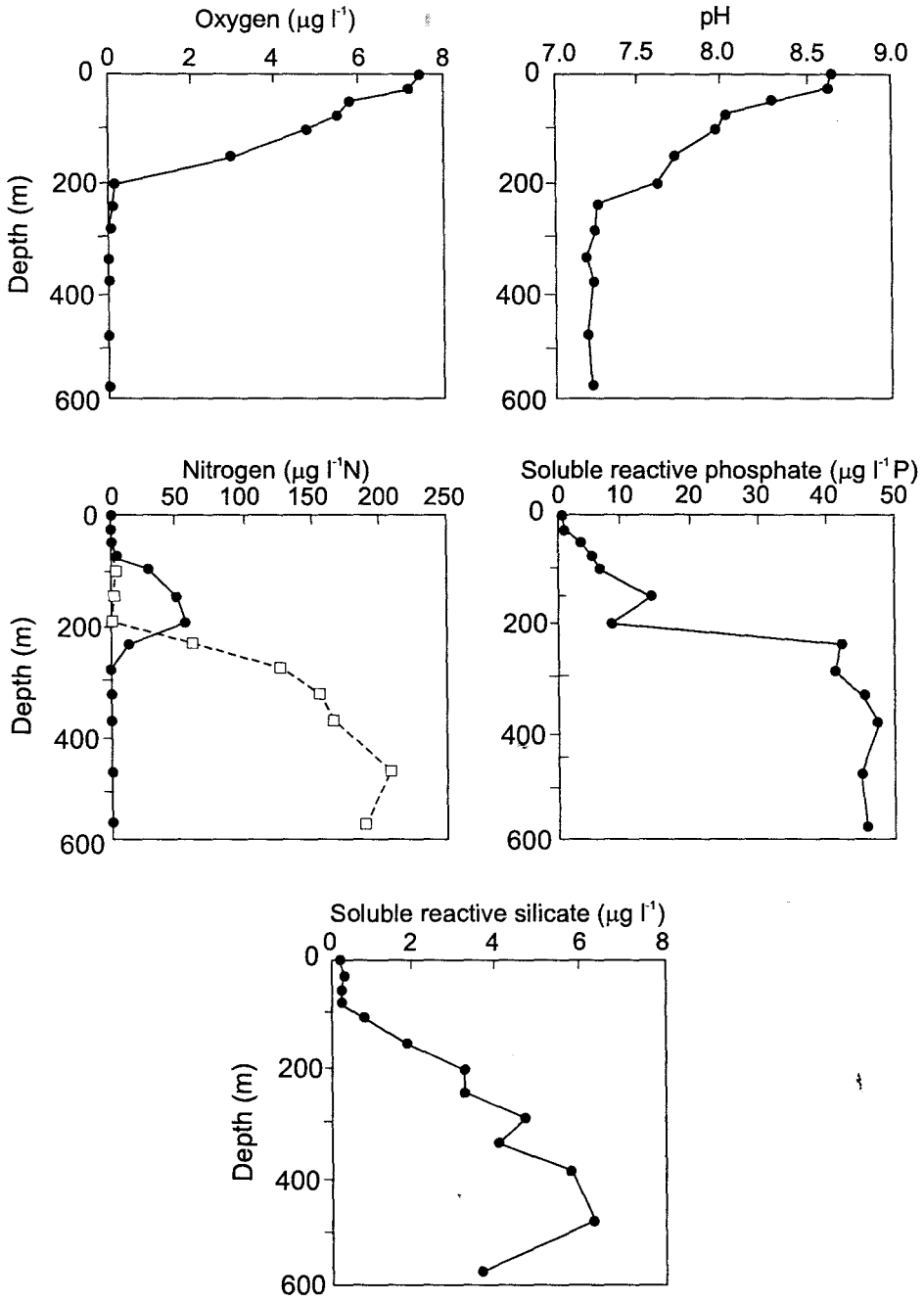


Figure 2.5. Depth distribution of major chemical parameters in Lake Malawi in May 1992. For nitrogen, • = total oxidised nitrogen and ☐ ammonia nitrogen. (Kachinjika & Patterson, 1995).

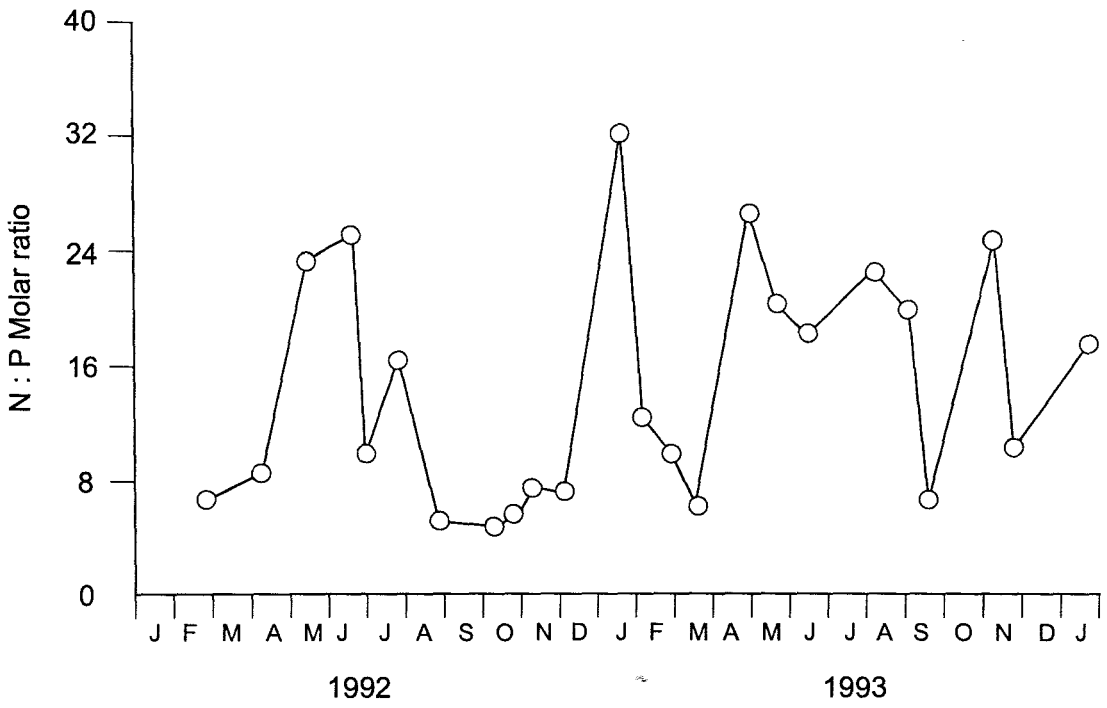


Figure 2.6. Molar N:P ratio-time plot at 75m depth from Lake Malawi derived from the ratio of molar total oxidised nitrogen to soluble reactive phosphate-phosphorus (PO_4-P) (adapted from Patterson & Kachinjika 1995).

Degnbol and Mapila (1982) estimated carbon (C) fixation values between 0.24 and 1.14 g C $m^{-2}.day^{-1}$, with mean value of 0.74 g C $m^{-2}.day^{-1}$ (total 271 g C $m^{-2}.year^{-1}$). Bootsma (1993) reported significantly lower values (0.66 g C $m^{-2}.day^{-1}$), attributable to the combination of lower wind speed and high temperature resulting in higher thermal stability of the water column and thereby restricting the upward movement of metalimnetic nutrients into the photic zone.

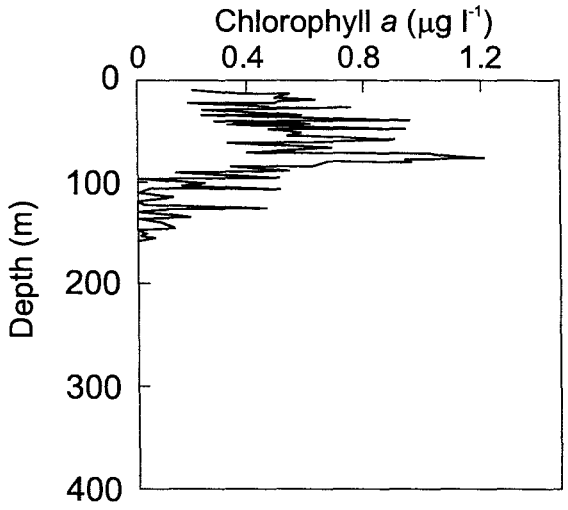


Figure 2.7. Depth distribution of chlorophyll *a* from Lake Malawi in May 1992 (adapted from Patterson & Kachinjika, 1995).

Patterson and Kachinjika (1995) reported higher values for primary production at 319.4 and 518.3 g C m^{-2}.$year^{-1}$ in 1992 and 1993, respectively. The high production value in the latter year was attributed to a high degree of seiching and nutrient loading. The high primary production values in the middle of 1992 and 1993 (see Figure 2.8b) were associated with periods when internal nutrient loading into the epilimnion was greatest (Patterson & Kachinjika 1995).

The spatial and temporal changes in nutrient load and primary production have an effect on secondary and tertiary consumers. Data collected on the vertical distribution of secondary consumers indicate that the crustacean zooplankton inhabit the upper 60-80m of the lake's water column, with maximum abundance occurring at a greater depth during the day than at night (Irvine 1995). Day-time maxima for the herbivorous and most abundant zooplankton, *Tropodiaptomus cunningtoni,* correspond well with sub-surface maxima for chlorophyll-*a*, although the copepod migrates to upper surface waters at night

– presumably a response to predation by *Chaoborus edulis* larvae (Irvine, 1995). It has been noted, however, that the temporal variation in crustacean standing-biomass is greater than the spatial variation; this appears to be a response to increases in phytoplankton production, which in itself is a response to increased mixing in June-July and the presumed increase in nutrient supply. Hence, when the lake becomes more strongly stratified abundance populations of the herbivorous zooplankton as well as secondary consumers, in the upper layer of the water column declines during February-May, with an overall reduction in phytoplankton, together with a greater preponderance of filamentous or colonial forms of phytoplankton dominated by cyanophytes (which are generally a poor source of food for the herbivorous zooplankton). Maximum populations of the herbivorous zooplankton are found during July-December. Figure 2.9 shows the seasonal variation in abundance of primary production, the herbivorous zooplankton *T. cunningtoni,* and larvae of *E. sardella* (which prey *on T. cunningtoni*) in the upper water column (60-80m depth).

Results from the ECOPATH modeling of the pelagic ecosystem of Lake Malawi by Allison *et al.* (1995) indicate that the primary production and the herbivorous and carnivorous zooplankton are under moderate to intense predation pressure. Since a total of 86 % of primary production and 67% of herbivorous zooplankton is consumed (Allison *et al.* 1995), the pelagic zone of Lake Malawi has been described as a food-limited system (Allison, *op. cit.).*

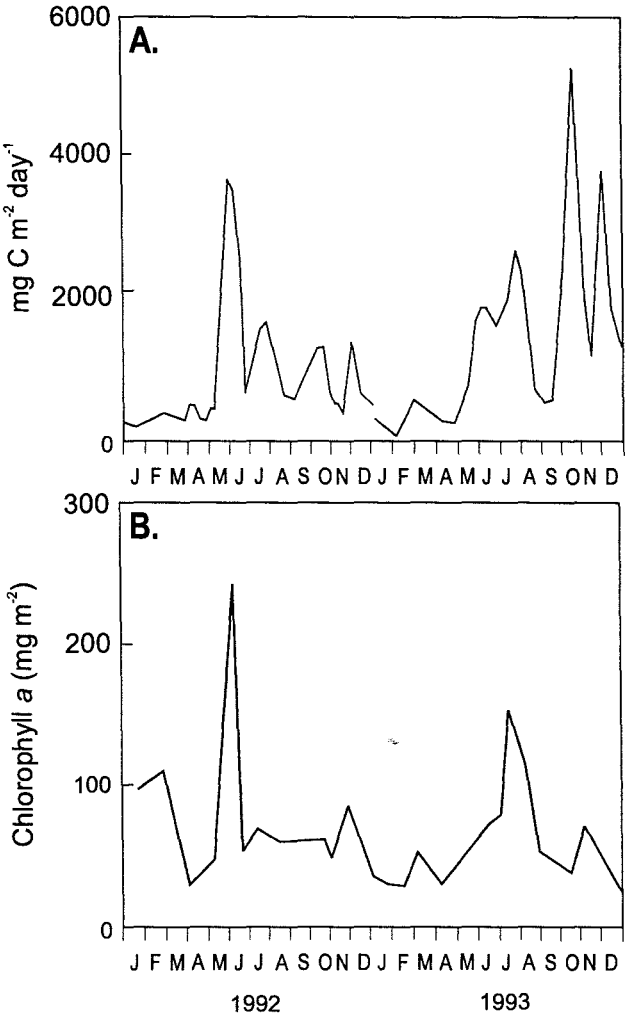


Figure 2.8. Seasonal changes in (A) estimated rate of primary production and (B) chlorophyll *a* in Lake Malawi (adapted from Patterson & Kachinjika 1995).

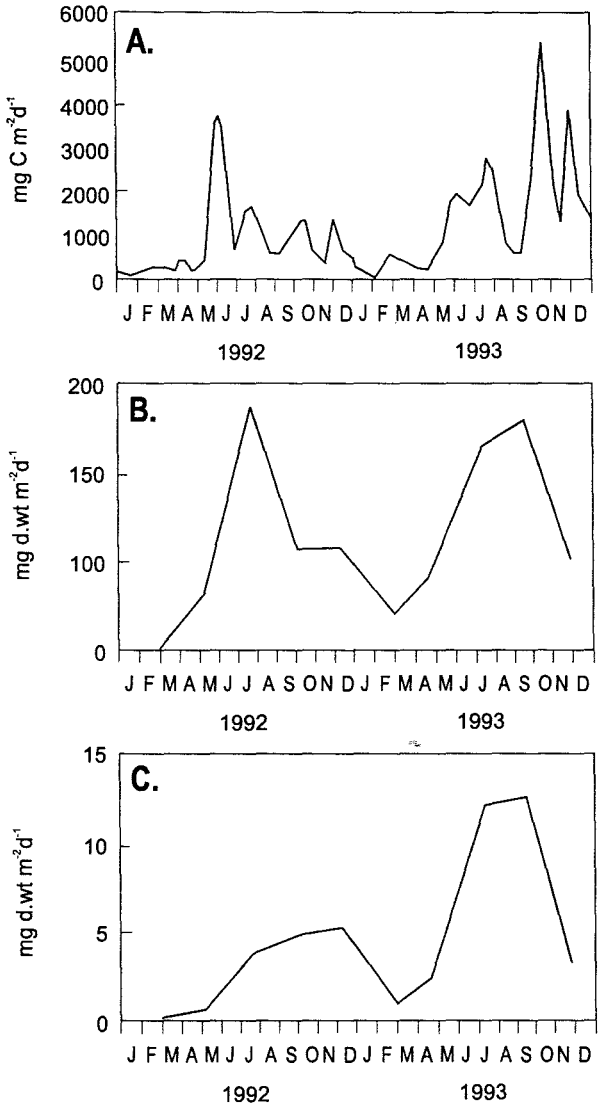


Figure 2.9. Seasonal variation for (A) primary production, (B) production of *T. cunningtoni* and (C) production of *Engraulicypris sardella* larvae in Lake Malawi (adapted from Allison *et al.* 1995).

CHAPTER 3

Age, growth and aspects of the reproductive biology of *Bathyclarias nyasensis* in Lake Malawi

3.1 INTRODUCTION

Studies on life history-traits such as growth and reproduction are indispensable for successful management of a natural fishery or an aquaculture facility (Wootton, 1990; Matthews, 1998). The catch that can be taken from a fishery depends largely on the growth of fish in the exploited population (Pitcher & Hart, 1982) and fish are recruited into a fishery through reproduction (Pitcher & Hart, 1982).

Many factors affect fish growth, these include endogenous factors such as the genetic make-up of a species, and exogenous factors such as food availability, temperature, salinity, and ammonia (Wootton 1990). While genetic factors determine an animal's potential for growth, variation in growth may largely be determined by exogenous factors of which temperature and food availability are considered to be the most important (Weatherley 1972). In subtropical environments, such as Lake Malawi where lake surface temperature varies only slightly at approximately 24 to 28.4°C (Patterson & Kachinjika 1995), food availability may be the most important environmental factor to regulate growth.

Calculation of age structure and growth rate in a population can be made if the age of fish sampled is accurately determined (Beamish & Mc Farlane 1987, Wootton 1990). Ageing of fish is less problematic in temperate and subtropical waters (Le Roux 1961, Bruton & Allanson 1974) than in tropical waters (Lowe 1952, Garrod 1959, Tweddle &Turner

1977, Morh 1994, Booth *et al.* 1995). Several authors have discussed the validity of annuli in otoliths, scales, spines, and vertebrae. In tropical waters attribute ring formation is generally attributed more to a "physiological winter", due to scarcity of food and to the periodicity of spawning, than to a climatic winter.

Otoliths, scales, spines and vertebrae are used to age fish, with varying degrees of success (Summerfelt & Hall 1987, Weatherley & Gill 1987). For example, scales have been found to underestimate longevity and therefore overestimate growth rate (Farade 1974, Pannella 1974 Hecht 1980a, Goeman *et al.* 1994, Quick & Bruton 1984, Booth *et al.* 1995). Spines, in particular, have been used to age catfish (e.g., *C. gariepinus*), but reabsorption and the resultant increase in lumen diameter renders them useless to age older fishes (Quick & Bruton 1984). Sectioned otoliths are currently considered the most suitable hard tissues for determining age of fish in tropical and subtropical areas (Hecht 1980a, 1980b, Beamish & McFarlane 1987, Hammers & Miranda 1991, Booth *et al.* 1995).

Growth and reproduction are complementary processes (Wootton 1990). The process of natural selection leads to selection for growth that tends to maximise the lifetime production of offspring (Matthews 1998). Further, within the framework of growth and reproduction, the onset of maturity represents a critical transition in the life history of an individual. At this stage, resources are partitioned between reproduction, survival and growth.

Timing of reproduction is another important life-history trait in fish. For each species or stock, the timing of annual spawning has evolved to ensure that the young hatch and

commence feeding at a time that is most conducive to their survival (Bye 1984). Thus there is a strong selection pressure on accurate reproductive control.

Life-history traits of *B. nyasensis* have not previously been investigated. This chapter provides information upon which to relate the feeding biology of the species to other important aspects of its life history.

3.2 MATERIALS AND METHODS

3.2.1 Age and growth

Samples of *B. nyasensis* were obtained during research and commercial trawl cruises of the FRU Ndunduma in the south east arm of Lake Malawi (Figure 2.1), on a monthly to bimonthly basis between December 1996 and November 1998. The FRU Ndunduma is a 17.5-m multipurpose research vessel powered by a single caterpillar engine of 386 hp.

Demersal trawling gear was used to obtain the samples. The gear used consisted of a Gulloppur bottom trawl net with a headrope of 23 m, with a vertical opening of 4 m and a cod-end mesh size of 38 mm. The trawling speed was approximately 3 - 3.5 knots and the duration of the research and commercial trawls were 0.49 $\pm$ 0.1 hours (range 0.25 – 0.67 hours, n=36) and 2.1 $\pm$ 0.84 hours (range 0.73 - 4.25 hours, n=49) respectively. The depths at which fishing took place was 35.9 $\pm$ 28.4 m (range 8 - 122m), and 53.6 $\pm$ 18.8m (range 8 - 98m) for research and commercial trawls, respectively.

Catches of *B. nyasensis* for the various hauls were variable and ranged from zero to more than 50 fish per haul. Where more fish were caught than could be processed between

hauls, samples were removed from all size classes. Twenty to 100% of the fish caught in each haul were collected and worked up.

Fish were measured for total length (TL) and standard length (SL) to the nearest mm and weighed whole to the nearest (g). Both pectoral spines and sagittal otoliths were removed from 247 specimens (223-1025 mm TL). After removal, the otoliths and spines were stored in marked envelopes for measurements, sectioning and age estimation. Otolith length was measured to the nearest 0.01 mm using Mitutoyo digitized calipers.

The relationship between weight and length of male and female fish was determined using the following formulae (Lagler *et al.* 1977):

$$W = aL^b \qquad \text{Equation 3.1}$$

where: W = weight (g);
L = total length (TL, cm);
and a and b are constants.

The relationship of otolith length to total length was estimated by the following equation (Griffiths & Hecht 1995):

$$OL = xL + z \qquad \text{Equation 3.2}$$

where: OL = otolith length (mm)
L = total length (mm)
and x and z are constants.

To estimate age, spines were mounted in clear polyester casting resin then, using a double-blade diamond-edged saw, sectioned to 0.2 - 0.5 mm at approximately $^2/_7$ of the spine length from the base as recommended by Bruton and Allanson (1980). Preparation of the otoliths followed that described by Griffiths and Hecht (1995), Booth and Merron (1996). The otoliths were burnt over a low-intensity ethanol flame until they turned light brown. This was done to enhance visibility of otolith rings. Care was taken not to char the otoliths, as this tends to obscure the internal structure and margin of otoliths. The otoliths were mounted in clear polyester casting resin rods and sectioned transversally through the nucleus to 0.2 - 0.5 mm, using a double-blade diamond-edged saw.

Otolith and spine sections were mounted on glass slides with DPX mountant and were viewed with a light microscope (Olympus BX 40), under transmitted light using variable magnification.

Comparison of hard tissues for age determination

In order to assess the suitability of spines and otoliths for ageing *B. nyasensis,* a subsample of sectioned sagittal otoliths and pectoral spines from 101 fish (223-805 mm TL) was used for comparison. The number of opaque zones on the two tissues was read on two occasions after three weeks without reference to the identity of the fish. A mean age was accepted if the number of rings for each of the two readings were equal or their difference was less than two.

Campana *et al.* (1996) noted that some measure of precision is necessary to assess the relative ease of determining the age using a particular structure, or to assess reproducibility of an individual's age determinations, and comparing the skill of one age

reader with that of another. There are two methods with which precision can be estimated: the average percent error method and the percent agreement method. Beamish & Fournier (1981) suggested that the index of average percent error (IAPE) is the better method for assessing the precision of age determinations compared to the percent agreement method, since the latter does not evaluate the degree of precision equally for all species. The average percent method can be calculated for age determination by the same reader or different readers and does not necessarily imply that the age estimates are accurate, but only relates to consistency between the age readings.

According to Beamish and Fournier (1981), if N fish are aged and R is the number of times each is aged, then X_{ij} is the ith age determination of the jth fish and X_j the average age calculated for the jth fish:

$$X_j = \frac{1}{R}\sum_{i=1}^{R} X_{ij} \qquad \text{Equation 3.3}$$

The average error in ageing the jth fish, as a fraction of the average of the age estimates, (APE) is

$$\text{APE} = \frac{1}{R}\sum_{i=1}^{R}\left(\frac{|X_{ij} - X_j|}{X_j}\right) \text{x } 100 \qquad \text{Equation 3.4}$$

The IAPE is calculated as

$$\text{IAPE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}\right] \text{x } 100 \qquad \text{Equation 3.5}$$

Greater precision is achieved as the percent error is minimised.

Chang (1982) suggested the use of a coefficient of variation (CV) for testing the reproducibility of ageing between readers. This can be done by replacing the average absolute deviation from the arithmetic mean in Equation 3.5 with the standard deviation. The percent error contributed by each observation to the average age-class may be estimated by an index of precision (D), which is the CV divided by $\sqrt{R}$, thus the percent error in each age can be obtained by multiplying the index of precision (D_j) by the average age for the jth fish.

Validation of annuli

The outer margins of spines and otoliths, sampled at monthly intervals were examined to determine periodicity of ring formation. To ensure that the margins were correctly identified, the margins were examined on two or three occasions. The composition of the outer margin was accepted if on at least two occasions similar identification (either opaque or translucent) was made. The number of spines or otoliths with opaque zones was expressed as a percentage of the monthly sample.

Growth parameter estimation

The hard tissue that provided greater precision as indicated by the lowest average percent error and CV was chosen for subsequent age analysis. Following Weyl (1998) a third reading was taken on the sample of the chosen hard tissue so that a mean of any of the two readings that were equal or less than two was taken as the final estimated age.

The recommendations by Punt and Hughes (1992) for determining and fitting appropriate growth models were followed in fitting models to data. The non-parametric one-sample-runs test was used to determine randomness and the Bartletts test was used to test for homodescacity (Hughes 1986). Variance estimates were calculated using the (conditioned) parametric bootstrap resampling method (Efron 1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were calculated from bootstrap data using the percentile method described in Buckland (1984). PC-YIELD 2.2 (Punt & Hughes 1992) was used to execute the procedure. This software uses a non-linear minimisation routine (simplex method) to obtain parameter estimates for selected growth models. While it was desirable to fit the von Bertalanffy growth model to the data, the model was inappropriate having large sum of squared residuals, and it was found that the four-parameter Schnute model (Schnute 1981) produced a better fit. The growth model is described by the following equation:

$$\ell(t) = [\ell_1 + (\ell_2^b - \ell_1^b) \frac{1 - e^{-a(t - t_1)}}{1 - e^{-a(t_2 - t_1)}}]^{1/b} \qquad \text{Equation 3.6}$$

where: $\ell(t)$ = the length at age t

t_1 = the smallest age in the sample

t_2 = the largest age in the sample

ℓ_1 = the value of $\ell(t)$ at time $t = t_1$

ℓ_2 = the value of $\ell(t)$ at time t = t2

a = parameter

b = parameter

3.2.2 Sexual maturity and reproductive periodicity

Fish were measured and weighed, to the nearest mm TL and (g), respectively, on a monthly basis. The fish were dissected and sexed, and the gonads were removed and weighed to the nearest 0.001 g. In order to determine size-at-maturity, the gonads were categorised as mature or immature following the criteria in Table 3.1.

Table 3.1. Macroscopic criteria used to stage the gonads of *Bathyclarias nyasensis* as immature and mature (modified from Bruton 1979). Gonads were placed in either of the two different categories if they fulfilled any of the detailed conditions.

Stage	Macroscopic appearance
Immature	**Males** • Minute gonads close under the vertebral column • Testes elongate threads • Sexual products have not yet begun to develop • Testes are transparent **Females** • Minute gonads close under the vertebral column • Ovaries elongate threads • Sexual products have not yet begun to develop • Ovaries are transparent or translucent pink • Eggs invisible to naked eye.
Mature	**Males** • Testes enlarged and white, opaque or pinkish orange, with gray proximal edging • Testes deflated, gray–white sacs • Testes turning darkish at margins **Females** • Eggs visible to naked eye as round and yellow • Ovary wall transparent • Ovaries distend the body cavity • Sexual products have been discharged, ovary dark red with a few remaining eggs.

To determine the mean length at 50% maturity, the proportion of sexually mature individuals (ψ) at length (L) was fitted to the logistic curve:

$$\psi = \frac{1}{1 + e^{-(L - Lm_{50})/\delta}} \qquad \text{Equation 3.7}$$

where: Lm_{50} = total length at 50% sexual maturity

δ = width of the logistic ogive.

The age at 50 % maturity was calculated from the length-at- 50% maturity using a transformation of the Schnute growth model, represented by:

$$t = \left[\frac{\ln\left(1 - \frac{(l_{(t)}{}^{b} - l_1^{b}) x (1 - e^{-a(t_2 - t_1)})}{l_2^{b} - l_1^{b}}\right)}{-a} \right] + t_1 \qquad \text{Equation 3.8}$$

where t = age at-50% maturity (years)

$\ell(t)$ = the length-at-50% maturity (mm)

t_1 = the smallest age in the sample

t_2 = the largest age in the sample

ℓ_1 = the value of $\ell(t)$ at time $t = t_1$

ℓ_2 = the value of ℓ (t) at time $t = t_2$

a = parameter

b = parameter

Temporal patterns in reproductive activity were assessed using monthly gonadosomatic index values (Wootton 1990). Gonadosomatic index (GSI) was expressed as:

$$GSI = \left[\frac{\text{Gonad weight (g)}}{\text{Total mass (g)}} \right] \text{x } 100 \qquad \text{Equation 3.9}$$

While the principal focus of the study of reproductive biology was to determine the sexual maturity and spawning periodicity of *B. nyasensis,* it was later considered that data on egg size and number and fecundity would confirm the life-history strategy *of B. nyasensis*. Egg size and number and fecundity, therefore, were determined on a limited number of specimens that were obtained and preserved during the study (n=5). While the fecundity estimates can at best be regarded as preliminary they do provide valuable inforrmation upon which to describe the life-history style of *B. nyasensis*.

Fecundity, the number of eggs per kg of fish (Encina & Granado-Lorencio 1997) was obtained by counting eggs that were preserved in 10 % formalin. The total weight of the gonads was taken and eggs from a 2 g subsample were counted. The total number of eggs per gonad was obtained by:

$$\text{Number of eggs per gonad} = \left[\frac{\text{Gonad weight (g) x number of eggs in subsample}}{2\text{ g}}\right] \quad \text{Equation 3.10}$$

and fecundity (eggs/kg) was obtained by:

$$\text{Fecundity (eggs/kg)} = \left[\frac{\text{number of eggs in gonad}}{\text{Total mass of fish} - \text{weight of gonads(kg)}}\right] \quad \text{Equation 3.11}$$

Since fish may lose condition during spawning (Encina & Granado-Lorencio 1997), monthly condition factors can be used to confirm seasonal spawning trends. Following the recommendations by Bolger and Connolly (1989), monthly condition factors (CF) were calculated as follows:

$$CF = \frac{\text{Body mass (g)}}{\text{Total length (cm)}^3} \quad \text{Equation 3.12}$$

3.3 RESULTS

3.3.1 Age and growth

The relationship between length and weight of *B. nyasensis* is summarised in Table 3.2 and shown in Figure 3.1.

Table 3.2. Length/weight relationship for *Bathyclarias nyasensis* from Lake Malawi (TL = total length (mm), Wt = weight (g)).

Sex	Relationship	r^2	p	n
Male	$Wt = 0.0045 \times TL^{3.113}$	0.972	<0.001	377
Female	$Wt = 0.0035 \times TL^{3.192}$	0.974	<0.001	458
Combined	$Wt = 0.0039 \times TL^{3.161}$	0.973	<0.001	835

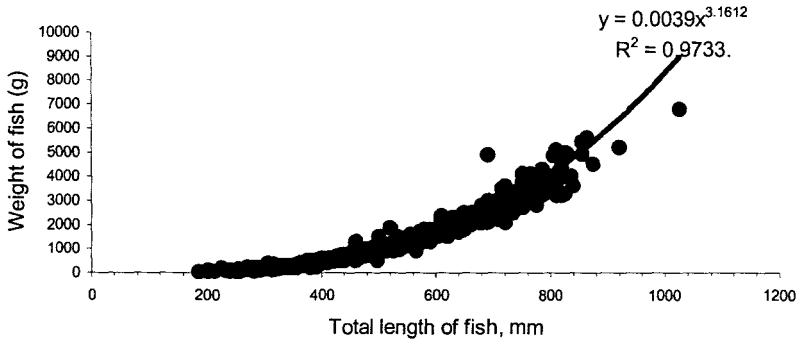


Figure 3.1. Length/weight relationship of *Bathyclarias nyasensis* (n=835).

The relationship of otolith length to fish total length relationship was given by the equation:

$$OL = 0.0008TL + 1.1978 \ (r^2 = 0.8974, n = 239) \qquad \text{Equation 3.13}$$

where: OL = otolith length (mm)

TL = length of fish (mm)

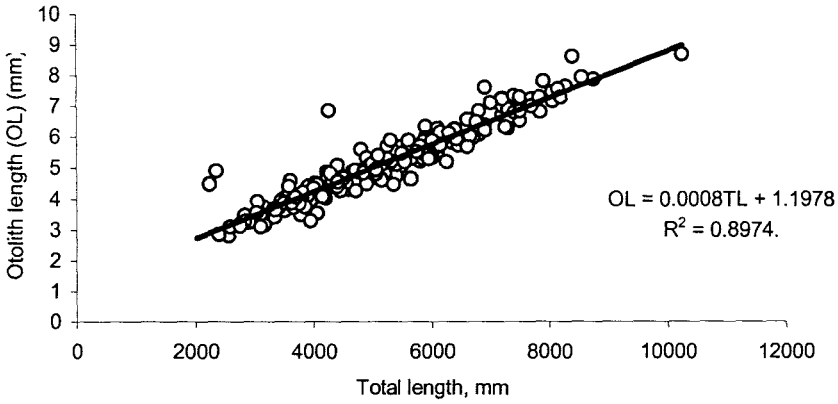


Figure 3.2. Relationship between otolith length/fish total length for *Bathyclarias nyasensis* (n=239).

Comparison of the hard tissues to estimate age

Of the 101 sectioned pectoral spines and sagittal otoliths used for comparison, 37 (36.6%) and 30 (29.7%) samples were rejected as unreadable, respectively. The high rejection rate of spines was a consequence of the reabsorption of material in the lumen (see Figure 3.3a). There was a marked dissimilarity in the number of rings between sectioned spines and otoliths (Table 3.3). A maximum age of 13 was obtained using the spines as opposed to 23 years using sectioned otoliths. Although the % APE, CV and index of precision (*D*) of spines and otoliths were not different (Table 3.4), otoliths only were used in subsequent analyses, since: a) spines showed reabsorption of growth zones with increasing lumen diameter (Figure 3.4); b) at least a high number of otoliths which could be aged reliably (Table 3.4), and c) otoliths showed discernible outer margins, unlike spines, which permitted use of marginal analysis for validation of annular rings.

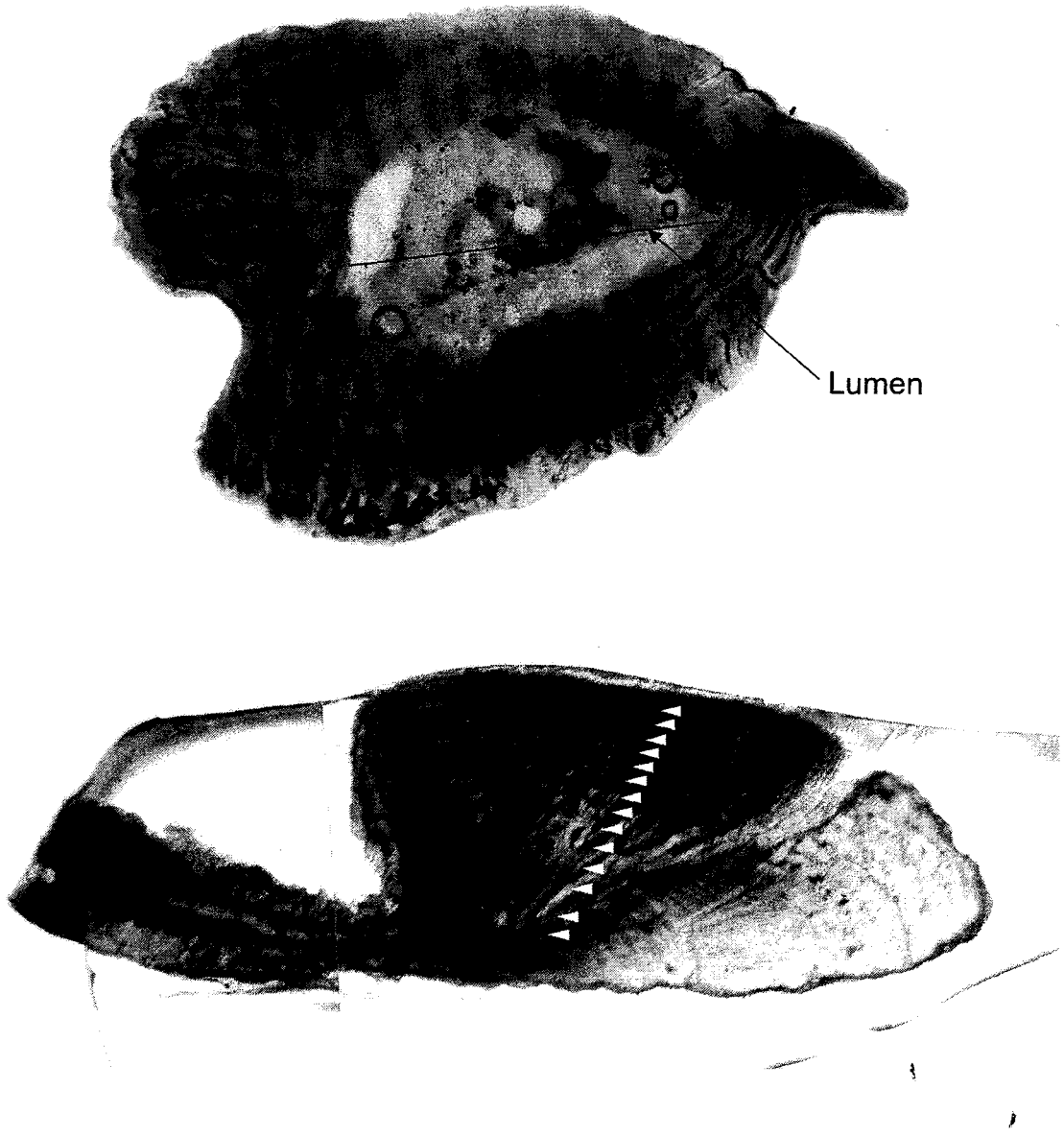


Figure 3.3. Photographs of (a) pectoral spine, and (b) sagittal otolith with 15 opaque zones from a 760 mm TL *Bathyclarias nyasensis*. Note that the size of the lumen in the spine (arrow) may have reduced the number of the opaque zones (x 100).

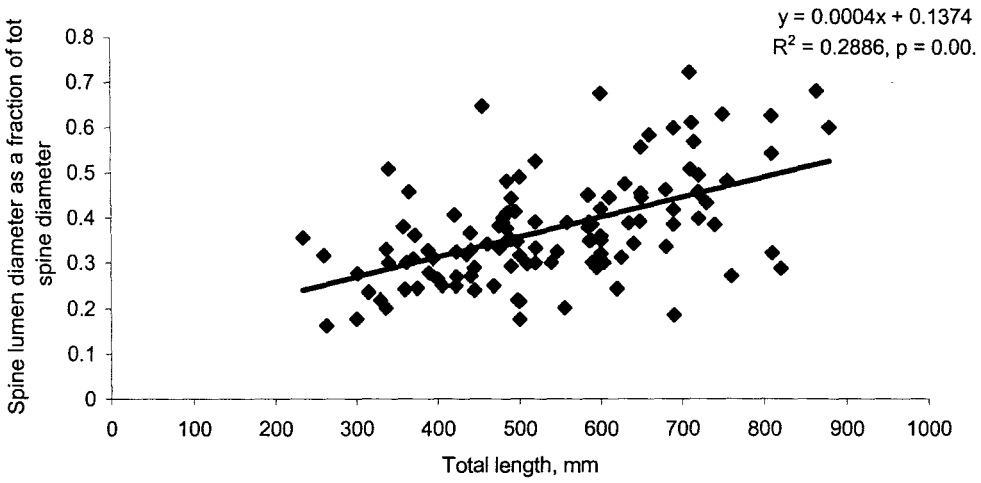


Figure 3.4. Ratio of spine lumen diameter to total spine diameter for different size classes of *Bathyclarias nyasensis* (n = 115).

Interpretation and validation of otolith growth zones

Growth zones in otoliths was noted optically as a succession of wide and opaque zones separated at regular intervals by narrower translucent zones (Figure 3.3b). Of the 247 single otoliths examined 70 (28.3%) were rejected as unreadable, while 15 (6.1 %) could not be aged reliably and were rejected. As a result, 162 (66 male and 96 female), provided reliable estimates and were used for estimation of growth parameters.

The monthly examination of the otolith margins revealed that two opaque zones are laid down annually, one during March and the other during August. Therefore, two opaque zones represent one year of growth and all counts of growth rings were divided by 2. A length-at-age key for *B. nyasensis* is presented in Table 3. 5.

Table 3.3. Sample size, total length (TL, range) and observed lengths-at-age (TL±standard error) determined from sectioned pectoral spines and sagittal otoliths of *Bathyclarias nyasensis* from Lake Malawi.

Age (year)	Sectioned spines			Sectioned otoliths		
	N	TL (Range) (mm)	Mean TL ± SE	N	TL (Range) (mm)	Mean TL ± SE
1	-	-	-	-	-	-
2	-	-	-	2	370 – 380	375 ± 9
3	4	320 – 440	373 ± 26	6	370 – 590	436 ± 35
4	7	360 – 510	438 ± 23	4	330 – 550	461 ± 47
5	4	350 – 400	379 ± 12	8	230 – 640	411 ± 40
6	6	220 – 490	362 ± 35	6	220 – 630	468 ± 63
7	6	420 – 600	504 ± 26	9	360 – 750	544 ± 42
8	10	450 – 810	571 ± 34	5	320 – 660	479 ± 59
9	1	630	630	7	440 – 690	559 ± 82
10	4	490 – 770	628 ± 58	6	420 – 740	559 ± 47
11	1	560	560	5	430 – 730	578 ± 53
12	-	-	-	-	-	-
13	3	690 – 730	713 ± 12	-	-	-
14				-	-	-
15				1	760	760
16				2	730 – 810	768 ± 38
17				2	690 – 750	720 ± 30
18				2	530 – 720	626 ± 94
19				-	-	-
20				-	-	-
21				-	-	-
22				-	-	-
23				1	790	790

Table 3.4. Summary of the results for the comparison of age estimates of *Bathyclarias nyasensis* using two different hard structures.

Hard structure	Average percent error (APE %)	Coefficient of variation (CV %)	Index of precision (D)	Number rejected as unreadable	% sample rejected for low reliability in age determination
Sectioned spines	14.8	10.5	7.4	36.6	29.7
Sectioned otoliths	14.2	10.0	7.1	29.7	7.0

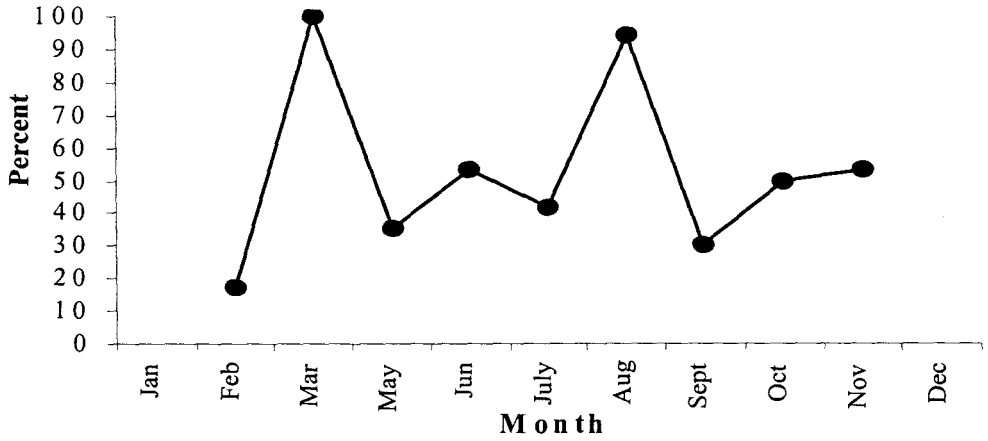


Figure 3.5. Monthly percent occurrence of an opaque margin in otoliths of *Bathyclarias nyasensis*(n = 130).

Growth parameter estimation

There were no significant differences in the growth models between male and female *B. nyasensis* ($p>0.05$). The growth parameters, their associated estimates of variation and confidence intervals from the Schnute model are summarised in Figure 3.6 and Table 3.6.

The near linear length-at-age growth curve after first year observed in this study has been observed in some populations of *Clarias gariepinus* in Southern Africa (Van der Waals & Schoonbee 1975, Clay 1984). Typically, in such growth curves, there is a period of rapid rate of growth in the first two years. After two years growth curve appear linear. In

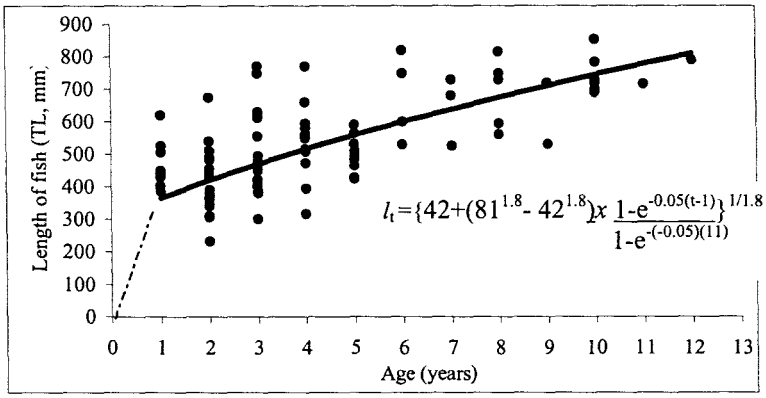
Table 3.5. Length-at-age key for *Bathyclarias nyasensis* from Lake Malawi.

Length (cm TL)	Age(years)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
20-29.9		1	1												
30-39.9	5	15	6	4	1										
40-49.9	7	9	15	3	9										
50-59.9	2	5	7	11	8	3	1	2	1						
60-69.9	1	3	4	3	2	3	2	1	0	1					
70-79.9			3	1	0	3	2	2	1	4	1	1			
80-102.5						1	0	2	0	1	0	3	0	1	
N	15	33	36	22	21	10	5	6	2	6	1	4	0	1	162

Table 3.6. Schnute model growth parameter estimate, standard error (SE) and 95% confidence interval (CI) for male and female *Bathyclarias nyasensis* (*Note*: L_∞ = asymptotic length).

	Males			Females		
Parameter	**Estimate**	**SE**	**95% CI**	**Estimate**	**SE**	**95 % CI**
a	-0.02	0.12	-0.21, 0.34	-0.05	0.09	-0.25, 0.11
b	1.20	1.58	-3.99, 4.00	1.76	0.66	0.58, 2.66
ℓ_1	40.74	2.77	34.63, 45.69	41.62	2.54	36.33, 95.03
ℓ_2	98.18	7.39	83.97,113.52	81.03	5.97	71.09, 95.03
L_∞	98.18	7.39	83.97,113.52	81.03	5.97	71.09, 95.03
t_o	N/A			N/A		
K	0			0		
t_1	1			1		
t_2	14			12		

(a)



(b)

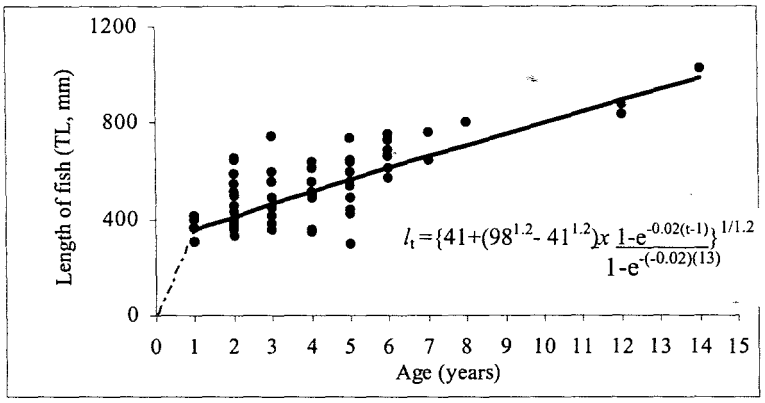


Figure 3.6. Observed individual lengths-at-age and Schnute growth curve for *Bathyclarias nyasensis*, determined from sagittal otoliths of (a) female and (b) male fish.

Clarias populations with such growth curves, length-at-age data did not fit the von Bertalanffy growth formula. In this study, the rapid growth rate was noticeable in the first year, and thereafter the growth curve appeared linear, accounting for a K value of zero.

3.3.2 Sexual maturity and reproductive seasonality

Of the 326 mature *B. nyasensis* sampled, 47 % were female and 53% were male. The sex ratio was 1:1.13 females to males, which was not significantly different from unity (χ^2 = 0.18, df = 1, >0.05). The length at 50 % maturity for males as estimated from the ogive was 532.5 mm TL, while for females it was 639.5 mm TL (Figure 3.7 a & b); from the Schnute growth model, these represented ages 4 and 7 years, for males and females, respectively.

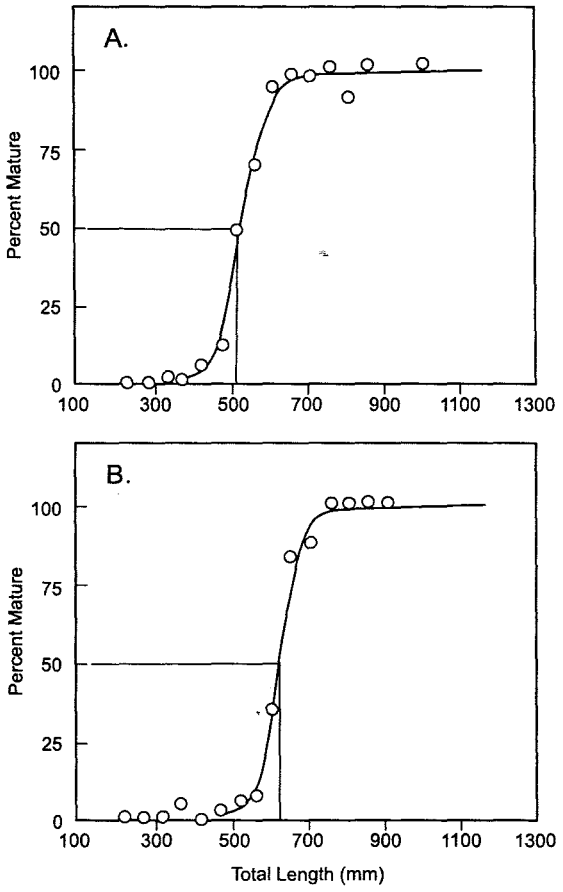


Figure 3.7. Sexual maturity in (a) male (n=363) and (b) female (n=454) *Bathyclarias nyasensis.*

It is apparent from GSI values (see Figures 3.8) that these fish breed during the summer, warm-wet period (December – February).

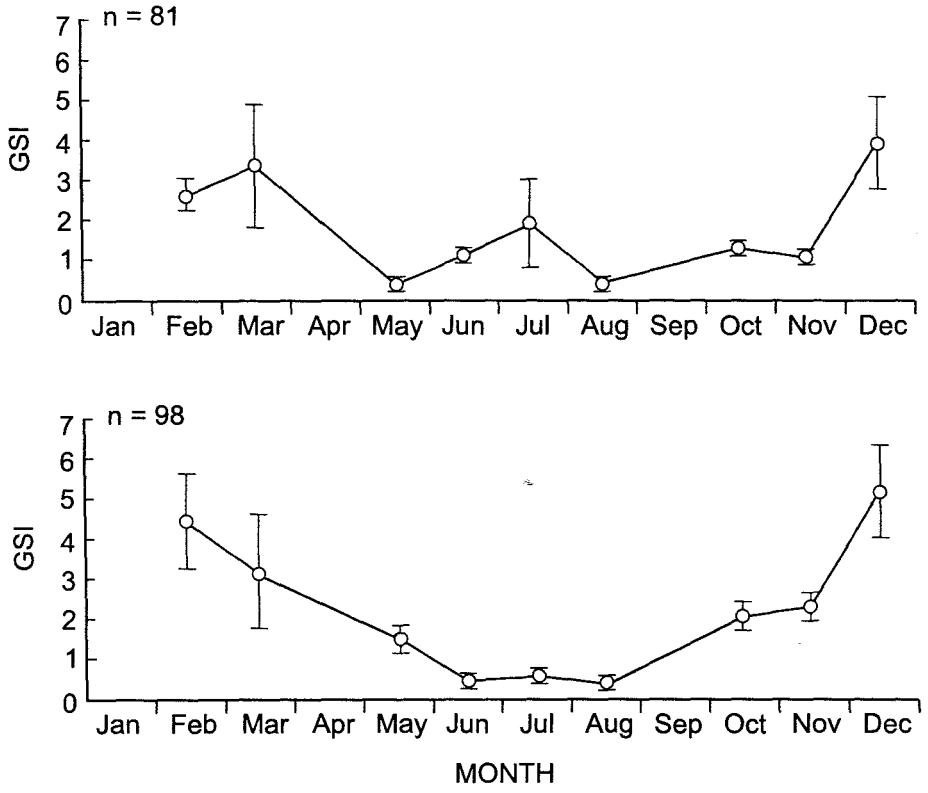


Figure 3.8. Mean monthly GSI values (± SD) for *Bathyclarias nyasensis* (top, males; bottom, females).

It can be inferred from Figure 3.9 that condition of fish dropped during the same warm-wet season. The mean condition factor of fish for the months October-December was significantly lower ($p<0.05$) than for the months July-September.

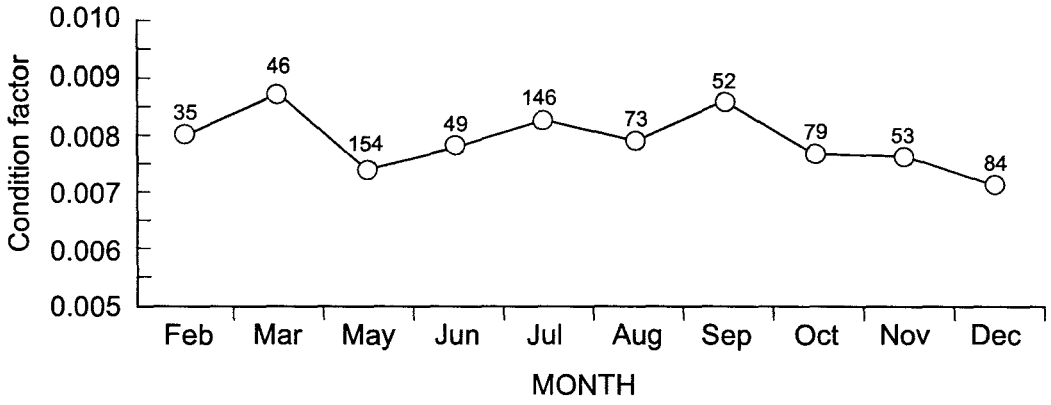


Figure 3.9. Condition factors (CF) of *Bathyclarias nyasensis* in different months (number of samples in each month is provided above the data point).

The mean fecundity value for *B. nyasensis* was calculated at 14267 (range 7485-18864 eggs/kg of mature fish); mean egg size was 2 mg (Table 3.7).

Table 3.7. Fecundity (eggs/kg) of *Bathyclarias nyasensis*

Specimen	TL (mm)	Wt of fish (kg) (minus gonad weight)	Wt of gonad (g)	No of eggs in 2 g sample	Mean egg weight (mg)	Total no. of eggs/ gonads	Fecundity (Eggs/kg)
1	985	5.836	164.19	729	2.74	59847	9974
2	660	2.026	73.78	984	2.03	36300	17285
3	605	2.285	64.86	1367	1.46	44332	18864
4	720	1.566	34.12	702	2.85	11976	7485
5	770	3.903	96.57	1584	1.26	76483	19121
6	820	4.604	96.04	1259	1.59	60457	12863
Mean (± SD)					2.0 (0.67)		14267 (4903)

DISCUSSION

Life-history traits of *B. nyasensis* have been previously reported by Bertram Ricardo *et al.* (1942), Lowe (1952) and Thompson *et al.* (1995). Bertram and Ricardo (1942) and Thompson *et al.* (1995) reported maximum lengths for these fish at 970 mm TL and 1070 mm TL, respectively. Lowe (1952) predicted that *B. nyasensis* had the potential to reach 300 mm in the first year. Lowe (*op cit.*) also reported that sexual maturity occurs at a size 500 mm TL and that spawning takes place in November. However, the observations by Bertram Ricardo *et al.* (1942), Lowe (1952) and Thompson *et al.* (1995) were anecdotal reports in their investigations on many fishes of Lake Malawi, and can not be used with confidence to describe the life history-style of *B. nyasensis.*

Since very little is actually known about the biology, in particular about the feeding biology of *B. nyasensis*, information on the African catfish *Clarias gariepinus,* another silurid, may provide insight into life-history traits of *B. nyasensis,* especially the environmental factors that are likely to affect growth and reproduction of the species. Comparative growth rate, and size-at-maturity of some *C. gariepinus* populations from South Africa are provided in Tables 3.8 and 3.9.

Table 3.8 shows a higher growth rate for *B.* nyasensis in the first year than for *C. gariepinus,* but significantly lower in subsequent years. The size-at-maturity of *B. nyasensis* was comparable to *C. gariepinus*, although bi-maturism (males and females maturing at different ages and sizes) was only was only observed in a limited number of *Clarias* populations.

Table 3.8. Comparative growth rates of *Bathyclarias nyasensis* and *Clarias gariepinus* populations (Bruton 1979, Quick & Bruton 1984) in South Africa (TL in cm and wt in g); (a) males and (b) females.

(a) Males

	Clarias gariepinus P.K. Le Roux Dam			*Clarias gariepinus* Lake Sibaya			*Bathyclarias nyasensis* (L. Malawi, this study)		
Year	TL	ΔTL	WT	TL	ΔTL	WT	TL	ΔTL	WT
1	21.3	21.3	53	24.0	24.0	97	35.5	35.5	301
2	32.1	10.8	198	39.9	15.9	419	40.9	5.4	468
3	41.3	9.2	446	51.7	11.8	843	46.1	5.2	680
4	52.0	10.7	939	57.5	5.8	1123	51.2	5.1	942
5	68.3	16.3	2263	62.9	5.4	1431	56.2	5.0	1259
6	80.3	12.0	3817	65.9	3.0	1623	61.1	4.9	1634
7	90.3	10.0	5575	69.5	3.6	1873	65.9	4.8	2067
8	96.4	6.1	6885	72.6	3.1	2107	70.7	4.8	2573

(b) Females

	Clarias gariepinus P.K. Le Roux Dam			*Clarias gariepinus* Lake Sibaya			*Bathyclarias nyasensis* (Lake Malawi, this study)		
Year	TL	ΔTL	WT	TL	ΔTL	WT	TL	ΔTL	WT
1	20.4	20.4	46	24.0	24.0	97	36.4	36.4	334
2	31.3	10.9	182	40.6	16.6	455	41.9	5.5	524
3	40.2	8.9	409	51.2	10.6	852	46.9	5.0	750
4	50.3	10.1	843	56.4	5.2	1107	51.5	4.6	1011
5	63.2	12.9	1762	60.8	4.4	1357	55.8	4.3	1306
6	76.0	12.8	3195	63.9	3.1	1552	59.9	4.1	1637
7	84.8	8.8	4551	64.8	0.9	1612	63.8	3.9	2002
8	89.7	4.9	5457						2396

Table 3.9. Length-at-first maturity of *Clarias* populations, as summarised by Bruton (1979) and Quick and Bruton (1984), compared to *Bathyclarias nyasensis* (this study).

Species	Male (cm, TL)	Female (cm, TL)	Place
C. anguillaris	-	20	Lake Chad, Chad
C. gariepinus	38	38	Zimbabwe
"	43-45	45-48	Vaal River, South Africa
"	35-45	35-40	Elands River, South Africa
"	26	26	Lower Shire River, Malawi
"	65-75	65-70	Hardap dam, Namibia
C. gariepinus	82-92	>74	P.K. le Roux Dam, South Africa
"	80-85	> 90	Verwoerd Dam, South Africa
"	35	35	Lake Sibaya, South Africa
C. lazera	-	25 (SL)	Lake Volta, North Africa
,,	65-70	65-70	Lake Rudolf
C. mossambicus	25-40	25-40	Lake Kyoga
"	50	50	Lake Victoria, East Africa
"	29	26	Lake Chilwa, Malawi
"	30-40	40-44	Lake Victoria, East Africa
C. senegalensis	32	32	Ghana
"	-	27	Lake Kossou, Ivory Coast
B. nyasensis	53	63	Lake Malawi, this study

Explanations of the growth rate of fish are made difficult by its genome, phenotypic plasticity of growth patterns, and the sensitivity of growth to environmental effects, including social interactions (Pudorm 1979). Most studies, therefore, emphasize the importance of environmental factors, such as food availability and temperature, as the

principal cause determining the growth rate of a species (Wootton 1990). Low food availability was regarded as the cause for slow growth of *C. gariepinus* in Lake Sibaya (Bruton 1979). Bruton (*op cit.*) noted that smaller fish in shallower water that preyed on fish grew faster than larger *C. gariepinus* found mainly in deeper waters and that relied on the low-standing crop of zooplankton. Poor food quality and low availability of large prey items was identified as the principal cause of low growth rates and the poor condition of large *C. gariepinus* in deep water. It seems probable that the slow growth rate of *B. nyasensis* (>2 years age) in Lake Malawi may be explained by a similar set of circumstances.

Size at maturity represents a critical stage in life, since food that was previously allocated to somatic growth and survival becomes allocated to reproduction as well (Matthews 1998). This stage occurs late in the life of *B. nyasensis* (mean age 6 years). It can be expected that before sexual maturity, growth may be rapid for up to six years. However, growth is rapid only during the first year; thereafter, it is significantly slower than in all *Clarias* populations for which growth estimates exist (cf. Table 3.7). Thus, it may be hypothesised that young *B. nyasensis* (one year old) must have access to a plentiful or relatively more nutritionally adequate food source, and, thereafter a change to another type of diet (which is not as plentiful or not nutritionally adequate) may occur, that manifests in a slower growth rate during subsequent years. This dietary shift seems to synchronise with the gradual habitat shift of older and larger fish into deep water (Figure 3.10), a typical ontogenetic diet, habitat shift phenomenon.

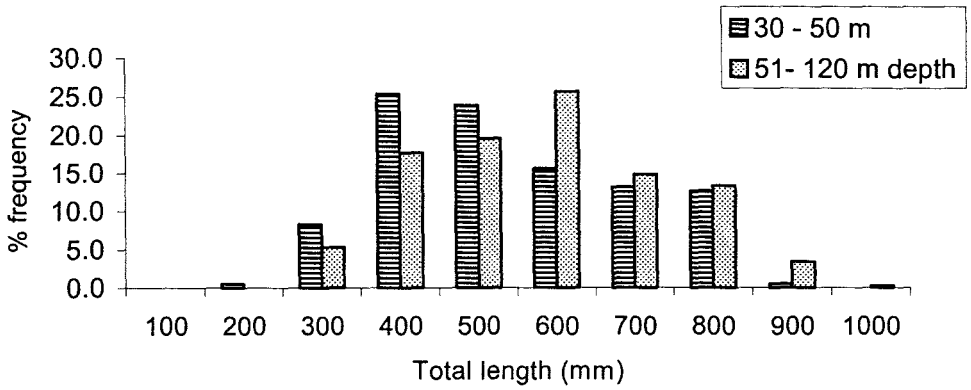


Figure 3.10. Size distribution of *Bathyclarias nyasensis* at different water depths. Note that the peak frequency for fish in shallower waters (30–50m) is for fish approximately 400 mm TL, in contrast to fish in deeper water, of approximately 600 mm TL, (n=775).

The breeding season of *B.* nyasensis (December to March) is typical of warm-water species regarded as summer spawners (Lagler *et al.* 1977). The low condition factor observed during the summer period (Figure 3.9) could confirm the summer breeding season on the assumption that the fish have diverted energy for gonadal development and spawning activity (Encina & Granado-Lorencio 1997). *C. gariepinus* in the Shire River, Malawi (Willoughbouy & Tweddle 1978), and in Lake Sibaya (Bruton 1979) also breed during the summer period (November to March), with peak breeding occurring in December. In Lake Sibaya, reproductive activity was related to rainfall and temperature. *C. gariepinus* spawned when water temperatures were approximately 22°C and usually after heavy rains at night (Bruton 1979). It seems probable that similar environmental cues that trigger spawning in *C. gariepinus* also trigger this event in *B. nyasensis* as the

spawning period of the latter coincided with the warm-wet season described in Chapter 2. Figure 3.11 shows that GSI increased in synchrony with the rise in temperature a rise temperature and amount of rainfall, particularly in December.

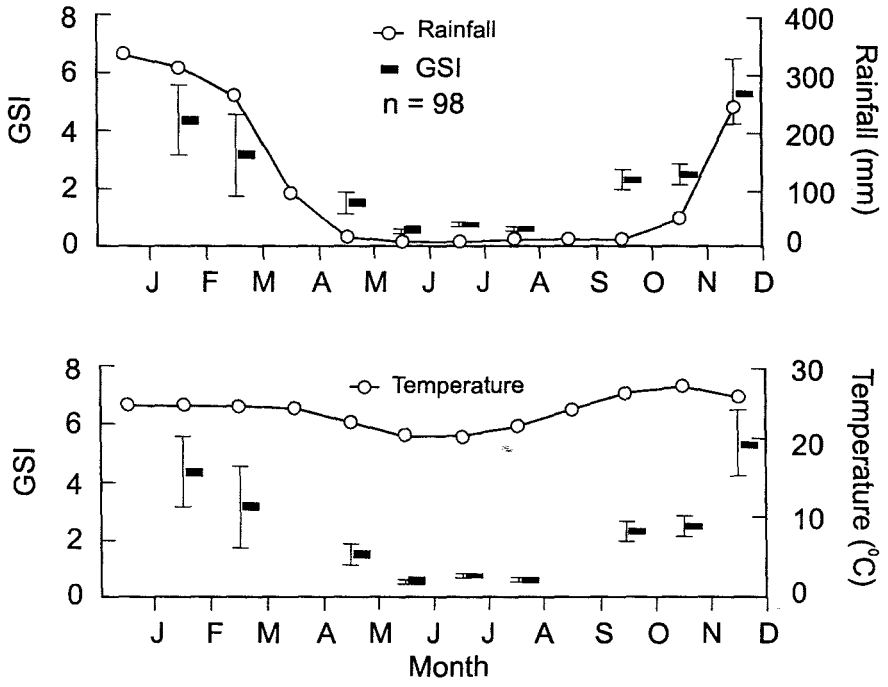


Figure 3.11. The temporal variation in gonadosomatic index (GSI) of *Bathyclarias nyasensis* and mean temperature (top) and monthly rainfall totals in Lake Malawi (bottom). Meteorological data obtained from the weather station at Salima (Paterson & Kachinjika 1995).

Life-history traits are "central to both theoretical ecology and resource management" (Winemiller & Rose 1992). Insights into the evolutionary response of life-history parameters to different environmental conditions and spatio-temporal changes usually come from two approaches: theoretical models of life history evolution (e.g., Roff 1984) and analyses of empirical patterns (e.g., Roff 1988, Paine 1990). Both of these approaches have rely to a large degree on the r-K continuum as proposed by Pianka (1970) or similar multidimensional schemes (e.g., bet-hedging) and iteroparity-semelparity (Schaffer 1974), and ALPREHOSRT (Balon 1975) as the basis for comparing alternative life history strategies. Winemiller (1989) and Winemiller and Rose (1992), suggested that the original r- verses –K dichotomy of reproductive strategies (Pianka 1970) failed to tie life-history traits to habitat; rather, the authors suggested three basic life history strategies in freshwater fish, viz. periodic, equilibrium and opportunistic strategies. A synthesis of the r-K, altricial-precocial and periodic, equilibrium and opportunistic life history strategies is provided below in an attempt to better define the life-history strategy of *B. nyasensis* in order that predictions of feeding strategies and suggestions for management can be made.

The first part of the r- and K-selection theory is based on assumptions about allocation of a population's resources between competitive and reproductive functions (Gadgil & Bossert 1970). Firstly, it is assumed that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. Secondly, it is assumed that that a species has only a fixed amount of resources available for survival and reproductive functions. These two assumptions result in an inverse relationship between the number of offspring and their average fitness (Crow & Kimura 1970). Therefore, the best reproductive strategy becomes a compromise between two conflicting demands: Production of the largest possible total number of offspring (r-selection), and

the production of offspring with the highest possible fitness (K-selection). The particular point of compromise for any species will be a function of the selection pressures operating on the species and, hence, would be that species' position on the r- and K-continuum.

The second part of the theory concerns the relationship between life history strategies of a species and the habitat that it occupies (Southwood *et al.* 1974, Southwood & Commins 1976). If mortality is variable and/or unpredictable (i.e., density independent), individual competitive fitness is of relatively lesser importance; then, the best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (r-selection).

The contrasting situation occurs in an environment wherein mortality is density dependent. Mortality under these circumstances will result in strong selection for individual fitness; there will be pronounced differences between the effect on different phenotypes. In stable environments, the optimal strategy is to produce offspring with substantial competitive ability (K-selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are points on a continuum. Species will always have a number of different selection pressures operating on them, both spatially and temporally. Natural selection will favor non-reproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages of the life history, thereby maximising overall survival (Crow & Kimura 1970). A change in allocation of a species' resources from reproductive to competitive activities enhances the chances of survival of

future offspring. As a result, organisms under different selection pressures will have characteristic life-history patterns. An r-selected species will employ strategies that tend toward productivity while K-selected species will have life strategies that tend toward efficient exploitation of a specific limiting resource (Pianka 1974).

A species that is exposed to a large component of non-selective or catastrophic mortality (an unpredictable environment) would have characteristics that are selected for increased productivity. An increase in productivity through reproductive activity generally implies: early maturity, rapid growth, production of larger numbers of offspring at a given parental size and maximum production of offspring at an early age (Gadgil & Bossert 1970). Other characteristics resulting from allocations of large portions of resources to reproductive activity are: small body size, high rate of mortality, and a shorter life span (Pianka 1974, Gadgil & Solbrig 1972). In terms of commonly measured population parameters in fishery biology, an r-selected species will have: a low age at first maturity, a high value of k from the von Bertalanffy growth equation, a small maximum size, high rates of instantaneous natural mortality (M), and low maximum age (Adams 1980).

Even in a stable environment where mortality is density dependent, increased allocation of resources towards competitive activities will only occur when two prerequisites are met (Schaffer & Gadgil 1975). The first is that the reproductive potential increases with some function of age. The second is that there is an additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with K-strategists are: delayed maturity, reduced growth rates, low mortality rates large body size and longer life span. In terms of fishery biology, K-strategists will therefore have: a high age at maturity, a low k value from the von Bertalanffy growth equation, a large maximum size, low natural mortality and a high maximum age (Adams 1980).

The concept of ALPREHORST homeorhetic states (Bruton 1989) reflects the epigenetic processes responsible for the r- and K-selection patterns. The arguments are that according to breeding modes and early ontogeny, the basis of epigenesis should be investigated if mechanism behind alternative life-history styles are to be elucidated, since the success of reproduction and early development determines the success of all subsequent events in life (Balon 1975, 1986). Hence "studies which deal only with the definitive phenotype (juvenile and adult) cannot possibly lead to an understanding of the self-organising processes of life" (Bruton 1989). Altricial fishes produce small, incompletely developed young and are generalists capable of surviving in unstable, crowded environments in which they are subjected to density-independent mortality. Precocial forms produce large, well-developed young and are specialists best able to survive in a stable environment that is characterised by density-dependent mortality.

In the triad life-history scheme proposed by Winemiller (1989) and Winemiller & Rose (1992), the "periodic" strategy describes fishes with delay maturation, in order to attain a size sufficient for the production of a large clutch and high adult survival during periods of sub-optimal conditions (e.g., winter, dry season, periods of reduced food availability). Species with a large clutch size frequently reproduce in synchronous spawning episodes. Synchronous spawning often coincides either with movement into favorable habitats or with favorable periods within the temporal cycle of the environment. Winemiller and Rose (*op. cit.*), also observed that in this group (despite the fact that egg size tends to be small) both larval and young-of-the-year growth rates tend to be relatively fast. This is presumed to reflect encounters with relatively high prey densities. Sinclair (1988) noted that in a stable population losses due to advection are ultimately balanced by the survival

benefits derived from the passage of some fraction of larval cohorts into suitable regions of habits.

In the "opportunistic" life-history strategy, fish appear to place a premium on early maturity, frequent reproduction during a spawning season, rapid larval growth, and rapid population growth and rapid population turn-over rates, all leading to a large intrinsic rate of population increase (Winemiller 1989). Such opportunistic fishes differ markedly from the r-strategists (Pianka 1970) in having the smallest, rather than the largest clutch sizes. Small fishes with early maturation, small eggs, small clutches and continuous spawning are well equipped to re-populate habitats following disturbances or else when faced with continuous high mortality in the adult stage (Lewontin 1965, in Winemiller & Rose 1992). This suite of life-history traits permits efficient colonization of habitats over relatively small spatial scales.

The "equilibrium" strategy (*sensu* Winemiller & Rose 1992) is largely consistent with the suite of characteristics often associated with a traditional K-strategy, i.e. adaptation to life in environments which are resource-limited and where mortality is density-dependent (Pianka 1970). Large eggs and high parental care result in reproduction of relatively small clutches. This results in larger or more advanced juveniles at the onset of independent life. However, the "equilibrium" strategy differs from the traditional K-strategy by involving only fish of small maximum size.

The di- and trichotomous traits of r- and K-selection, and the altricial-precocial and the triad scheme of the "periodic", "opportunistic" and "equilibrium" are summarised in Table 3. 10.

Table 3.10. Predicted life-history traits in the r-K, altricial-precocial, "periodic", "opportunistic" and "equilibrium" strategies.

Life history strategy	Size-at-maturity	Number of eggs	Maximum size	Growth rate
r- selected	Small	high	small	high
K-selected	Large	low	large	low
altricial	Small	high	small	high
precocial	Large	low	large	low
"periodic"	Large	high	large	high in larvae and "young of the year"
"opportunistic"	Small	low	small	high
"equilibrium"	Large	low	small	low

In comparison with other open-water species in Lake Malawi (Table 3.11), the r-K selection life history theory fails to explain the life-history traits of *B. nyasensis*. The relatively large size-at-maturity, large maximum size and relatively slow growth rate are indicative of a K-selected species. However, the high fecundity and smaller egg size are traits of r- selected strategists. Table 3.10). Similarly, the relatively large size at maturity and the high fecundity of *B. nyasensis* (assuming that the number of eggs/kg fish weight obtained accurately represents the species' fecundity), in comparison to other open-water species of Lake Malawi (Table 3.11), suggest that the altricial-precocial dichotomy also does not explain in a straightforward manner the differences in life-history strategies between these species. However, the altricial-precocial scheme does seem applicable when comparing the life-history traits of *B. nyasensis* with those of *C. gariepinus*.

Table 3.11. Life history traits of *Bathyclarias nyasensis* (this study) compared to some open water species of Lake Malawi and *Clarias gariepinus* in South Africa .

Species	K	L_∞ (mm , TL)	Fecundity eggs/kg (± SD)	Egg wt (mg)	Size-at-maturity (mm, TL)
Bathyclarias[a] *nyasensis*	-	800-1070	14267 (4903)	2	500-650
Engraulicypris sardella[b]	0.47-1.64	113	-	-	-
Copadichromis quadrimaculatus[b]	0.65-0.78	120-190	649 (217)	41	150
Diplotaxodon 'big eye'[b]	-	-	602 (172)	41	110
Diplotaxodon elongate[b]	0.84	196	366 (147)	46	140
Rhomphochromis ferox[b]	0.24	490	461 (79)	68	200-250
Rhamphochromis longiceps[b]	0.45	250	288 (44)	70	170
Synodontis njassae[b]	-	-	66733(27423)	0.16	110
Clarias gariepinus[c]			60,000	1.6	200-900 (mean 42) [d]

[a] this study

[b] Thompson *et al.* (1995)

[c] Hecht (1996)

[d] Mean size-at-maturity computed from Table 3.8.

The lower fecundity and the relatively larger size at sexual maturity places *B. nyasensis* on the precocial end of the continuum, while higher fecundity and the smaller size at maturity places *C. gariepinus* on the altricial end of the continuum. Relative to open-waters species of Lake Malawi, it is intriguing to note that *B. nyasensis* perfectly fits the Winemiller (1989) and Winemiller and Rose (1992) "periodic" strategy, viz. maturing at a relatively large size, having a high fecundity, large maximum size, and a high growth rate in the first year.

On the basis of life-history strategies discussed above, a suite of ecological characteristics for *B. nyasensis* may be put forward as hypotheses. Being on the precocial side of the

continuum, relative to *C. gariepinus,* it could be predicted that *B. nyasensis* is more of a specialist in terms of feeding as compared to *C. gariepinus* and that the species lives in a more predictable environment than *C. gariepinus* (Bruton 1989). On the basis of the "periodic" strategy, the larvae and early juveniles may in fact possess fast growth (Winemiller & Rose 1992) and some fraction of the larval cohort may characteristically pass into suitable regions or habitats (Sinclair 1988). A high growth rate for early juveniles is supported by the high growth rate of first year *B. nyasensis* recorded in this study.

In conclusion, results from the study of aspects of age and growth permit the prediction that *B. nyasensis* undergo ontogenetic diet changes that may be synchronised with a habitat shift. If the hypothesis is accurate then this may explain the rapid growth of fish in the first year and slow growth in subsequent years. The current analysis of life-history strategies shows that life history style of *B. nyasensis* does not fit the r-K selection strategy, but fits the "periodic" strategy proposed by Winemiller and Rose (1992) which further supports the ontogenetic, habitat shift of *B. nyasensis.*

CHAPTER 4

Morphological features and structures associated with feeding

4.1 INTRODUCTION

Morphological features and body structures have been used in numerous studies to predict fish feeding habits (Al-Hussaini 1949, Nagelkerke 1997). This is possible as the foraging behaviour of a fish might determine its body shape/form or vice versa (Motta & Kotrschal 1992). However, comparative studies between morphology and food choice have thus far yielded varied success (Felley 1984, Goudling 1985, Grossman 1986, Kotrschal 1989, Motta *et al.* 1995). Sibbing and Nagelkerke (1997) summarised four major bottlenecks that obscure clear relationships between form and function.

Firstly, food habits are often deduced by comparing morphological features of fish with large phylogenetic distances (Douglas & Matthews 1992, Felley 1984, Findley & Black 1983, Strauss 1987). Morphological differences, between fishes with long separate evolutionary histories may dominate, constrain or obscure the relationship between structural and ecological features.

Secondly, too few food properties have been taken into account. Food size is often the only parameter measured and used to relate feeding habits to morphological features. Fish, on the other hand, have to cope with a large set of food properties. For example, dragonfly larvae and bivalve molluscs can be very similar in size but they differ widely in velocity, mechanical features and habitat, and fish may require different adaptations to feed effectively on either of these food types.

Thirdly, too few structural parameters critical to total foraging and food processing have been considered (Kotrschal 1989, Wainwright & Richard 1995, Webb 1984). Mouth size is often the only morphological feature considered (e.g., Norton 1995). Fish with similar mouth sizes, however, can have very different body shapes, resulting in different foraging capabilities (e.g., pursuing prey).

Lastly, most studies have focused on the direct correlation between morphological features and ecological parameters, rather than searching for functional relationships and explanations (Keast & Webb 1966, Felly 1984, Barel *et al.* 1989, Douglas & Matthews 1992, Motta *et al.* 1995). Large eyes, for example, may improve vision, but as long as it is not known which aspects of the eye contribute to which aspects of vision (e.g., resolution or sensitivity) it is impossible to predict what the effect of a larger eye may have on the organism's foraging performance.

Despite such limitations the ecomorphological method, among others, can be a useful tool in predicting diet, provided the bottlenecks are circumvented (Nagelkerke 1997). This study was undertaken to predict food and feeding habits of *B. nyasensis*. This was deemed particularly important since the information obtained in this study would provide insight into the mechanisms employed by *B. nyasensis* to successfully secure its food. To improve the precision of the predictions, the limitations listed above were handled in the following way:

1. Morphological characters and features of *B. nyasensis* were investigated on a comparative basis with *Clarias gariepinus*. There is a close phylogenetic relationship between *B. nyasensis* and *C. gariepinus* (see Chapter 1). Moreover, the morphology,

feeding ecology and form-and-function relationships of *C. gariepinus* have been the subject of much research (Murray 1977, Bruton 1979); more is probably known of the food habits of the latter species than any other fish of the suborder Siluroidei (Hecht 1996). Thus, this allow for valid comparisons.

2. Fish feeding (i.e., foraging and processing) consists of a chain of subactions (Holling 1966, Atema 1971), *viz.* search, detection (encounter), approach, intake (capture), size selection, mastication, transport, mechanical breakdown (mastication), swallowing and chemical breakdown (digestion). To increase the effective utilisation of particular food types, animals have to specialise in specific subactions according to the cumulative challenges imposed by specific food types (Sibbing & Nagelkerke 1997). For example, successful pursuit and capture techniques are required by piscivores, while molluscivores require mechanical breakdown equipment. In this study morphological characters were examined according to the subactions summarised in Figure 4.1.

3. The selection of structural features with which to compare the feeding abilities of the two species were based, as much as possible, on tested relationships between form and function (Hoogenboezem *et al.* 1991). Such relationships provide evidence for the significance of structural parameters in: (a) functioning of the feeding subsystems, b) the total feeding performance, and (c) in adjusting feeding behaviour to ecological parameters, e.g. food size, density, distribution, motility, habitat, mechanical and chemical properties (Nagelkerke & Sibbing 1996).

The prediction of the diet of *B. nyasensis* is based on a comparative morphological study between *B. nyasensis* and the closely related *C. gariepinus*; the null hypothesis is that the morphological features of the two species are not significantly different.

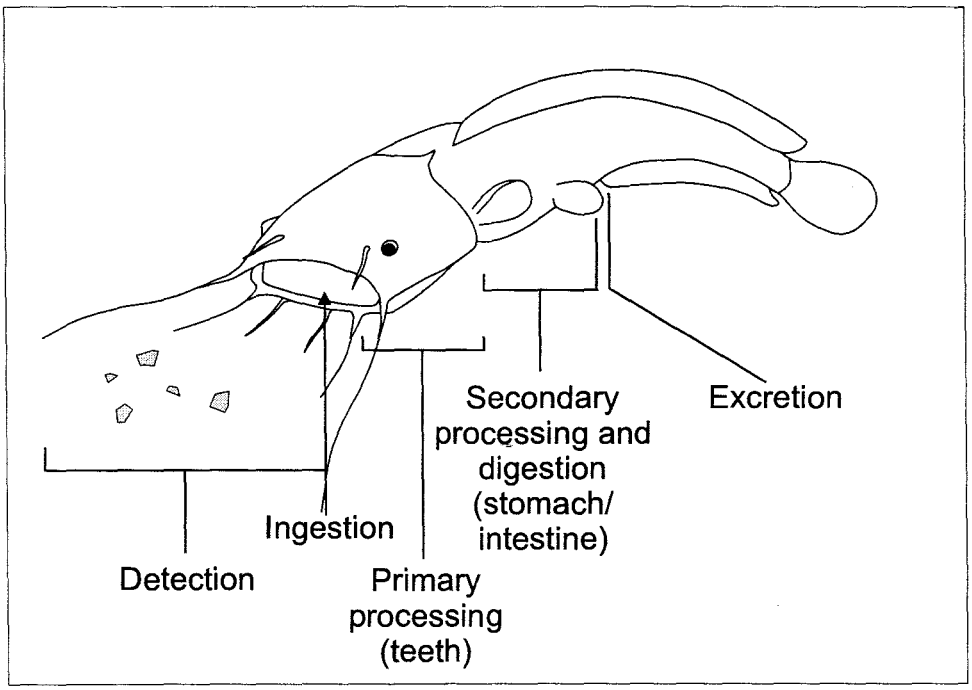


Figure 4.1. Subactions that directed the selection of morphological features that were studied.

4.2 MATERIALS AND METHODS

Specimens of *B. nyasensis* were collected from the study area in Lake Malawi (Figure 2.1), while *C. gariepinus* were obtained from fish ponds at Bunda College (Figure 2.1) and the Experimental Fish Farm at Rhodes University, South Africa.

For the quantitative analyses, 27 measurements were taken from 62 specimens of *B. nyasensis* (264 – 649 mm TL) and 56 specimens of *C. gariepinus* (205-472 mm TL). Measurements (Figure 4.2) were made on either fresh or thawed specimens. Standard length (SL) and total length (TL) were taken to the nearest mm using a measuring board. Head length (HL), body width (BW), interorbital width (IOW), eye diameter (ED), mouth width (MW), mouth depth (MD), length of opercular bone (OPL), depth of opercular bone (OPD), length of lower jaw (LJ), length and width of premaxillary tooth plate (PML, PMW), length and width of vomerine tooth plate (VTL, VTW), length of nasal barbel (NB), length of maxillary barbel (MB), length of outer mandibular barbel (OM), length of inner mandibular barbel (IM), length of anal fin (AFL), length of anal fin base and (AFB), depth of caudal peduncle (DCP), length of caudal fin (LCF), length of first gill arch (GARCH), and length of three gill rakers (GRLE), two on the lower and one on the upper arm of the first gill arch (Figure 4.3), were measured using vernier callipers to the nearest 0.01 mm .

Total filtering area (FILTERA) was computed from the two areas of trapezium formed by the upper and lower arms of the first gill arch. The gill raker at the inflection point between the upper and lower arms was the longer length, and the gill rakers at the tip of each arm were the shorter distances of the trapeziums (Figure 4.3). Overall filtering area was the summation of the two areas (see review by Gerking 1994). Distance between the first six gill rakers on the lower arm of the first gill arch (GRKD) was measured using a stereomicroscope fitted with an ocular micrometer.

The volume of the buccal cavity (BCV) was estimated by pouring an agar paste into the mouth of fish. After it had set, the fish were cut open and the agar removed. The volume

of the buccal cavity was estimated by the amount of water displaced by the coagulated agar. The gut length (start of oesophagus to end of intestine) of 202 individuals of *B. nyasensis,* ranging from 205 to 940 mm TL, was also measured in the field.

To determine ontogenetic changes in feeding modes, models were fitted to the relationships between total filtering area (FILTERA), buccal cavity volume (BCV) and fish size.

For interspecific differences in tooth size on the maxillary, vomerine, palate, dentary and pharyngeal tooth pads, teeth were measured from seven specimens of *B. nyasensis* (356 to 509 mm TL) and 7 *C. gariepinus* (352 to 560 mm TL). Teeth were cleansed by imbedding the tooth pads in 10% hydrogen peroxide for at least 12 hours before air-drying them. Teeth were finally sputter coated with gold and observed in a JEOL JSM 840 scanning electron microscope. Micrographs of teeth were taken from at least 2-4 randomly chosen areas of each tooth pad. Length, basal diameter and number of teeth from each micrograph were obtained using the Sigma Scan ^{TM}/Image Software program Version 1.20.99. In total, 2626 and 2812 teeth of *B. nyasensis* and *C. gariepinus* respectively, were measured.

Tissue from the circum-oral barbels of four specimens of *B. nyasensis*, ranging from 510 to 660 mm TL, was prepared for scanning electron microscopic studies. The tissue (±2 mm^3) was fixed in 2.5% glutaradyhyde in 0.1 M phosphate buffer for a minimum of 4 hrs, dehydrated in a series of increasing concentrations of ethanol, followed by three increasing concentrations of amyl acetate in ethanol and finally in 100% amyl acetate. The tissue was critical-point dried in a Polaron critical-point dryer using liquid CO_2. It

was sputter coated with gold and observed under a JEOL JSM 840 scanning electron microscope.

Parts of the alimentary tract from 11 specimens of *B. nyasensis*, ranging from 510 to 775 mm TL, and three *C. gariepinus*, ranging from 320 mm to 440 mm TL, were taken for histological examination. Tissue was taken from the middle region of the oesophagus, the fundic region of the stomach, and the anterior and middle regions of the intestine of each specimen (Figure 4.4). Tissue was fixed in Bouin's solution for 24 – 72 hours, and in the absence of Bouin's in 10% buffered formalin for one week and was thereafter stored in 70% propanol following the method of R. Cross (Electron Microscopy Unit, Rhodes University, pers. comm.). For histological preparation, tissue was prepared according to Bancroft and Stevens 1982. Tissue was placed in buffered formalin, then in a series of increasing concentration of alcohol. Thereafter, tissue was placed in chloroform and embedded in wax blocks. The tissue was sectioned at approx. 2 microns thickness. After de-waxing, tissue was placed in a series of decreasing series of alcohol concentration and was finally stained with haematoxylin and eosin.

To compare goblet cell distribution and dimensions from the intestinal region, three specimens each of *B. nyasensis* and *C. gariepinus* were used. Distribution of goblet cells was determined by counting the cells from three randomly selected mucosal areas of each specimen. Cell distribution was expressed as the number of goblet cells per length of the epithelium. Lengths and widths of 79 and 59 goblet cells from *B. nyasensis* and *C. gariepinus* were measured, respectively.

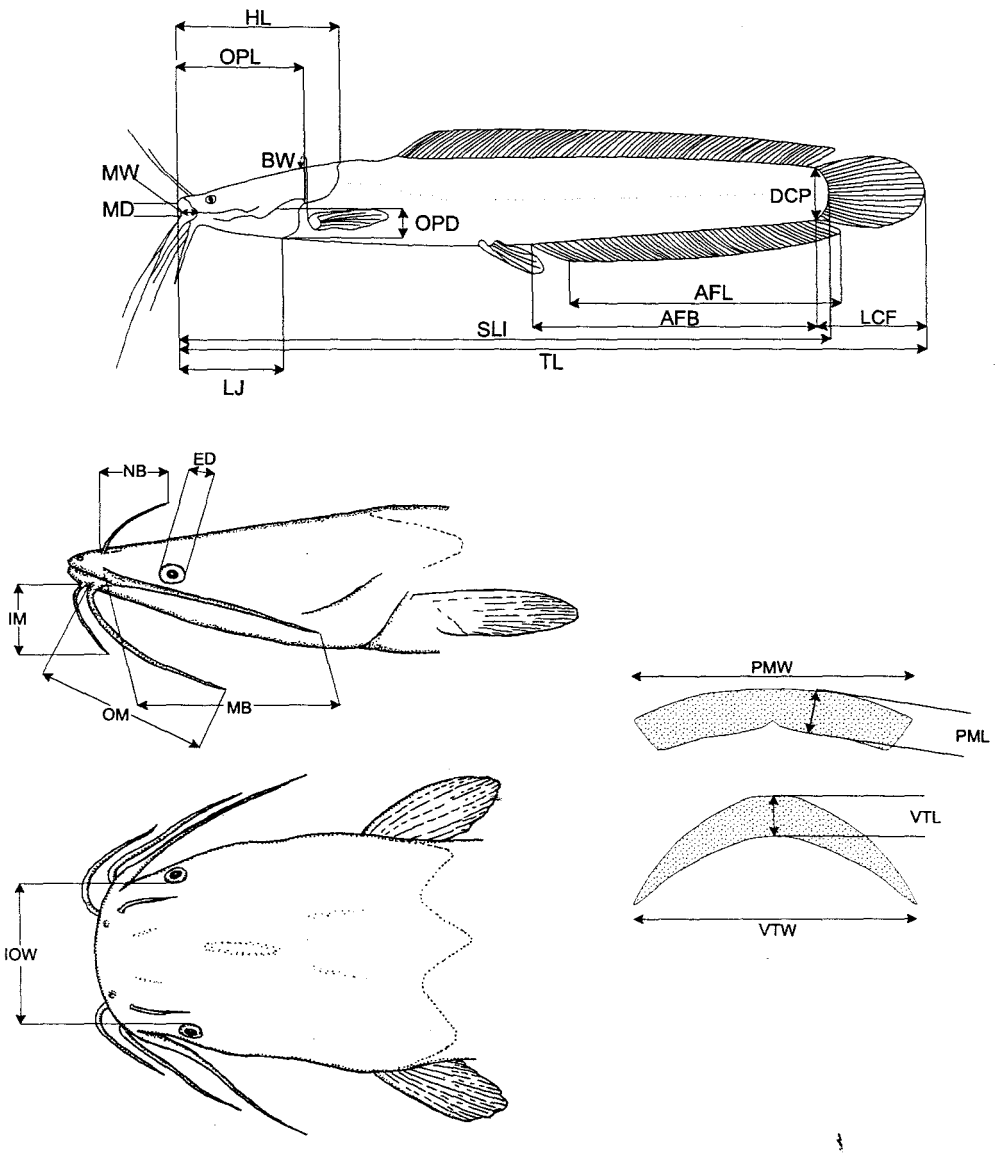


Figure 4.2 Measurements that were taken on *Bathyclarias nyasensis* and *Clarias gariepinus*. OPL = length of opercular bone; OPD = depth of opercular bone; MW = mouth width; MD= mouth depth; LJ = length of lower jaw; NB = length of nasal barbel; IM = length of inner mandibular barbel; OM = length of outer mandibular; MB = length of mandibular barbel; SL = standard length; TL = total length AFB = area of anal fin; DCP = depth of caudal peduncle; LCF = length of caudal fin; HL = head length; BW = body width; PMW = premaxillary tooth plate width; PML = premaxillary tooth plate length; VTW = vomerine tooth plate width; VTL= vomerine tooth plate length.

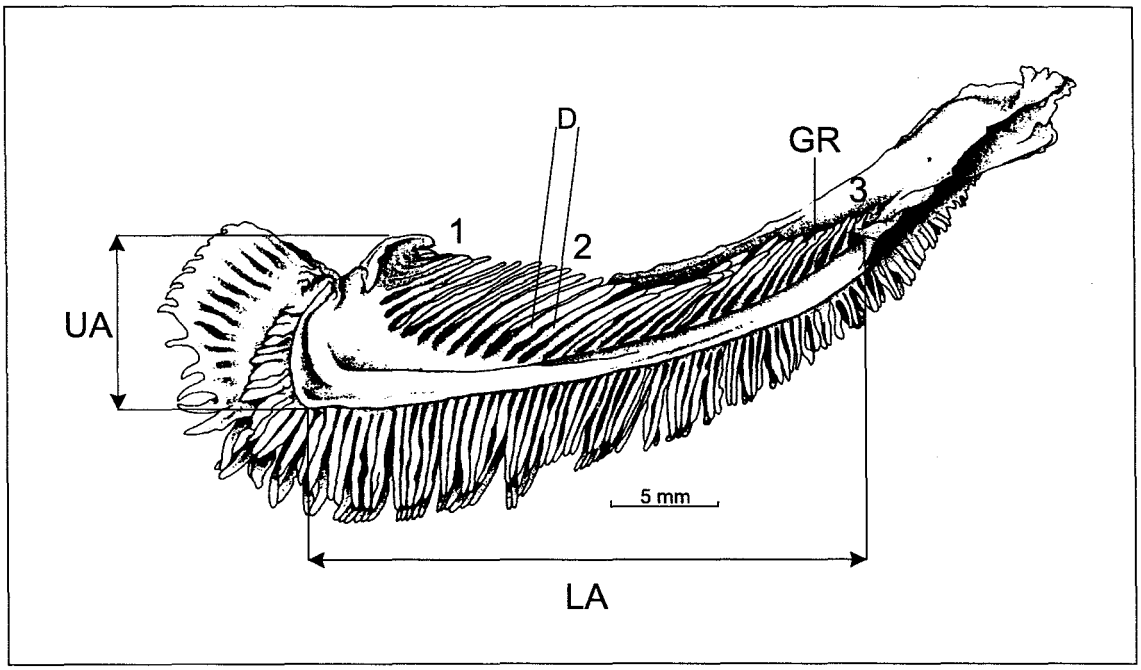
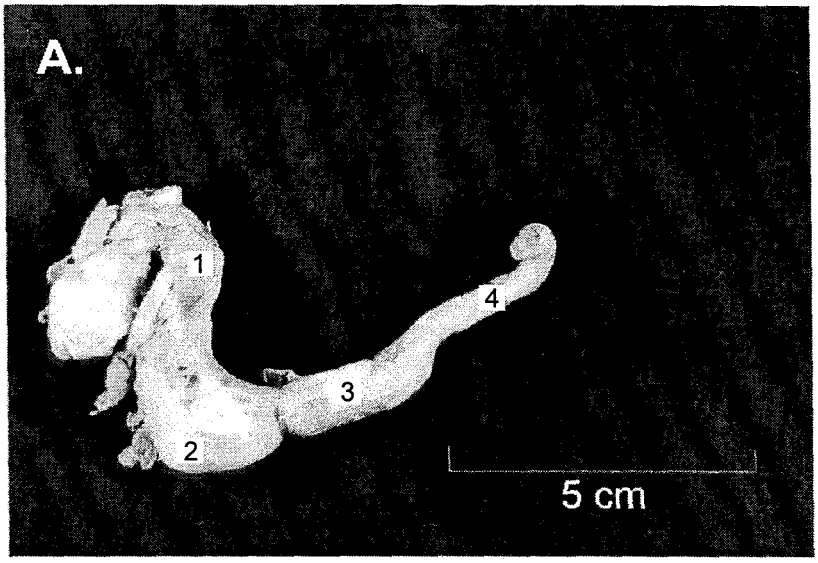


Figure 4.3. Measurements that were taken on the gill raker apparatus of *Bathyclarias nyasensis* and *Clarias gariepinus*. GR = gill rakers; UA = upper arm of gill arch; LA = lower arm of gill arch; D = distance between gill rakers; 1 and 3 are points where the short distances for the upper and lower arm trapeziums, respectively, were measured. 2 is the point where the long distance for both the upper and lower arm trapeziums was measured (Illustration of gill raker apparatus redrawn from Teugels 1986).

Statistical analysis

For comparative purposes, the morphometric measurements were standardised to different parts of the body according to Humphries (1993), Sibbing and Nagelkerke (1996) and Anseaume and Teugels (1999) (Table 4.1).



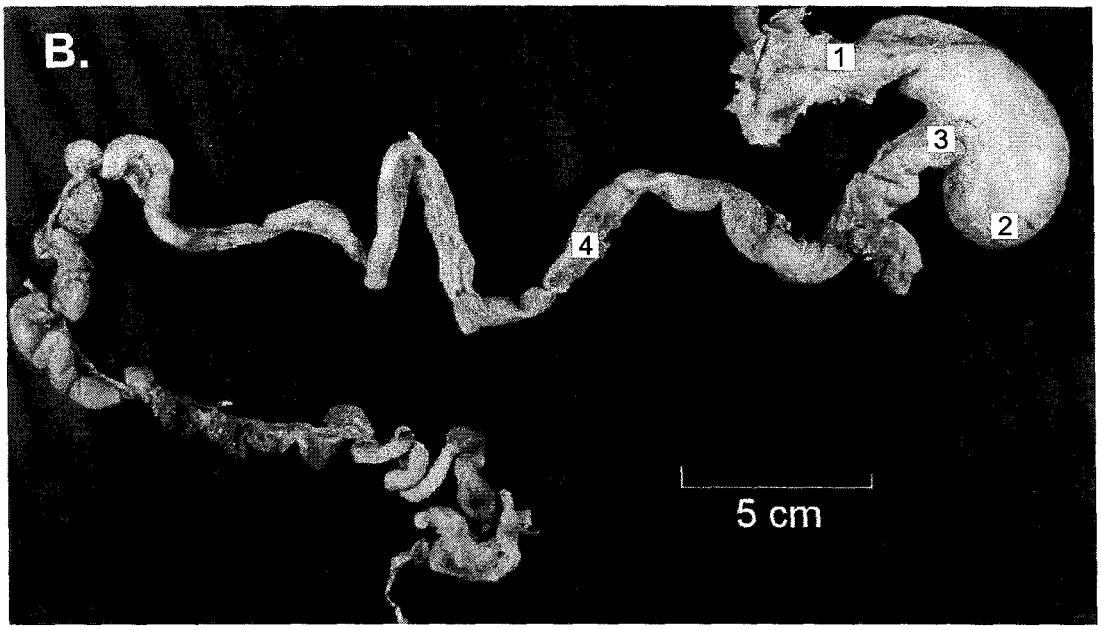


Figure 4.4. Gut areas from which tissue was taken for histological analyses: (A) *Clarias gariepinus* and (B) *Bathyclarias nyasensis*. 1 = oesophageal region, 2 = fundic region, 3 = anterior part of intestine, 4 = middle part of intestine.

Table 4.1. Standardised metric measurements used in the study (after Humphries 1993, Sibbing & Nagelkerke 1996, Anseaume & Teugels 1999).

Parameter	Ratio
standard length (SL)	-
head length (HL)	HL/SL
body width (BW)	BW/HL
Interorbital width (IOW)	IOW/HL
eye diameter (ED)	ED/SL
mouth length(ML)	ML/SL
mouth width (MW)	-
mouth depth (MD)	(MW X MD)/SL
length of lower jaw(LJ)	LJ/SL
length of nasal barbel (NB)	NB/SL
length of maxillary barbel (MB)	MB/SL
length of outer mandibular barbel (OM)	OM/SLL
length of inner mandibular barbel (IM)	IM/SL
depth of caudal peduncle (DCP)	DPC/SL
length of caudal fin (LCF)	LCF/SL
length of first gill arch (GARCH)	GARCH/SL
mean length of three gill rakers (GRLE)	GRLE/SL
mean interraker space of the first six gill rakers on the first gill arch (GRKD)	GRKD/SL
filtering area (FILTERA)	FILTERA/SL
total length of gill arch(upper and lower) (GARC)	GARC/SL
length of anal fin (AFL)	-
length of anal fin base (ABL)	AFL X ABL/SL
area of anal fin (AFA)	100 X AFLX ABL/SL^2
volume of buccal cavity (BCV)	BCVOL/SL
length of premaxillary tooth plate (PML)	PML/SL
width of premaxillary tooth plate (PMW)	PMW/SL
length of vomerine tooth plate (VTL)	VTL/SL
width of vomerine tooth plate (VTW)	VTW/SL

Univariate and multivariate analyses were used to test for differences between morphometric ratios of *B. nyasensis* and *C. gariepinus*. For univariate analysis all the morphometric ratios were tested for normality (Zar 1984). Ratios can cause statistical problems because of the underlying correlation between the numerator and denominator

(Reist 1984). However, since most of the calculated ratios were normally distributed (even without ln-transformation), and were only used for univariate comparisons, their use was considered justified (Sibbing & Nagelkerke 1997).

Differences in means of normally distributed ratios were tested using t-test for independent samples and non-normally distributed parameters were tested non-parametrically using a Mann-Whitney U-test for two samples (Zar 1984).

For multivariate analyses, the ratios were subjected to principal component analysis (PCA) (Rognon *et al.* 1998, Sibbing & Nagelkerke 1997, Motta & Kotrschal 1992). The STATISTICA software program (Statsoft Inc.) was used to undertake the PCA. The coefficients with absolute values equal to or greater than 0.6 were included in the analysis. In PCA, the ratios may fall into one of four categories:

1) A character in the two species extracted in the same factor and having same sign indicates that the character is in the same vector direction. The character is taken to be same in the two species.

2) A character in both species is positive but in different factors, means that the character is on different axes but the direction of the vectors is the same. There is a minor difference of the character in the two species.

3) A character in the two species has different signs and is extracted in the same factor means that the character has different vector direction and is regarded as completely different.

4) A character in the two species has different signs and is extracted in different factors has different vector directions but in different factors. The character is different but the difference is minor compared to 3.

A t-test for independent samples (Zar 1984) was used to test for differences in the distribution, length and width of goblet cells from the middle region of the intestine.

4.3 RESULTS

Results from the univariate analysis (Table 4.2) showed significant ($p<0.05$) interspecific differences in characters related to prey search and detection (eye diameter, interorbital width, circum-oral barbels), food capture (anal fin area, length of caudal fin), prey grip (length and width of premaxillary and vomerine tooth plates) and food ingestion (filtering area, buccal cavity volume, and length of lower jaw). Character relationships used were identical to those defined by Nagelkerke (1997).

The results showed that the eyes of *B. nyasensis* are significantly larger ($p < 0.05$) than those of *C. gariepinus*. Furthermore, the eyes of the former are laterally positioned while those of *C. gariepinus* are anterio-dorsally positioned (Bruton 1979, Figure 4.5), accounting for the significantly larger ($p<0.05$) interorbital width in *B. nyasensis* in comparison to *C. gariepinus*. Teugels (1983) used eye position as one of the diagnostic features to distinguish the genus *Dinotopterus (synonymy = Bathyclarias)* from *Clarias* and *Heterobranchus*. While characters related to mouth size (mouth width (mw) x mouth diameter (md)/sl) were not significantly different ($p>0.05$), the mouth of *B. nyasensis* is typically terminal, while the mouth of *C. gariepinus* is subterminal (Figure 4.6).

Table 4.2. Differences between morphometric ratios in *Bathyclarias nyasensis* and *Clarias gariepinus*. SL = standard length, HL = head length.

	Bathyclarias nyasensis			*Clarias gariepinus*				
Variables	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**	**n**	**p value**	**Significant (S)/ non- significant (NS)**
Head length/SL	0.32	0.120	62	0.29	0.023	56	0.068	NS
Head width/SL	0.60	0.079	44	0.60	0.04	42	0.755	NS
Body width/HL	0.72	0.366	18	0.61	0.038	14	0.281	NS
Interorbital width/HL	0.52	0.190	62	0.40	0.027	56	0.000	S
Eye diameter/SL	0.03	0.010	62	0.02	0.009	56	0.003	S
Mouth width x mouth diameter/SL	0.23	0.073	44	0.27	0.074	42	0.050	NS
Lower jaw length /SL	0.16	0.059	62	0.14	0.024	56	0.007	S
Nasal barbel length/SL	0.14	0.081	62	0.08	0.02	56	0.000	S
Mandibular barbel length/SL	0.32	0.168	62	0.21	0.033	56	0.000	S
Inner mandibular barbel length/SL	0.12	0.059	62	0.11	0.019	56	0.268	NS
Outer mandibular barbel length/SL	0.20	0.094	62	0.16	0.029	56	0.005	S
Depth of caudal peduncle/SL	0.09	0.044	62	0.08	0.007	56	0.155	NS
Length of caudal fin/SL	0.12	0.047	62	0.14	0.012	56	0.028	S
100 x Anal fin length x Anal fin base /SL^2	14.42	3.618	18	19.09	1.670	14	0.000	S
Gill raker distance /SL	0.001	0.000	18	0.002	0.000	14	0.087	NS
Filtering area/SL	0.79	0.473	62	0.42	0.160	56	0.000	S
Buccal cavity Volume/SL	0.21	0.171	62	0.12	0.043	56	0.000	S
Premaxillary tooth plate length/SL	0.04	0.007	44	0.05	0.008	42	0.000	S
Premaxillary tooth width/SL	0.33	0.035	44	0.29	0.021	42	0.000	S
Vomerine tooth plate length/SL	0.032	0.062	44	0.04	0.011	42	0.000	S
Vomerine tooth width/SL	0.28	0.047	44	0.25	0.011	42	0.000	S

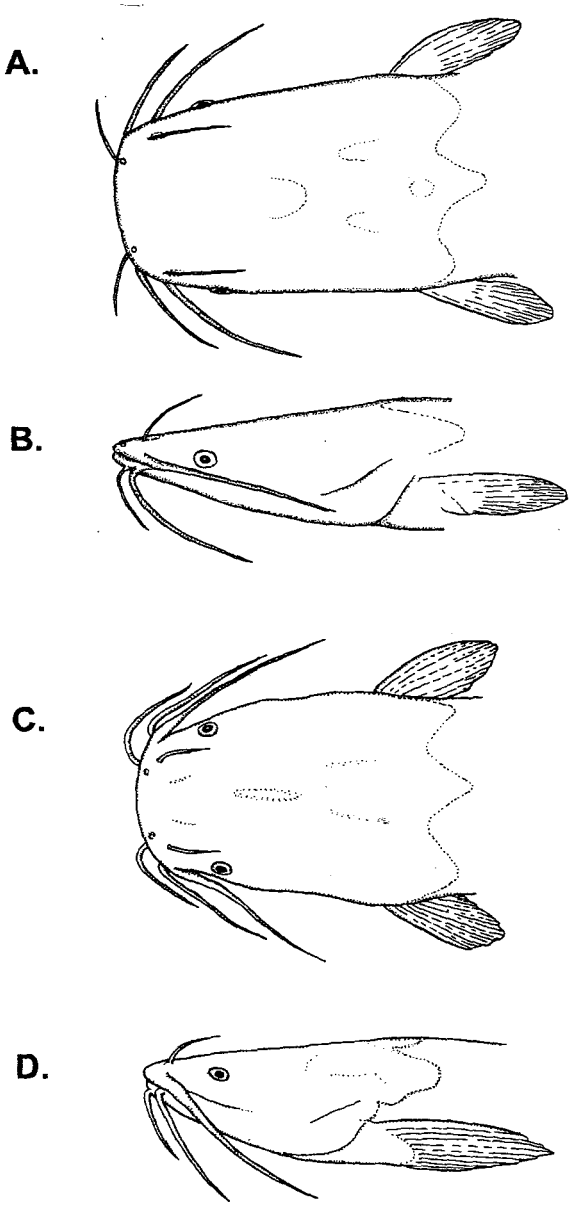


Figure 4.5. Eye position in *Bathyclarias nyasensis* (A & B) and *Clarias gariepinus* (B & C). Note the laterally positioned eyes in (A) and (B) compared to (C) and (D).

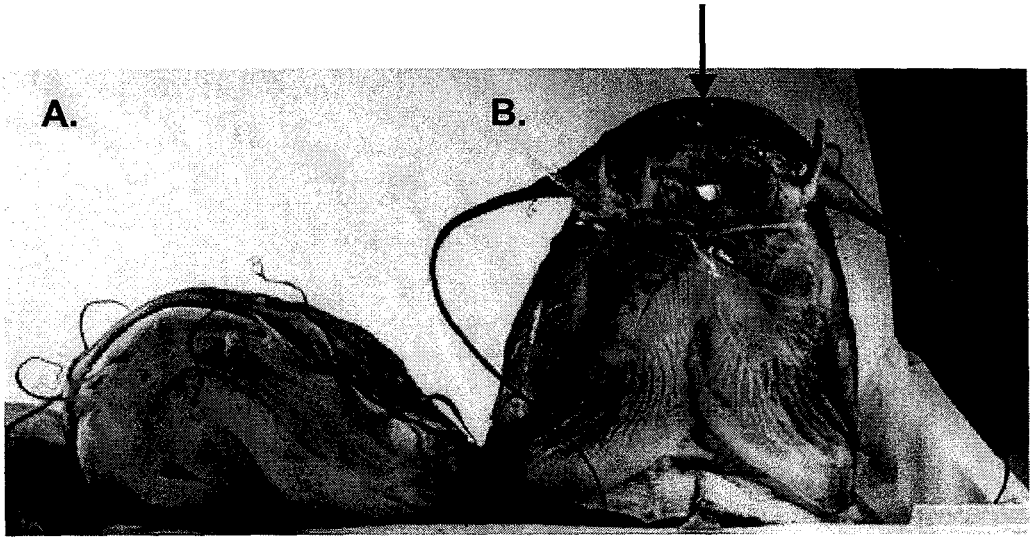


Figure 4.6. Terminal mouth *Bathyclarias nyasensis* (A) and subterminal mouth *Clarias gariepinus* (B) (note the fleshy lips in *Clarias gariepinus* - arrow).

Except for the inner mandibular barbels, all the pairs of circum-oral barbels of *B. nyasensis* were significantly longer ($p<0.05$) than in *C. gariepinus*. Taste buds consisting of distinct swellings on the outer surface of the epidermis were observed on barbels of both *B. nyasensis* and *C. gariepinus* (Figure 4.7).

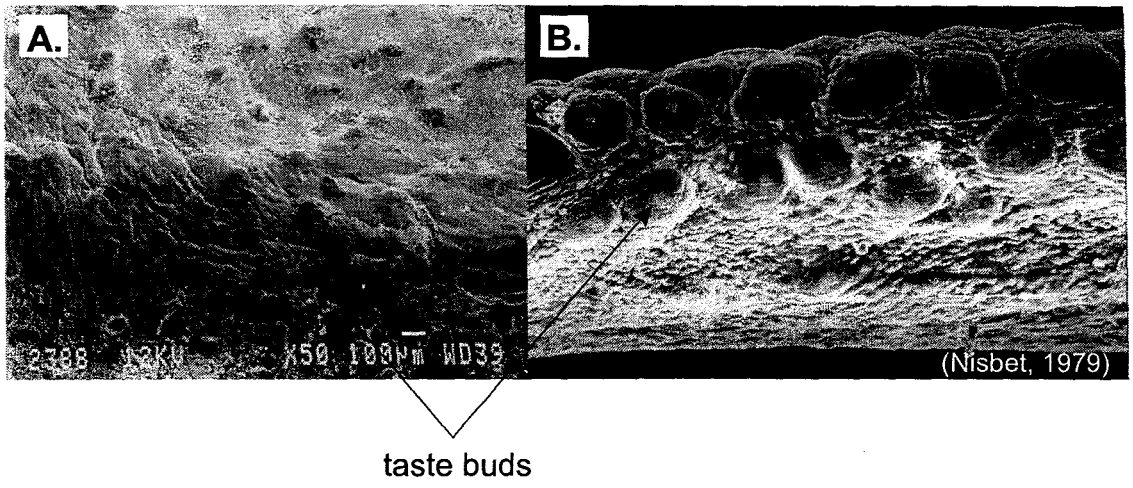


Figure 4.7. Taste buds on the circum-oral barbels of adult *Bathyclarias nyasensis* (A) and *Clarias gariepinus* (B).

The caudal fin of both species is rounded. Caudal fin length and the anal fin area were significantly larger in *C. gariepinus* ($p<0.05$) than in *B. nyasensis*. The length (breadth) of the premaxillary and vomerine tooth plates of *B. nyasensis* was significantly smaller

($p<0.05$) than in *C. gariepinus*. However, the width of the premaxillary and vomerine tooth plates was significantly greater ($p<0.05$) in *B. nyasensis* than in *C. gariepinus* (Figure 4.8).

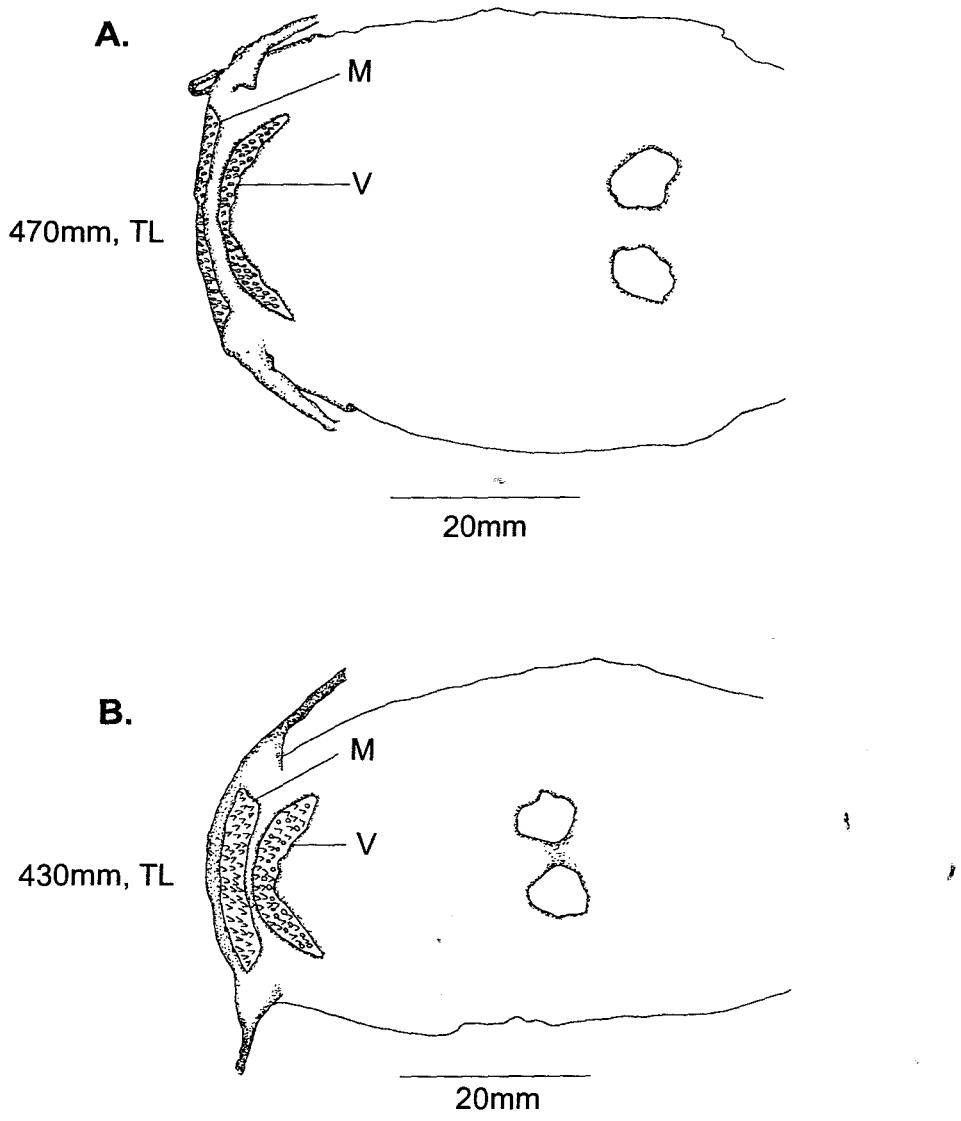


Figure 4.8. The premaxillary (M) and vomerine (V) bands in adult *Bathyclarias nyasensis* (A) and *Clarias gariepinus* (B). Note the broad bands in *Clarias gariepinus*.

Premaxillary, vomerine, dentary, pharyngeal and teeth from upper palates of *C. gariepinus* were significantly stouter and longer ($p<0.05$) than in *B. nyasensis*, and except for the premaxillary and pharyngeal teeth, were more sparsely distributed in the latter than in *C. gariepinus* (Table 4.3).

Table 4.3. Length (*u*m), base diameter (*u*m) and number of teeth per mm^2 in *Bathyclarias nyasensis* and *Clarias gariepinus*.

		Bathyclarias nyasensis					***Clarias gariepinus***					
Type of teeth	**Dimension**	**Mean**	**S.D.**	**Minimum**	**Maximum**	**n**	**Mean**	**S.D.**	**Minimum**	**Maximum**	**n**	**p value**
Premaxillary	Length	943.15	469.34	126.23	1989.30	313	1025.99	491.76	282.77	2579.77	262	0.0396
	Base diameter	189.75	79.44	64.28	388.80	336	289.42	114.48	110.73	678.87	277	0.0000
	No/mm2	4.95	3.22	1.25	9.99	13	2.76	2.79	0.75	10.03	15	0.0650
Vomerine	Length	496.08	207.01	126.23	1246.24	136	1100.24	462.54	202.71	2322.27	248	0.0000
	Base diameter	214.60	101.25	76.26	483.66	186	445.20	155.59	17.21	1110.26	287	0.0000
	No/mm2	5.94	3.07	1.64	12.42	13	1.69	1.37	0.87	5.85	19	0.0000
Upper palates	Length	345.56	221.31	85.11	1418.09	202	694.38	388.58	153.76	2144.71	267	0.0000
	Base diameter	73.83	39.43	23.16	290.57	267	195.51	96.93	68.86	452.81	387	0.0000
	No/mm2	19.48	15.22	3.13	54.38	14	7.16	7.78	1.64	27.09	15	0.0100
Dentary	Length	490.30	165.87	188.80	1074.63	271	1086.54	500.53	336.01	2467.16	324	0.0000
	Base diameter	180.69	90.64	3.16	542.04	303	291.78	172.80	104.86	860.05	277	0.0000
	No/mm2	6.13	1.94	1.32	8.11	14	3.75	1.84	1.08	6.32	11	0.0049
Pharyngeal	Length	323.72	114.53	107.49	738.00	310	612.77	239.22	192.74	1350.79	238	0.0000
	Base diameter	92.17	42.11	33.72	206.14	302	210.36	74.99	44.52	404.05	245	0.0000
	No/mm2	5.20	5.16	0.63	19.84	17	4.24	4.15	1.19	16.01	18	0.5501

The teeth are unicuspid in both species. The pharyngeal and teeth from upper palate of *C. gariepinus* are backwardly directed (Figure 4.9C2 & 4.10B2). The vomerine teeth of both

species were molar-like, with few conical teeth at the distal margins (Figure 4.9B1 & B2). Similar modifications were observed at the posterial margins of the dentary tooth plates (Figure 4.10A1 & A2).

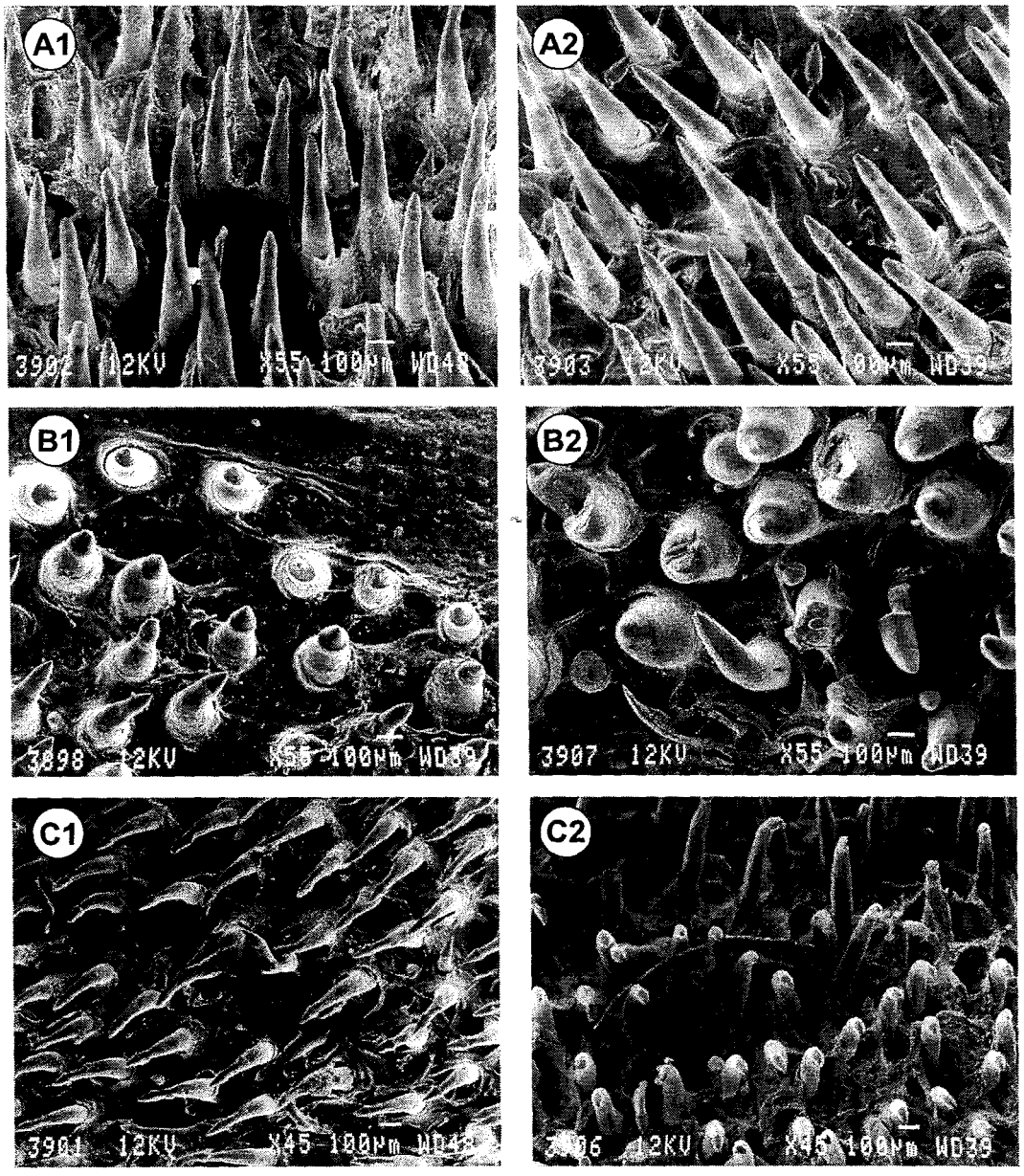


Figure 4.9. Teeth in a 474 mm TL specimen of *Bathyclarias nyasensis* (A1, B1, C1) and a (406 mm TL) specimen of *Clarias gariepinus* (A2, B2, C2) A1, A2 = premaxillary; B1, B2 = vomerine, C1, C2 = teeth from the upper palates.

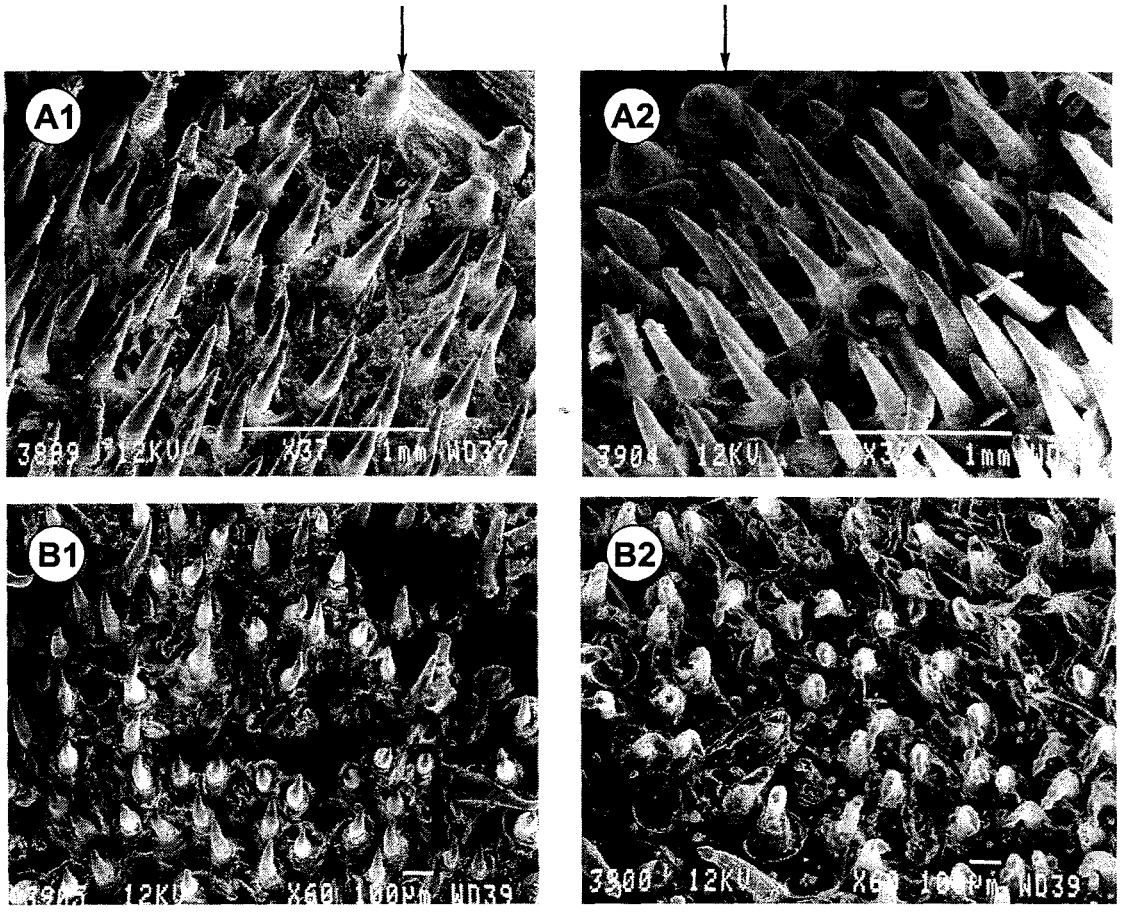


Figure 4.10. Teeth in a 474 mm TL *Bathyclarias nyasensis* (A1, B1) and a 406 mm TL *Clarias gariepinus* (A2, B2). A1, A2 = dentary; B1, B2 = pharyngeal teeth. Note the molariform teeth in A1 and A2 (dentary, arrow) and the highly recurved teeth in pharyngeal teeth of *Clarias gariepinus*.

While the distance between gill rakers of the two species was not significantly different ($p>0.05$), the total filtering area (FILTERA) and buccal cavity volume (BCV) of *B. nyasensis* were significantly larger ($p<0.05$) than in *C. gariepinus*. In both species the FILTERA and BCV changed ontogenetically, but in different fashions. A logistic model described the ontogenetic change in the filtering area of *B. nyasensis* (Equation 4.1):

$$\text{Filtering area (FILTERA)} = \left(\frac{1}{1+e^{-(TL-539.40)/105.2}}\right) \times 1676 \text{ mm}^2 \quad r^2 = 0.93 \text{ (n = 62)}$$

Equation 4.1

where: TL = total length of fish (mm)

In *C. gariepinus* the relationship was best described by a multiplicative model (Equation 4.2):

$$\text{Filtering Area (FILTERA)} = 0.001TL^{2.01} \text{ mm}^2 \qquad r^2 = 0.87 \text{ (n = 56)}$$

Equation 4.2

where: TL = total length of fish (mm)

Figure 4.11 shows the logistic model (Equation 4.1) and multiplicative model (Equation 4.2) fitted to filtering area data of *B. nyasensis* and *C. gariepinus*.

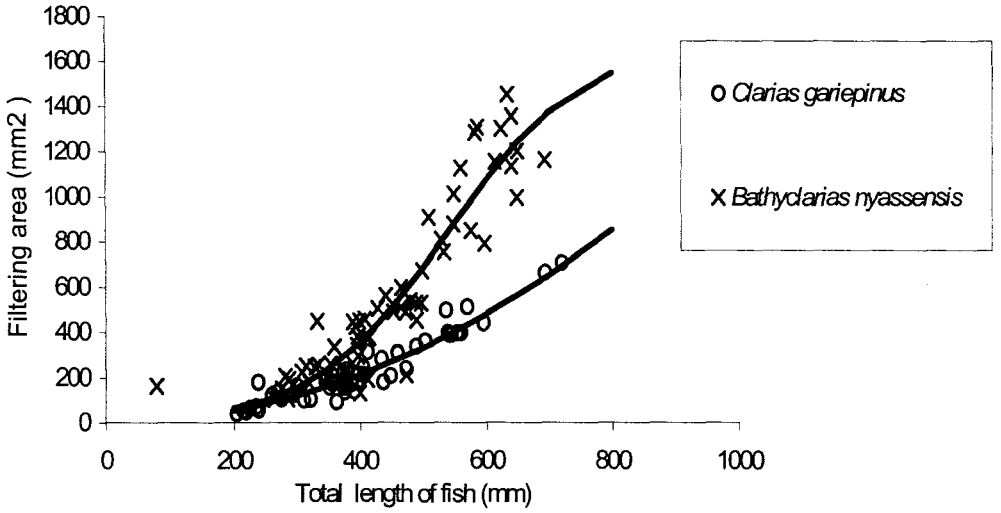


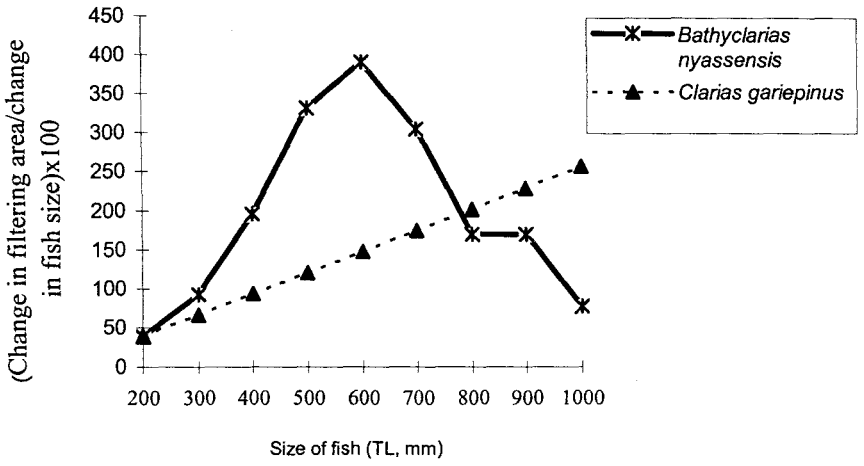
Figure 4.11. Changes in filtering areas in *Bathyclarias nyasensis* and *Clarias gariepinus.*

From Figures 4.11 and 4.12, it can be demonstrated that as the fish increased in size, the rate of change in filtering area in *B. nyasensis* reached a maximum between 500 and 600 mm TL, while in *C. gariepinus* it increased steadily.

Ontogenetic changes in the buccal cavity volume of *B. nyasensis* were described by an exponential equation:

$$\text{Buccal cavity volume (BVC)} = e^{(0.79+0.007TL)} \text{ mm}^3 \quad r^2 = 0.83 \text{ (n = 62)}$$

Equation 4.3



where TL = total length of fish in mm.

Figure 4.12. Change in filtering area per change in fish size in *Bathyclarias nyasensis* and *Clarias gariepinus.*

In *C. gariepinus* this was defined by a multiplicative model (Equation 4.4):

$$\text{Buccal cavity volume (BCV)} = 0.00007TL^{2.19} \text{ mm}^3 \quad r^2 = 0.84 \text{ (n = 56)}$$

Equation 4.4

where TL = Total length of fish in mm

The models described by equations 4.3 and 4.4, and graphically presented in Figure 4.13, show a significant change in buccal cavity volume in *B. nyasensis* between 500 and 600 mm TL.

Results of the principal components analysis showed that, only characters associated with the subaction prey capture (anal fin area and length of caudal fins) were not different. Characters related to food search and detection (barbels) (Factors 1 and 2 in Table 4.4 and Figure 4.14), prey grip (vomerine tooth plate) (Factors 4 and 5, Table 4.4) and food ingestion (filtering area and buccal cavity volume (Factors 1 and 2, Table 4.4 and Figure 4.14) were different. Thus, it could be suggested that the differences observed in univariate analysis in food search and detection, prey grip and food ingestion are unequivocal.

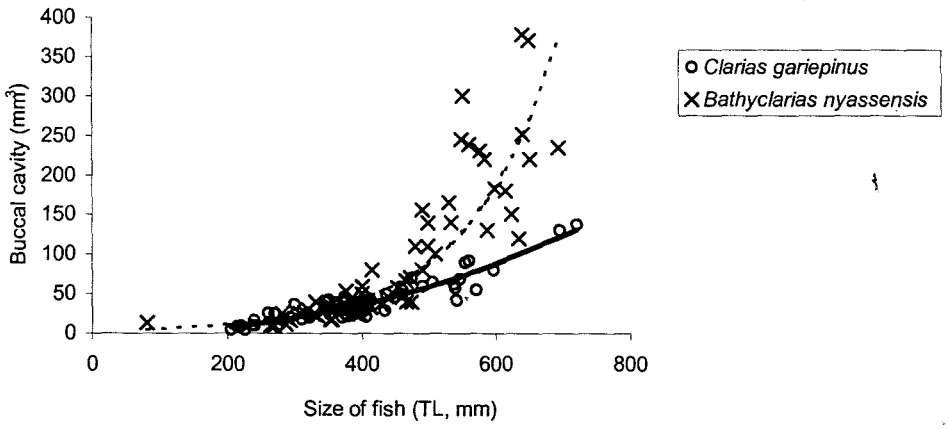


Figure 4.13. Changes in buccal cavity volume in *Bathyclarias nyasensis* and *Clarias gariepinus*.

The relative gut length (RGL) of *B. nyasensis* was significantly greater ($p<0.05$) than what was recorded for *C. gariepinus* (Table 4.5).

Table 4.4. Factor loadings in the first seven principal components (PC). The factor loading with the absolute values ≥ 0.6 are given in bold. If such a value did not occur in the first seven factors, the characters are not shown. A character starting with C- refers to *Clarias gariepinus* and B- to *Bathyclarias nyasensis*; sl = standard length.

	Factors						
	1	2	3	4	5	6	7
Characters/% Variance	**21.7**	**18.3**	**14.4**	**9.5**	**8.7**	**6.8**	**5.1**
C-nasal barbel/sl	0.209	**-0.891**	-0.011	0.009	0.001	-0.298	-0.076
C-maxillary barbel/sl	0.170	**-0.860**	0.148	-0.186	-0.039	-0.028	0.060
C-inner mandibular barbel/sl	0.149	**-0.871**	0.119	-0.286	0.135	-0.089	-0.098
C- outer mandibular barbel/sl	0.116	**-0.748**	0.291	-0.354	0.189	0.111	-0.256
C-filtering area/sl	-0.532	**0.636**	-0.139	0.383	-0.163	0.087	-0.126
C- buccal cavity volume/sl	-0.510	**0.685**	-0.013	-0.104	-0.474	-0.023	0.014
C- length premaxillary tooth plate/sl	-0.088	-0.120	-0.212	0.320	-0.337	**-0.655**	0.242
C- width premaxillary tooth plate/sl	0.083	0.057	-0.200	-0.225	-0.605	-0.519	0.178
C- length of vomerine tooth plate/sl	0.298	-0.081	0.297	0.076	-0.633	-0.325	-0.169
B- headlength/sl	**-0.866**	-0.153	0.365	0.149	0.154	-0.140	0.123
B- body width/sl	**0.612**	0.538	0.341	0.056	0.185	-0.198	-0.146
B- lower jaw length/sl	**-0.809**	-0.122	0.440	0.149	0.139	-0.291	0.023
B-nasal barbel/sl	**0.705**	0.520	0.354	-0.114	0.155	0.069	-0.010
B-maxillary barbel/sl	**0.633**	0.458	0.491	-0.084	0.243	0.014	-0.101
B-inner mandibular barbel/sl	**0.686**	0.531	0.356	-0.155	0.173	-0.022	-0.069
B- outer mandibular barbel/sl	**0.725**	0.365	0.469	-0.233	0.030	0.027	-0.132
B- depth of caudal peduncle/sl	-0.373	-0.070	0.044	**-0.685**	-0.035	0.235	0.303
B-100 x anal fin length/sl^2	-0.214	0.080	**0.813**	-0.152	0.090	-0.452	0.102
B-gill raker distance/sl	-0.184	-0.101	**0.854**	0.105	-0.181	0.250	0.072
B- filtering area/sl	**-0.847**	-0.047	0.123	0.345	0.279	-0.087	0.123
B- buccal cavity volume/sl	**-0.886**	0.062	0.157	0.259	0.213	-0.043	-0.001
B- length of premaxillary tooth plate	**0.681**	0.336	0.148	0.249	0.311	0.052	0.218
B- premaxillary tooth plate width/sl	0.259	0.046	0.372	**0.716**	-0.277	-0.178	-0.372
B-vomerine tooth plate/sl	0.329	0.344	0.139	**0.739**	-0.299	0.120	0.234
B-vomerine tooth plate width/sl	-0.300	0.217	-0.052	-0.084	0.482	0.006	**-0.660**

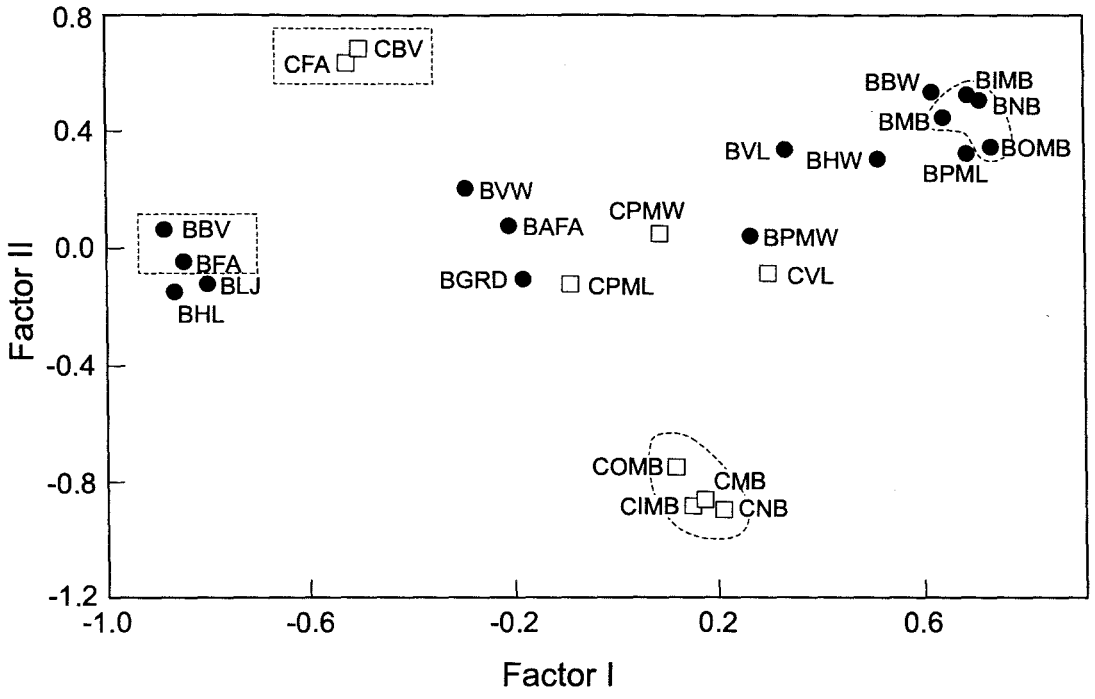


Figure 4.14. Principal component analysis for characters in factors 1 and 2 in Table 4.4. □= *Clarias gariepinus*, and • = *Bathyclarias nyasensis.* The characters that are different are shown by different enclosures. These are barbels (COMB, CMB, CIMB, CNB vs. BOMB, BMB, BIMB, BNB), buccal cavity volume (CBV vs. BBV) and filtering area (CFA vs. BFA). First letter C of each character refers to Clarias gariepinus, B refers to *Bathyclarias nyasensis*. OMB = outer mandibular barbels; MB = maxillary barbels; IMB = inner mandibular barbels; NB = nasal barbels; BV = buccal cavity volume and FA = filtering area.

Table 4. 5. The relative gut lengths (RGL) of *Bathyclarias nyasensis* and *Clarias gariepinus.*

Species	Mean	S.D.	n	p-value	Author
Bathyclarias nyasensis	1.27	0.24	202	0.0039	This study
Clarias gariepinus	0.93	0.32	4		Computed from RGLs reported by Kruger & Mulder (1973), Stroband & Kroon (1981) and Uys (1989).

While ontogenetic changes were noted in filtering area and buccal cavity volume in *B. nyasensis,* the RGL showed no such changes (Figure 4.15).

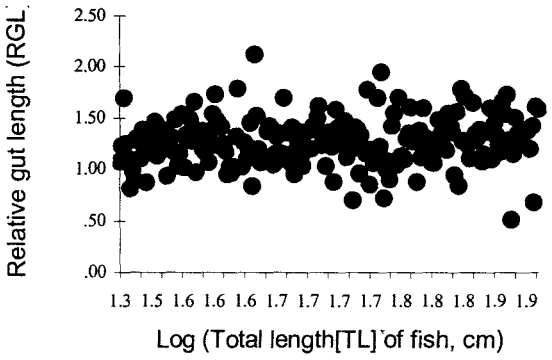


Figure 4.15. Relative gut length (RGL) of *Bathyclarias nyasensis.*

The oesophagus of both *B. nyasensis* and *C. gariepinus* are short, muscular and dilatable and open into a distensible flask-like stomachs. Histological examination showed that both species have the following basic layers: epithelium, lamina propria-submucosa, tunica muscularis and adventitia or serosa. In *C. gariepinus* the mucosal folds appear deeper and more numerous than in *B. nyasensis* (Figure 4.16A & B).

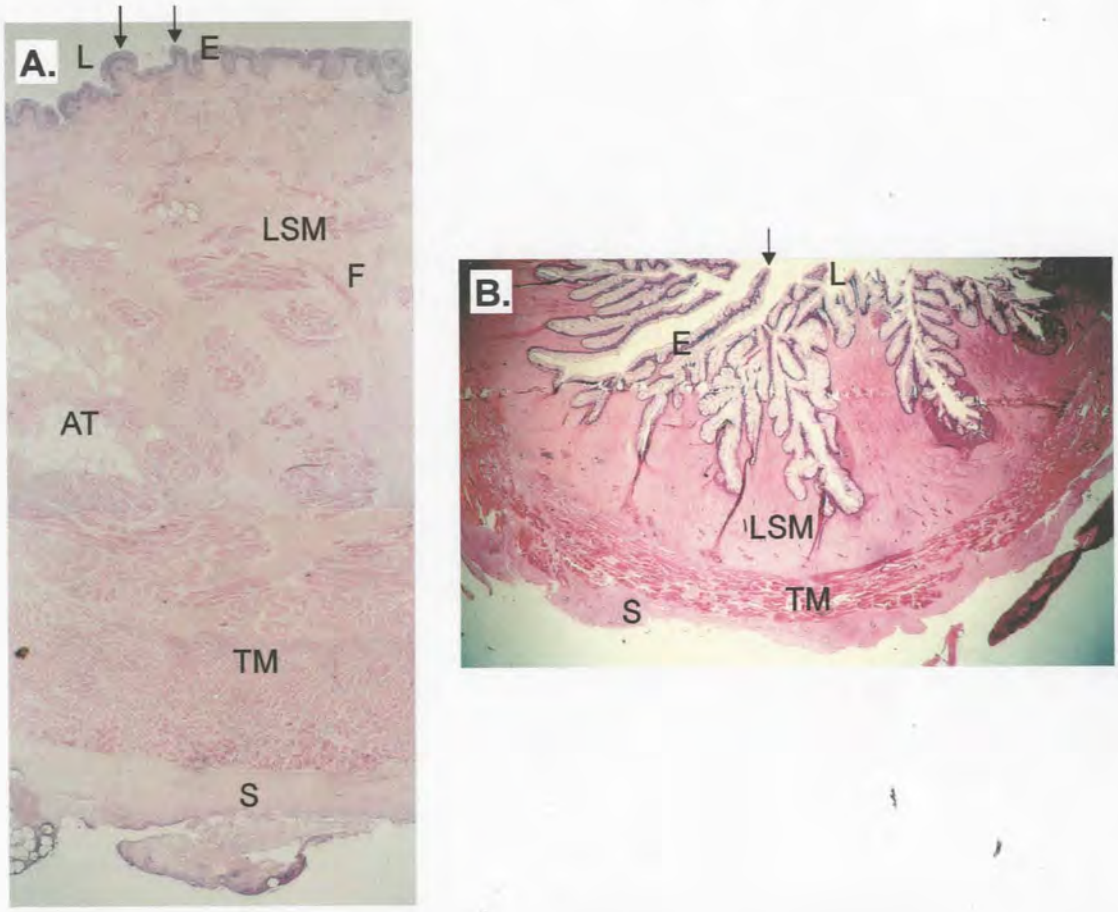


Figure 4.16. The oesophageal layers in (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus* (x 20, haematoxylin and eosin (H&E)). E = epithelium, LSM = lamina propria-submucosa, TM = tunica muscularis and S= serosa or adventitia. L = lumen side of the oesophagus. Clumps of adipose tissue (AT), and muscle fibres (F) are noted in (A) *Bathyclarias nyasensis.* Note the deeper folds in B. *Clarias gariepinus* compared to *Bathyclarias nyasensis* (arrow).

The epithelium of the oesophagus consisted of three components: a surface layer of simple squamous cells, a mid-layer containing mucous cells and a basal layer of undifferentiated cells (Figure 4.17A & B).

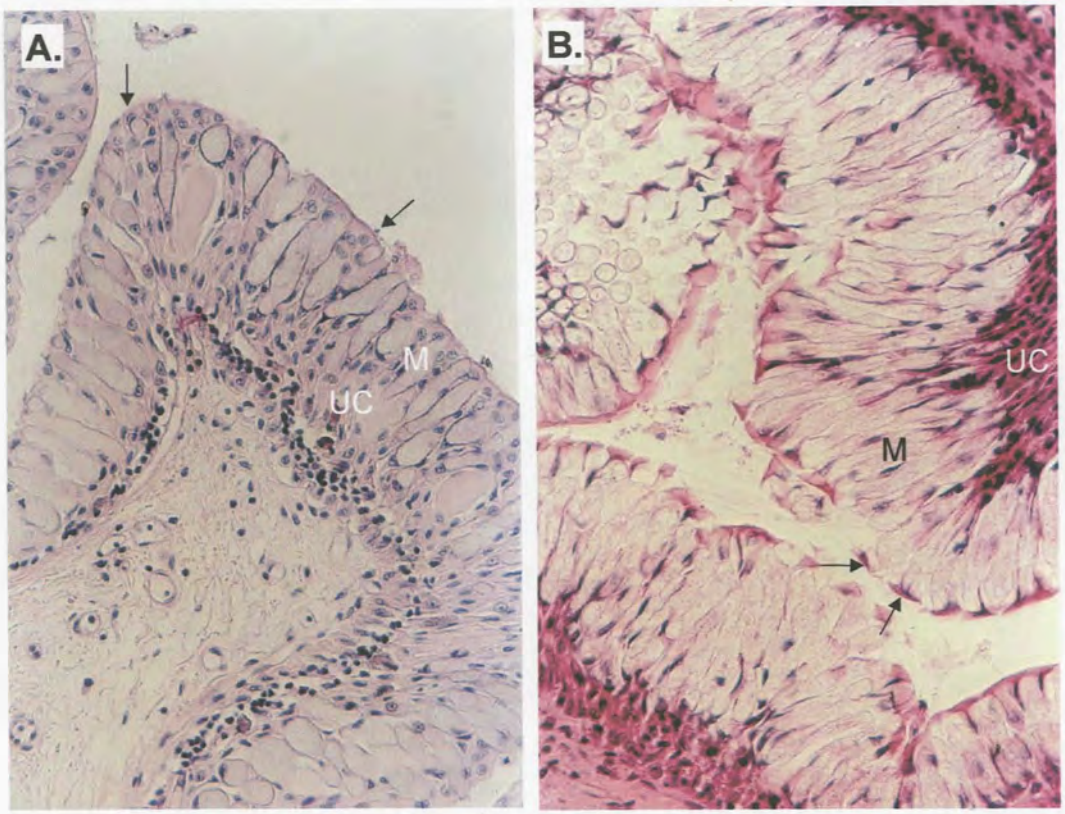


Figure 4. 17. The squamous cells (arrow), midlayer mucous cells (M) and undifferentiated cells (UC) in (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus* (x 200, H&E).

A distinct junction between the lamina propria and the submucosa was not observed. The lamina propria-submucosa contained no mucous cells, but projected into the mucosal folds. There were neither glands nor muscularis mucosae in the wall of the oesophagus of both species. There was a strong component of fibers in the lamina-propria-submucosa of *B. nyasensis* (Figure 4.16*)*. The tunica muscularis of both species consisted of striated or skeletal muscle (Figure 4.18 A & B).

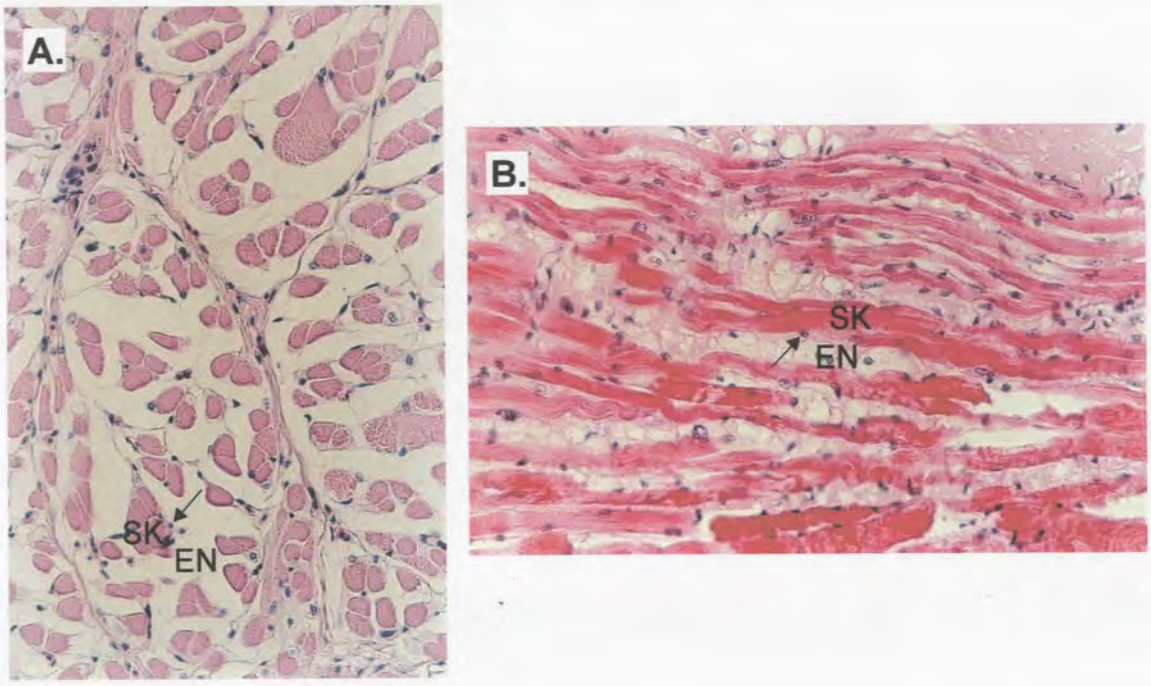


Figure 4.18. The skeletal muscles (SK) of (A) *Bathyclarias nyasensis* (traverse section) and (B) *Clarias gariepinus* (longitudinal section). Note the peripheral location of the nuclei (arrow) and the endomysium (EN) occupying the spaces between the muscle fibers (x 200, H & E).

The primary folds or rugae of the fundic region of the stomachs of both species appeared subdivided into extensive networks of secondary folds. Four basic layers were distinguished: – the mucosa, submucosa, tunica muscularis and serosa. The mucosa included simple columnar epithelium and a lamina propria (Figure 4.19 A & B).

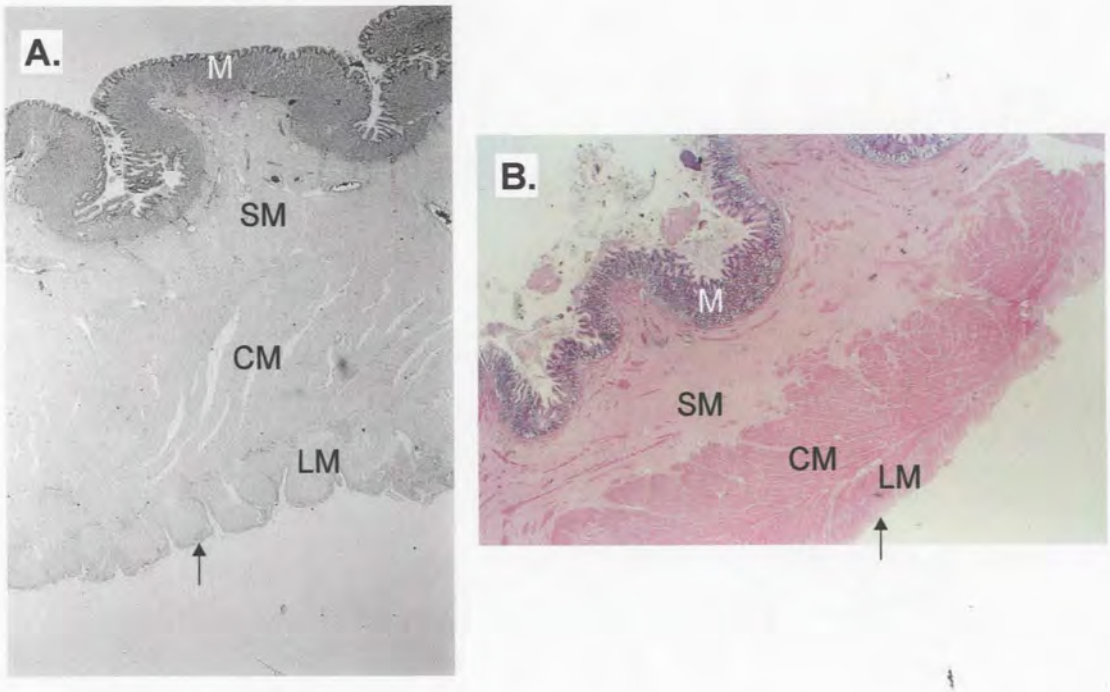


Figure 4.19. The basic layers in fundic region of the stomachs of (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus*: mucosa (M), submucosa (SM), circular muscle (CM), longitudinal muscle (LM) and this serosa (arrow) (x 20 H&E).

The gastric mucosa of both species consisted of simple columnar cells and glandular cells (Figure 4.20A & B). Only one type of glandular cell was observed. The cells were centrally nucleated and resembled the structure of parietal or oxyntic cells of higher vertebrates (Wheater *et al.* 1987).

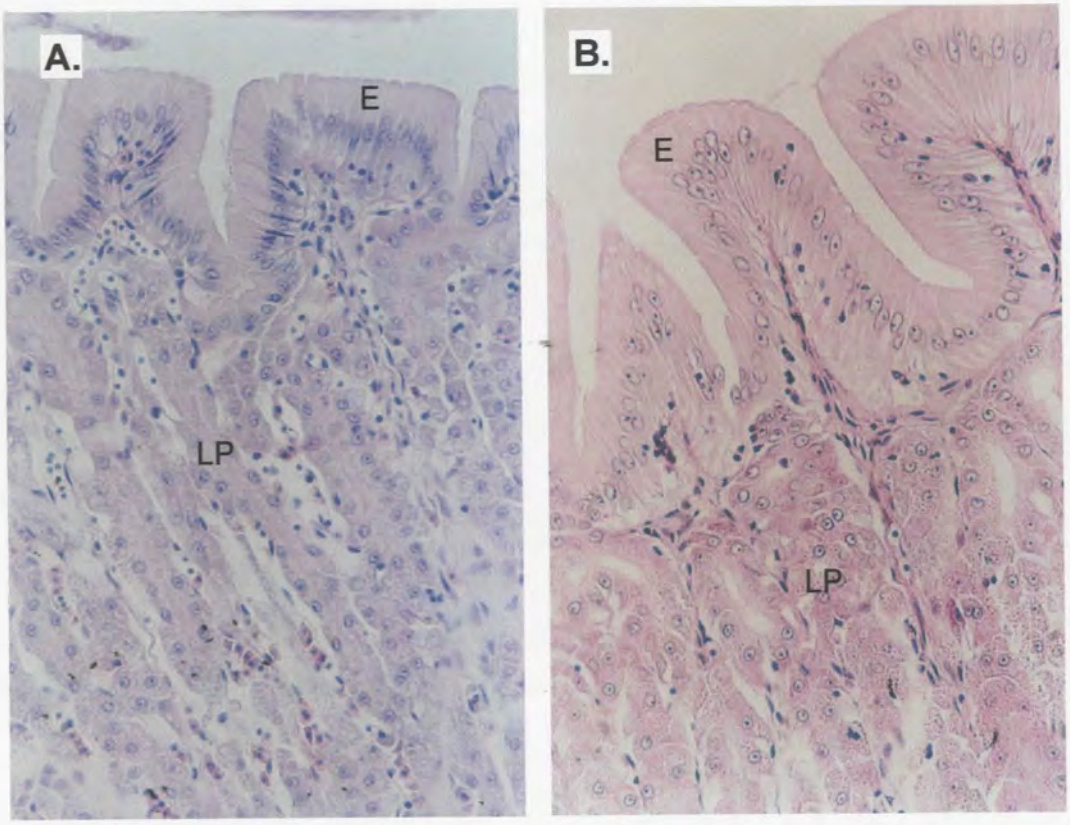


Figure 4.20. The simple columnar epithelium (E) and the underlying glandular cells in the lamina propria (LP) of (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus* (x 200, H&E).

The stomach musculature of both species consisted of centrally nucleated spindle-shaped smooth muscles (Figure 4.21A & B).

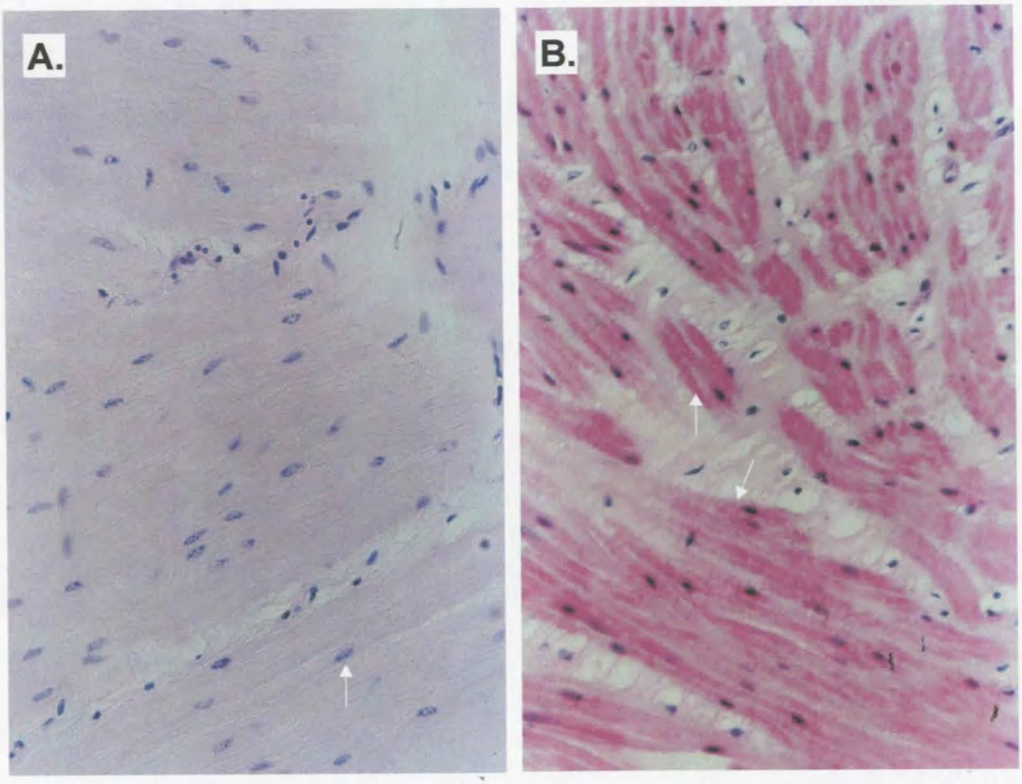


Figure 4.21. The centrally nucleated smooth muscles in the stomach fundic regions of (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus.* Note the nucleus (arrow) in the spindle shaped muscle fibers (x 200 H&E).

In both *B. nyasensis* and *C. gariepinus* the middle region of the intestine consists of the following layers: columnar epithelium, lamina propria-submucosa, tunica muscularis and serosa. In relation to the whole intestinal wall, the villi of *B. nyasensis* were significantly shorter ($p<0.05$) while the musculature and submucosa in this species were significantly longer ($p<0.05$) than in *C. gariepinus* (Figure 4.22A & B, Figure 4.23A & B, Table 4.6).

Table 4.6. Proportion of different layers of the intestine in relation to the total intestine wall in *Bathyclarias nyasensis* and *Clarias gariepinus*

	Bathyclarias nyasensis			***Clarias gariepinus***			
Layer	**Mean value**	**S.D.**	**n**	**Mean value**	**S.D.**	**n**	**p**
Serosa	0.049	0.027	9	0.011	0.012	10	0.000886
Outer longitudinal layer	0.1	0.03	9	0.001	0.003	10	0.0000
Inner circular layer	0.18	0.037	9	0.027	0.011	10	0.0000
Submucosa	0.024	0.022	9	0.004	0.006	10	0.012268
Villi	0.51	0.12	9	0.93	0.027	10	0.0000

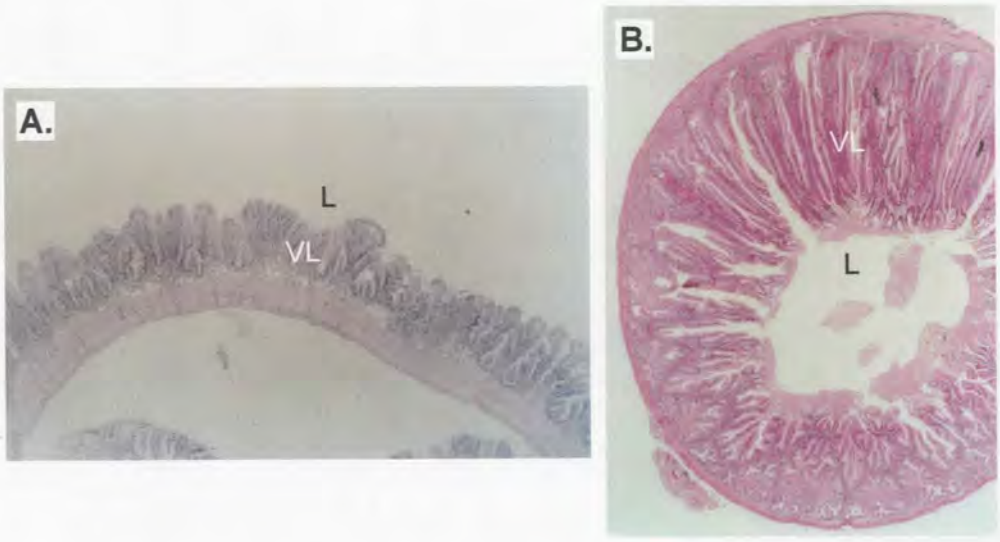


Figure 4.22. The intestinal wall showing relatively shallower villi (VL) in (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus*. L is the lumen side of the intestine (x 20, H&E).

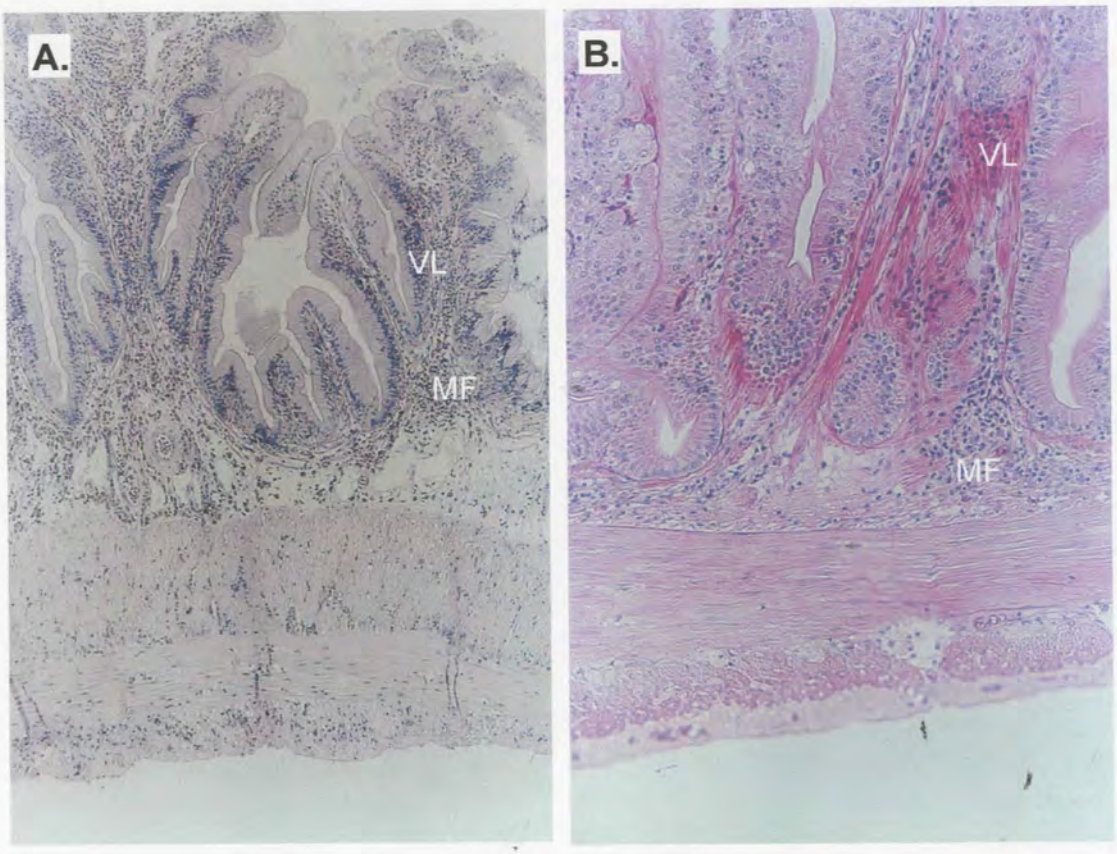


Figure 4.23. The mucosal folds (MF) projecting into villi (VL) in (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus* (x 200, H&E).

The intestinal columnar epithelium (with absorptive cells) is lined with brush border microvilli. The goblet cells are scattered along the sides of the crypts and tips of the folds (Figure 4.24).

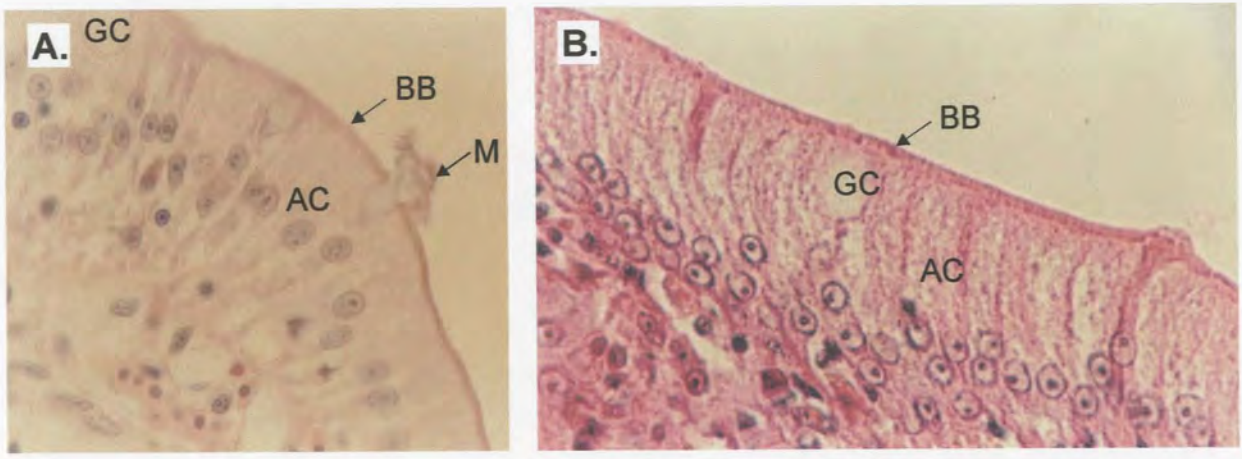


Figure 4.24. Columnar absorptive cells (AC) lined with brush borders (BB) in the middle region of intestine of (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus*. The goblet cells (GB) can be seen between the absorptive cells. Note mucous (M) being discharged from a goblet cell in (A) *Bathyclarias nyasensis* (x 1000 H&E).

The columnar absorptive cells in *B. nyasensis* were significantly taller ($p<0.05$) in *B. nyasensis* than in *C. gariepinus* (Table 4.7).

Table 4.7. Length of absorptive columnar epithelium cells in *Bathyclarias nyasensis* and *Clarias gariepinus.*

Species	Mean size (*um*)	S.D.	Minimum size	Maximum size	n	p value
Bathyclarias nyasensis	45	6.96	30	52	15	0.04
Clarias gariepinus	39	6.35	29	50	10	

Furthermore, the goblet cells in *B. nyasensis* were significantly wider ($p<0.05$) and longer ($p<0.05$) than in *C. gariepinus* (Table 4.8), although the distribution of the cells in the two species was not different ($p>0.05$) (Table 4.8).

Table 4.8. Mean goblet cell dimensions (in *u*m) and number *per um* within the mid region of the intestine of *Bathyclarias nyasensis* and *Clarias gariepinus.*

	Clarias gariepinus	*Bathyclarias nyasensis*	p value
Mean width (*um*)	9.17	10.64	0.0002
S.D.	2.05	2.30	
Minimum	5	7	
Maximum	15	17.5	
n	59	79	
Mean length (*um*)	13.38	15.78	0.0001
S.D.	3.61	3.52	
Minimum	7.5	10	
Maximum	30	22.5	
n	59	79	
Mean number per (*um*)	0.046	0.052	0.3200
S.D.	0.19	0.17	
Minimum	0.02	0.03	
Maximum	0.09	0.09	
n	17	17	

The lamina propria and submucosa of the mid intestinal region of both species are indistinguable and are formed of a meshwork of connective tissue fibres and blood vessels intermingled between epithelial cells. The musculature consists of an inner circular muscle and the outer, less developed longitudinal muscle. The outermost serosa consists of a layer of loose connective tissue (Figure 4.25).

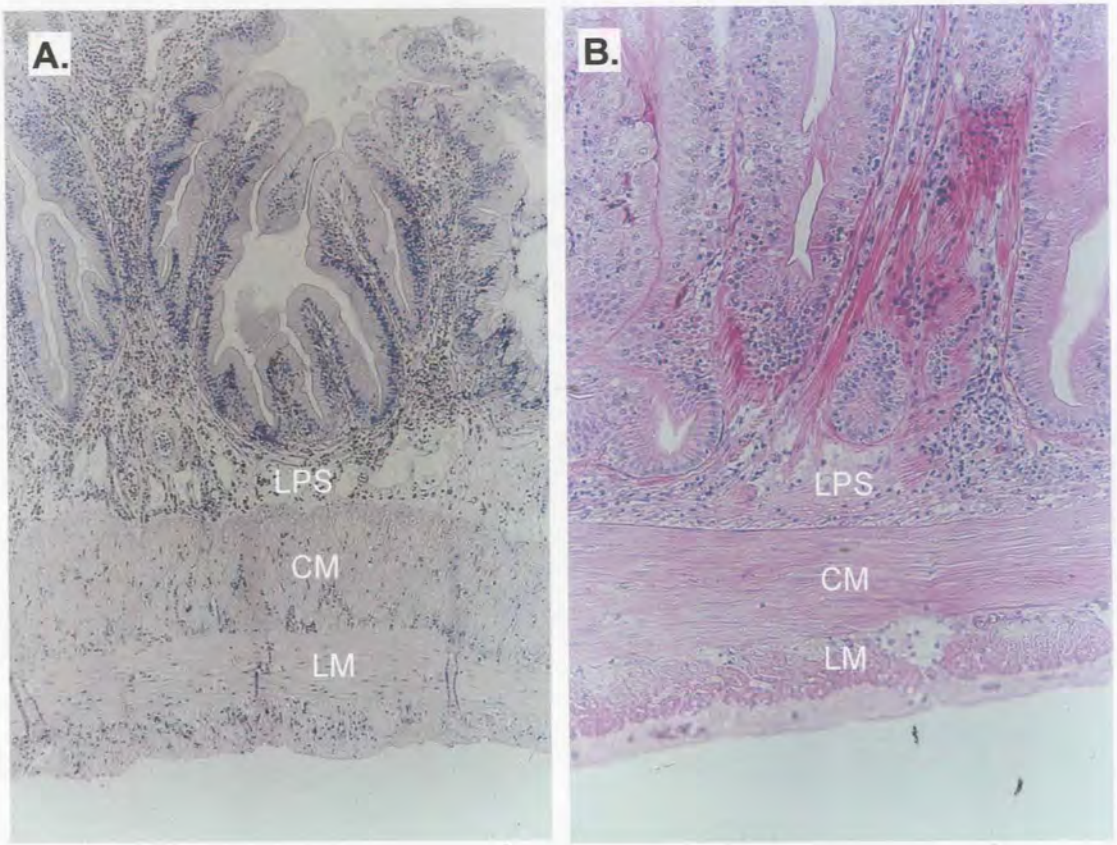


Figure 4.25. The layers in the mid region of the intestine of (A) *Bathyclarias nyasensis* and (B) *Clarias gariepinus*: the lamina propria - submucosa (LPS), circular muscle (CM), and longitudinal muscle (LM) and serosa (S) (x 200 H&E).

4.4 DISCUSSION

The observed morphological differences between *B. nyasensis* and *C. gariepinus* in size and position of eyes, mouth type, size of circum-oral barbels, filtering area and buccal cavity volume, size of teeth and tooth plates and relative gut length (RGL) may reflect interspecific differences in food and feeding habits of the two species.

Large eyes are associated with predatory behaviour (Fryer & Iles 1972), especially planktivory, where they may be used to provide accurate depth perception needed to judge prey size (Pietsch 1978). Moreover, larger eyes are typical of bathypelagic species (Gerking 1994) and are required by fish to feed on epibenthic zooplankters in low light intensity (Nagelkerke 1997). Dorsal eyes on the other hand are typical of benthic fishes (Hynes 1970, Gerking 1994).

Consistent with the suggested functions relating to eye size and position, Bruton (1979) hinted that the relatively small eyes of *C. gariepinus* were not functionally used for sight, as an antero-dorsal field of view would not allow for a direct anterior, posterior and ventral vision. Bruton (*op cit.*) observed that hungry swimming fish often bypassed stationery prey unless the prey made some direct contact with some part of the predator's body. Given that the eyes of *B. nyasensis* are significantly larger ($p<0.05$) than those of *C. gariepinus* and are laterally positioned, may suggest that they are used for food searching in a bathypelagic environment.

Barbels occur in many groups of fishes as accessory feeding structures possessing sensory organs (Lagler *et al.* 1977). In members of the order Siluriformes they serve as a set of "tongues" with a combined gustatory and tactile function (Atema 1971). Taste buds that were observed on the circum-oral barbels of *B. nyasensis* and *C. gariepinus* are

characteristic of siluroid catfishes (Atema 1971, Nisbet 1979, Tilney & Hecht 1990, Booth 1996). Bardach and Atema (1971) suggested that taste buds have a mechano as well as a chemosensory function. Touch sensitivity arises from the nerves innervating the taste buds, which radiate to the surrounding regions (Lagler *et al.* 1977). The gustatory (taste) system is involved in food detection, selection and ingestion, and in protection against noxious substances, while olfaction is possibly involved in responses associated with food detection, fright, mating, spawning, territorial and homing behaviour (Hara 1994).

Gosline (1973) and Bruton (1979) described the circum-oral barbels of clariids as forwardly directed "seines" and probes, respectively, which assist the fish in the capture of mobile and sedentary prey. The relatively longer barbels in *B. nyasensis* suggest that the sense of taste and touch are more acute in this species than in *C. gariepinus*. Furthermore, Bruton (1979) hypothesised that *C. gariepinus* use barbels to scan large volumes of water. Given that *B. nyasensis* has significantly longer ($p<0.05$) barbels than *C. gariepinus*, it is suggested that the former can scan a much larger volume of water than *C. gariepinus.*

A vertically directed mouth enhances surface feeding while a subterminal mouth enhances bottom feeding (Gerking 1994). The subterminal mouth of *C. gariepinus* is more suited for benthic feeding and the hypertrophied fleshy lips may serve as "shock-absorbers" when the fish forces its snout into the ground. In contrast, the mouth of *B. nyasensis* is terminal and more suitable in the pelagic environment.

The family Clariidae belongs to the superorder Acanthopterygii where suction is the most widespread feeding system (Alexander 1967). In catfishes, the buccophyrangeal chamber

is increased by lowering the hyoid apparatus, thus creating a strong negative pressure in the vicinity of the food that is consequently carried towards the mouth in the current (Gosline 1973). Increasing buccal-cavity volume (Pietsch 1978) can increase suction pressure. Hence, it may be expected that *B. nyasensis*, with its significantly larger ($p<0.05$) buccal cavity volume, is more efficient at suction feeding than *C. gariepinus*.

The notable changes that occur in the buccal cavity volume of *B. nyasensis* between 500 – 600 mm TL suggests a greater reliance on suction feeding at this size. These changes synchronise with changes in filtering area. Filtering area is a function of the gill rakers. This suggests that gill rakers play a role in feeding in *B. nyasensis*. The role of gill rakers in particulate feeders is questionable (Drenner *et al.* 1987, Langeland & Nost 1995); however, their role as filtering devices in filter-feeding species is well established (Mummert & Drenner 1986, MacNeil & Brandt 1990, Qin & Fast 1997). As gill rakers seem to play a role in feeding in *B. nyasensis*, suggests that, just as in *C. gariepinus* (Murray 1975), they may be used as filtering devices. The fact that changes in filtering area and buccal cavity volume synchronise with change in growth rate and a possible habitat shift (Chapter 2), suggests that at this fish size (500 – 600 mm TL), *B. nyasensis* changes to a diet that requires intense filter feeding.

Tooth plate arrangement and tooth size may be used to predict feeding habits (Fryer & Iles 1972, Blaber *et al.* 1994). Larger tooth plates may aid in holding and crushing large mobile prey, while smaller plates indicate a propensity for smaller less mobile soft-bodied invertebrate prey (Blaber *et al* 1994). *C. gariepinus* takes mainly fish and seems to use the vomerine plates to crush and grip prey (Bruton 1979). This may explain why the species has broad premaxillary, mandibular and vomerine tooth plates. Given that the

tooth plates in *C. gariepinus* are significantly broader ($p<0.05$), it can be predicted that *B. nyasensis* has an inclination to feed on smaller less mobile invertebrate prey.

Generally, teeth on the outer jaws and pharyngeal bones of piscivorous species are stout (Fryer & Iles 1972), unicuspid (Greenwood 1973), sharp and backwardly directed (Fryer 1957, Fryer & Iles 1972). Large sharp teeth are adaptations for grasping large swimming prey (Chao & Musick 1977), while recurved and pointed teeth are primarily used to hold prey that may be swallowed whole (see review by Mullaney & Gale 1996). Posteromedial orientation (backward recurving) of teeth may facilitate entry of large prey items into the mouth, hindering or preventing their anterior escape (Mullaney *op. cit.*) Where holding may be done by the hyoid apparatus or the pharyngeal bones, the stout upper pharyngeal teeth can rasp and tear flesh of the prey that is pressed against them (Fryer & Iles 1972). In contrast, teeth in plankton feeders teeth are greatly reduced and the pharyngeal bones are scarcely used for mastication (Fryer & Iles 1972).

The significantly longer and stouter ($p<0.05$) premaxillary and dentary teeth and the observed recurved palatine, pharyngeal and vomerine teeth of *C. gariepinus* are a perfect adaptation to its reported piscivorous feeding mode (Bruton 1979). Consistent with the findings on tooth plate sizes, the significantly ($p<0.005$) smaller, straight teeth in *B. nyasensis* suggest a propensity for invertebrate prey.

The heterodont dentition (with molar-like teeth and few conical teeth on distal margins) on the vomerine tooth plates of both *B. nyasensis* and *C. gariepinus* indicates an adaptation for a wide-spectrum diet including snails. Given that molluscs form part of the diet of *C. gariepinus* (Bruton 1979), it is likely that they are also part of the diet of *B. nyasensis*.

Relative gut lengths (RGLs) can be used to describe the feeding ecology of a species. Uys (1989) compiled a summary of relative gut lengths of fishes (Table 4.9).

Table 4.9. Fish species ranked according to their mean relative gut length (RGL) with reference to their feeding habits (compiled by Uys (1989) and this study).

Species	RGL	Feeding ecology	Author
Labeo rosae	17.30	Detritivore	Kruger & Mulder, 1973
Labeo capensis	14.90	Detritivore	Kruger & Mulder, 1973
Labeo umbratus	10.00	Detritivore	Kruger & Mulder, 1973
Oreochromis mossambicus	7.90	Herbivore	Kruger & Mulder, 1973
Tilapia rendalli	7.20	Herbivore	Kruger & Mulder, 1973
Cyprio carpio	2.20	Omnivore	Kruger & Mulder, 1973
Chondostromus nasus	2.05	Omnivore	Junger *et al*, 1989
Erimyzon sucetta	1.76	Omnivore	Ribble & Smith 1983
Barbus holubi	1.70	Omnivore	Kruger & Mulder, 1973
Bathyclarias nyasensis	**1.27**	**Omnivore**	**this study**
Rutilis rutilis	1.25	Omnivore	Junger *et al*, 1989
Abramis brama	1.19	Omnivore	Junger *et al*, 1989
Clarias gariepinus	**1.18**	**Carnivore**	**Kruger & Mulder, 1979**
Barbus kimberleyensis	1.14	Carnivore	Kruger & Mulder, 1979
Tinca tinca	1.13	Carnivore	Junger *et al*, 1989
Blicca bjoerkna	1.08	Omnivore	Junger *et al*, 1989
Clarias gariepinus	**1.07**	**Carnivore**	**Kruger & Mulder, 1979**
Rutilis rutilis	1.05	Omnivore	Al Hussaini, 1949
Eutropius depressirostris	1.04	Carnivore	Kruger & Mulder, 1979
Leusciscus cephalus	1.01	Omnivore	Junger *et al*, 1989
Barbus matozzi	0.96	Carnivore	Kruger & Mulder, 1979
Clarias gariepinus	**0.96**	**Carnivore**	**Uys, 1989**
Lepomis auritus	0.91	Carnivore	Ribble & Smith 1983
Abramis ballerus	0.82	Carnivore	Junger *et al*, 1989
Aspius aspius	0.79	Carnivore	Junger *et al*, 1989
Ictalurus natalis	0.78	Carnivore	Ribble & Smith 1983
Pelecus cultratus	0.78	Carnivore	Junger *et al*, 1989
Gobio gobio	0.72	Carnivore	Al Hussaini, 1949
Micropterus salmoides	0.72	Carnivore	Ribble & Smith 1983
Esox americanus	0.58	Carnivore	Ribble & Smith 1983
Clarias gariepinus	**0.45**	**Carnivore**	**Stroband & Kroon, 1981**
Aphredoderus sayanus	0.40	Carnivore	Ribble & Smith 1983
Percina nigrofasciata	0.37	Carnivore	Ribble & Smith 1983
Anguilla rostrata	0.31	Carnivore	Ribble & Smith 1983

Fish with a RGL of <1 were classified as carnivorous. Those with RGLs between 1 and 1.2 were classified as carnivorous/omnivorous, fish with RGL between 1.2 and 2.2 as omnivorous, those with a RGL between 7 and 8 as herbivorous and fish with a RGL >10 as detritivores. *B. nyasensis* and *C. gariepinus* have RGLs of 1.27 $\pm$ 0.24 and 0.93 $\pm$ 0.32 and, therefore are considered to be omnivorous and carnivorous/omnivorous, respectively. It should be noted that while ontogenetic changes in filtering area and buccal cavity suggests diet changes when *B. nyasensis* attain 500-600 mm TL, the RGL does not change with fish size (Figure 4.15) suggesting that there is no change in the basic composition of the diet.

Histological examination of the oesophageal region, the stomach fundic region and the middle part of the intestine showed structures that are typical of teleost fishes. The presence of squamous epithelial and mucous cells is characteristic of the oesophageal region of teleost fishes and has been observed in *C. gariepinus* (Sis *et al.* 1979) and other species (Morrison & Wright 1999).

Similarly, striated or skeletal muscles observed in the oesophagus of both species is typical for this region of the alimentary tract (Fänge & Grove 1979). These muscles are voluntary in nature (Wheater *et al.* 1987) and may thus allow for rejection/acceptance of undesired/desired food items. Histological differences between the two species seem to lie in the complexity and type of the folds and the presence or absence of fibers in the lamina proria-submucosa. Folds allow distension during swallowing and therefore provide a large surface area for the passage of food (Clarke & Witcomb 1980). *C. gariepinus*, with its greater folding of the lamina propria-submucosa, would therefore have better distensibility to allow a larger portion of food per given time than *B. nyasensis*. On the other hand, *B. nyasensis* seem to compensate for the shorter folds by

having muscle fibers interspersed within the collagen connective tissue. These fibers, which were not observed in *C. gariepinus* allow for elasticity (Caceci 1998) of the oesophagus, thereby allowing passage of a large portion of food per time.

The fundic region of the stomach of the two species showed columnar epithelial cells, gastric glands in the lamina propria and a musculature which is typical of this region. The tall columnar epithelial mucus-secreting cells are shed continuously and are replaced by cells from the gastric pits (Wheator *et al.* 1987). Mucus may have assorted digestive functions and aid in lubrication (Clarke & Witcomb 1980, Anderson 1990, Murray *et al.* 1996).

The gastric glands of both *C. gariepinus* and *B. nyasensis* are of a uniform nature and show no differentiation into peptic or oxynctic cells, and have a granular nature. Fänge & Grove (1979) reviewed the ultrastructure of gastric glands in teleosts. At their bases the cells contain zymogen-like secretory granules and a rich endoplasmic reticulum. These ultrastructural features are consistent with the hypothesis that they are active in both acid production and in the synthesis of pepsinogen. Pepsinogen is activated to pepsin in an acid environment. Pepsin is an endopeptidase that attacks peptide linkage of most proteins. Due to the similar structure of the gastric glands in *B. nyasensis* and *C. gariepinus* with those in most fishes suggests that they also secrete both pepsinogen and hydrochloric acid.

The simple intestinal columnar epithelium with a brush border of microvilli present in both *B. nyasensis* and *C. gariepinus* is typical of absorptive tissue in teleosts (Fänge & Grove 1979). Al-Hussaini (1949) termed the columnar epithelial cells of this region the "columnar absorptive cells", emphasising their function other than their shape. The

significantly taller ($p<0.05$) villi in *C. gariepinus* suggest a larger surface area for absorptive functions than in *B. nyasensis*. However, the significantly taller ($p < 0.05$) absorptive cells of *B. nyasensis* may imply higher efficiency in absorptive functions than in *C. gariepinus*. Al-Hussaini (1949) observed that the filamentous processes of absorptive cells are not separate intercellular spaces but one continuous space filled with fluid, which freely communicates with the tissue fluid in the sub-epithelial core, either by diffusion through the permeable basement membrane or by actual minute perforations. Thus, this "excretory area" or the surface area which the substances may diffuse from the absorptive cells to body fluids, is enormously increased by the tapering of the basal portions of the epithelial cells. Therefore, fish with shorter absorptive cells would, accordingly, have a smaller excretory area. The significantly taller absorptive cells in *B. nyasensis*, would imply larger excretory area suggesting a high efficiency in absorptive function, thereby compensating for the short villi.

Furthermore, the significantly ($p<0.05$) larger proportion of intestinal musculature in *B. nyasensis* in comparison to *C. gariepinus* would limit distensibility, and therefore the size of food items that could pass through the intestine of *B. nyasensis*. However, the significantly larger ($p<0.05$) goblet cells of *B. nyasensis* may be an adaptation to cope with a large amount of food per unit time. The structure and function of goblet cells has been well described by Al-Hussaini (1949), Clarke and Witcomb (1980) and Wheater *et al.* (1987). These "flask"-shaped cells are attached to the basement membrane, and have the same length as the columnar cells. The distended apical cytoplasm contains a dense aggregation of mucigen granules which, when released by exocytosis, combines with water to form mucus. The width of goblet cells depends on their mucus content (Clarke & Witcomb 1980). Hence, by having significantly wider ($p<0.05$) goblet cells, *B. nyasensis* emits more mucus than *C. gariepinus*. Mucus aids in emulsifying food into chyme or

lubricating faecal substances (Clarke & Witcomb 1980). Hence, it can be suggested that the relatively (though theoretical) higher amount of mucus emitted by *B. nyasensis* would allow this species to handle a large quantity of food.

Al-Hussaini (1949) emphasised the importance of considering the intestinal mucosal area in relating gut length to fish diet. He found that a large area compensated for shorter intestinal lengths. Using this logic, it can be expected that the significantly shorter ($p<0.05$) RGL of *C. gariepinus* would be compensated for by taller villi projections. However, the differences in the size of absorptive and goblet cells suggests that the differences in observed in RGL reflect differences in digestive capabilities of the two species.

Overall, the results from the histological examination lead to similar observations made by Uys (1989) i.e., that there is very little interspecific variation in the digestive histology of teleosts. Rather, the main interspecific differences may lie in the gross, morphological adaptations (e.g., presence or absence of stomach, RGL. etc.) and in the rapidity of the functional development of the digestive organs in the early life-history stages. The microscopic structures of *B. nyasensis* and *C. gariepinus* do not seem to differ in any significant way from each other. Fänge and Grove (1979) noted that the basic gut plan of species of the same origin is similar, and that the minor modifications due to diet are superimposed on the plan. If this hypothesis is accepted, then the modifications due to diet may have led to significant differences in RGL of *B. nyasensis* and *C. gariepinus*. As the two species belong to the same family, Clariidae, the basic/histological structure has remained intact. Admittedly, these conclusions remain speculative as the whole digestive system and its ultrastructure was not considered in this study.

Finally, a comparison of the structures associated with feeding between *B. nyasensis* and *C. gariepinus* and the observed and predicted feeding habits of the two species respectively are presented in Table 4.9.

Table 4.9. A comparison of the structures associated with feeding between *Bathyclarias nyasensis* and *Clarias gariepinus* (from Bruton 1979, and this study).

	Clarias gariepinus		***Bathyclarias nyasensis***	
Morphological feature	**Description of morphology feature**	**Observed diet/feeding strategy**	**Description of morphology feature**	**Predicted food habit/feeding strategy**
Eyes	Small	Eyes not used in detecting food	Large	Eyes probably used in detecting food
Mouth type	Subterminal	Bottom feeding		Predator- feeding in water column
Premaxillary and vomerine tooth plates	Large	Suitable for capturing and holding large moving prey	Small	Suitable for small moving prey and invertebrates
Vomerine teeth	Heterodont large, recurved incisors and molariform	Piscivorous, diet including molluscs	Heterodont, straight and relatively smaller incisors , and molariform	Molluscs included in diet
Maxillary teeth	Stout and long	Piscivorous,	Stout but relatively slender, and shorter	Less inclination to feeding on fish than *C. gariepinus*
Pharyngeal teeth	Highly recurved and stout	Used in holding, rasping/tearing flesh	straight and slender, small	May not be used in rasping or tearing prey
Mandibular teeth	Stout and long	Piscivorous	Small, sharp but relatively short and slender	Less reliant on fish prey
Barbels	Relatively short	Ambush predator, fish prey	Significantly long	Can scan a wider volume of water, may include fish in diet
Filtering area	Small	Filter feeding, crustacea	Large	Filter feeding, crustacea changes in filtering ability at 500 – 600 mmTL
Buccal cavity volume	Small	No "special" requirement for suction in life	Large	Suction required particularly when fish reach 500-600 mm TL
Relative gut length	Variable (0.9 to 1.8), but short 0.93±0.32	Carnivorous/ Omnivorous	Long, 1.27±0.24	Omnivorous

From this summary, the size of eyes and barbels, and the mouth type of *B. nyasensis* suggests use of sight and touch to detect prey in the water column. The size of teeth and various tooth plates suggest *B. nyasensis* has the capability to handle both large and small prey, with a propensity towards small prey. The type of teeth suggests that molluscs may form part of the diet. The relative gut length suggests omnivory, with ability to switch between planktivory and piscivory. Changes in buccal-cavity volume and filtering area suggests a significant change to planktivory by filter feeding at between 500–600 mm TL.

CHAPTER 5

The diet of *Bathyclarias nyasensis*

5.1 INTRODUCTION

Studies of food habits of fishes are essential for understanding the functional role of fishes in aquatic ecosystems (Sedberry 1983). Studies in this field can be placed into two categories: those which examine the diet of a fish population with the view of assessing the species' nutritional standing in the context of the fish community as a whole, and those that attempt to estimate the total amount of food consumed by a population. Studies in the first category may consider seasonal variation in the diet and/or a dietary comparison between different subgroups of the same species, e.g., year classes or different species living in the same or comparable habitats. The second category of studies are usually conducted over repetitive 24-hr diel periods (Chapter 6). In both instances the aim may be to discern whether or not there is competition for food (Hyslop 1980), resource partitioning and prey selectivity (Sedberry 1983) or else to define predator-prey relationships.

Competition for food can be important where the resource may be limiting and where there is a high level of dietary overlap among species (Sedberry 1983). Resource partitioning is widely accepted as being the prime mechanism allowing the co-existence of species assemblages and communities (Ross 1986). Depending on fish assemblages, resource partitioning can occur along different axes, such as prey category, or space and time (Ross 1986). Ross (1986) and De Pirro *et al.* (1999) considered prey type and space as the most important axis, while in some cases, time can be the more important (Sagar & Glova 1994). Recently, Yuma *et al.* (1998) noted an additional axis in shrimp-eating cichlids in Lake Tanganyika, in which the resource is partitioned by different capturing techniques. For example, some species randomly prey on shrimp that have escaped during

forages by other fish. Alternatively, some fish may for instance position themselves behind other foraging fish and capture shrimp that have escaped from fish in front. Yet another strategy is to sort through the debris in which the shrimp have hidden themselves after the forages of other fish.

For individual fish, survival, growth and reproduction are dependent on the intake of energy and nutrients by means of its feeding activities (Wootton 1990). The diet must, therefore, contain the correct proportions of nutrients, and the nutrients must be able to be digested and absorbed in a form that makes them available to provide energy to the animal (De Silva & Anderson 1995). The capacity of different species to utilise energy contained in different nutrients varies considerably. For example, some species are able to use carbohydrates as a major energy source, while others use carbohydrates poorly and rely, to a greater extent, on protein for energy. The quality of a diet, therefore, is a function of how well a particular feed meets the energetic requirements of an animal (De Silva & Anderson 1995).

The diet of a species may also change as a consequence of habitat shifts, on a seasonal basis or in a diel cycle, and it may also change ontogenetically. Ontogenetic dietary shifts are usually associated with morphological changes (Wootton 1990), particularly an increase in mouth size and improved locomotory ability (Easton & Orth 1992). Ontogenetic changes may also be accompanied by changes in feeding behaviour. Drenner *et al.* (1982) observed that *Sarotherodon galilaeum* of different sizes displayed different feeding behaviours. Fish <20 mm SL, fed on zooplankton as obligate particulate feeders, while fish between 20-42 mm SL were either particulate or filter feeders, while those >62 mm SL were obligate filter feeders. These feeding modes were accompanied with changes in types of prey taken: particulate feeders were size selective and had highest feeding electivities for large-sized zooplankton species, while filter feeders had highest

feeding electivities for zooplankton species with poor escape ability. Zale (1987) reported similar results regarding *Oreochromis aureus.*

A habitat shift that may lead to dietary switches may be related to ontogenetic changes (ontogenetic habitat shift) or may be a response to predation risks. Fish may shift to a habitat where they are less vulnerable and where the prey items are different. These predator-mediated habitat and dietary shifts have been observed in *Galaxias gracilis* (Rowe & Chisnall 1996) and *Lepomis macrochirus* (Mittlebach 1986).

Prey availability is another factor that triggers diet changes following the shift to a different habitat. Young *et al.* (1997) observed that the southern bluefin tuna preyed on fish in inshore region, while squid and macro-zooplankton were the main prey items in offshore regions. It was proposed that the low abundance of shoaling fish in the offshore regions forced the tuna to rely on the alternative prey.

Seasonal changes in diet have been observed in many species and fish communities including: *Trachinotus marginatus* (Monteriro–neto & Cunha 1990), the demersal fish community of the outer continental shelf of the middle Atlantic bright (Sedberry 1983); the red seabream, *Pagrus major* (Shinamoto & Watanabe 1994); the South African anabantid, *Sandelia bainsii* (Mayekiso & Hecht 1986); and largemouth bass *Micropterus salmoides* (Ward & Newman 1998). Workers attributed seasonal dietary changes to prey availability and temperatures that affect metabolism and feeding rate, and therefore the diversity of prey items.

Although fish morphology can provide circumstantial evidence regarding the diet of fish (see Chapter 4), such inferences must be confirmed by direct evidence of what is eaten (Wootton 1990). The objective of this chapter therefore, is to ascertain the diet of *B. nyasensis* of different

sizes, in different seasons, and caught from different water depths. The study also investigates (using findings from other studies) whether or not intraspecific or interspecific competition and resource partitioning with co-occurring species does occur. This would allow us to elucidate the ecological role of *B. nyasensis* as well as to test the hypothesis that the observed ontogenetic changes in buccal cavity volume/filtering area (Chapter 4) are reliable indicators of an ontogenetic dietary shift.

5.1.1 A brief review of methods used in studying the diet of fish

The analysis of the food consumed by fish is based on identification of stomach contents since digestion in the stomach is generally less advanced than in the remainder of the alimentary canal. The quantitative and qualitative methods of studying food composition have been reviewed extensively be several workers (Hynes 1950, Hyslop 1980, Tudorancea *et al.* 1988, Wootton 1990, Konchina & Pavlov 1995, Cortès 1997, Hansson 1998). A synoptic review of the methods is provided below.

Percent frequency of occurrence represents the number of fish (i.e. stomachs) in which a particular food item was found expressed as a percent of the total number of feeding individuals. This method allows for a qualitative characterisation of the diet, i.e., the selection and commonness of prey in the diet of the predator. One problem with the method is its failure to account for the volumetric or gravimetric proportion of the prey. A prey item may have the same percent frequency of occurrence in two different species, but the prey item in these species may be very different volumetrically/gravimetrically.

The numerical method is the number of a given food item in relation to the total number of all consumed prey expressed as a percentage. The main problem with this method is the overemphasis

on small prey items that may supply little total energy in comparison to a large prey item. In addition, the method cannot be used when prey is highly digested or does not form discrete units, for example when fish feed on macrophytes, detritus, or gelatinous zooplankton.

The volumetric and gravimetric methods express the proportion of a given prey to total volume or weight of the prey items in the gut as a percentage. Measurement of volume of prey is done either by the replacement method or based on three measurements of discrete prey items (length, width, and height), which is not always possible. Modifications of the volumetric method include the points method wherein the volume of prey item with respect to total volume of prey is estimated visually and expressed as a percentage. In the gravimetric method, the weight of prey items is taken. The problem with both volumetric and gravimetric methods is the overemphasis of large prey items that may not actually be the preferred prey.

Owing to the inherent problems of the different methods, a number of compound indices that incorporate one or more of the methods have been developed. One of these is the index of relative importance (IRI) (Hyslop 1980), commonly used:

$$IRI = (\%N + \%V) \times \%F \qquad \text{Equation 5.1}$$

where: % N = percent total numbers
% V = percent volume
% F = percent frequency of occurrence

In some cases where there is a great disparity in the size of individual prey items such as zooplankton and fish, the numerical method is omitted from equation 5.1, such that the IRI is calculated as:

$$IRI = \%V \times \%F \qquad \text{Equation 5.2 (Palomares } et\ al. \text{ 1997)}$$

Cortès (1997) noted that the IRI values make comparisons between food types difficult, and suggested that the IRI be expressed on a percent basis, such that %IRI for a specific prey category $_i$ (% IRI_i) becomes:

$$\% IRI_i = 100 IRI_i \sum_{i=1}^{n} IRI_i \qquad \text{Equation 5.3}$$

where n = the total number of food categories considered at a given taxonomic level.

Cortès (1997) also observed that many feeding studies attempt to describe variations in stomach contents owing to season, size, location, habitat or other factors only on a qualitative basis, and do not provide statistical support for their conclusions. He reviewed the statistical methods that have so far been used in diet studies, including multivariate analysis of variance (MANOVA) and hypothesis-free canonical discriminant analysis. Cortès (*op cit.*) also suggested that when stomach contents are expressed numerically or as occurrences, a multi-way contingency-table analysis based on log-linear models could be used. In this method, the significance of the interactions (e.g., prey type by season, to test if there are significant seasonal differences in diet of fish) is tested by individually deleting them from the log-linear models. A post-hoc test is then run to detect the specific differences. One advantage of this technique is that it allows one to readily identify the rows (e.g., prey types) and columns (e.g., season) most responsible for the dietary differences. Details on the use of contingency-table analyses may be found in Zar (1984).

5.2 MATERIALS AND METHODS

Fish were obtained from the south east arm of Lake Malawi, between latitudes 13°50'S and 14°59'S and longitudes 34°01'E and 35°04'E (Figure 2.1), at depths between 10 and 83 m. All specimens were collected on board the R/V Ndunduma, using a bottom trawl net, at a trawling speed as described in Chapter 3. Fish were weighed and measured to the nearest (g) and (mm), then dissected and the stomachs removed. Stomachs that appeared to have no contents were cut open to check if there were any traces of food. Stomachs with visible contents were immediately preserved in 10% formaldehyde for later analysis in the laboratory. Out of 776 fish that were dissected, 343 with identifiable stomach contents were analysed.

In the laboratory, a longitudinal incision was made in the stomach wall to expose the contents. Large prey items were removed using forceps, while small food particles were flushed into containers using water. Stomach contents were examined under a dissecting microscope. Identification of prey items was made to the lowest taxon possible. Prey items were placed in a single petri dish and sorted into different taxonomic categories. The relative volume of each prey category was estimated visually. Prey items in each category were then counted. Where small prey items (e.g., zooplankton) were numerous, they were placed in a known volume of water and thoroughly mixed by swirling the water, of which 10 % removed for sorting and enumerating. At most this dilution was done twice.

Stomach contents were analysed for the whole sample, fish size, season and in relation to water depth using three methods:

(a) Frequency of occurrence: The number of stomachs in which a prey item occurred was expressed as a percentage of the total number of stomachs in the sample.

(b) Numerical occurrence: For each prey item, the number of individuals was expressed as a percentage of the total number of all prey items recorded.

(c)Volumetric method: The relative volume of each prey item was expressed as the percentage of the volume of the stomach contents. In this method, all the prey items were put together in a single petri dish to visually estimate the initial volume. The prey items were then sorted into various taxonomic categories, and their relative volume visually estimated.

Due to large differences between individual zooplankton and fish prey, partial digestion of the larger prey items, such as small fish and insects, the numerical method significantly overemphasized the importance of zooplankton. The IRI, therefore, was computed using equation 5.2. Percent IRI (equation 5.3) was also computed to estimate the relative importance of prey item categories in the whole sample, per size class, per season and in relation to water depth.

Although only 44.2% of the total number of fish were analysed the size range for which the contents were analysed is a fair representation of the population size range that was obtained in the study (Figure 5.1).

To confirm the predicted ontogenetic changes in diet, fish with stomach contents were categorised into six size groups (Table 5.1).

To determine whether there is any evidence of a seasonal shift in diet, fish of two size categories (200-399 mm, and 400-865 mm TL) were placed into three seasonal climatic categories (see Chapter 2): Cold-dry (CD, July-October), warm-wet (WW, November-March) and warm-dry

(WD, April-June) (Table 5.2). Size distribution of fish that were examined and those that were analysed for stomach contents in each season is presented in Figures 5.2a, b and c.

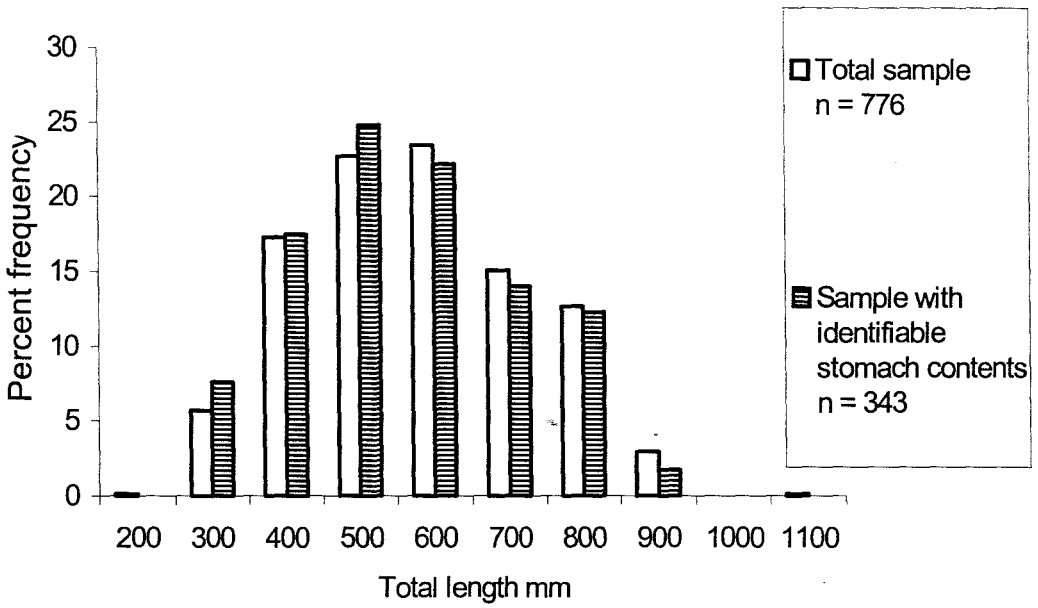


Figure 5.1. Size frequency distribution of total sample of *Bathyclarias nyasensis* that were examined and those with identifiable stomach contents.

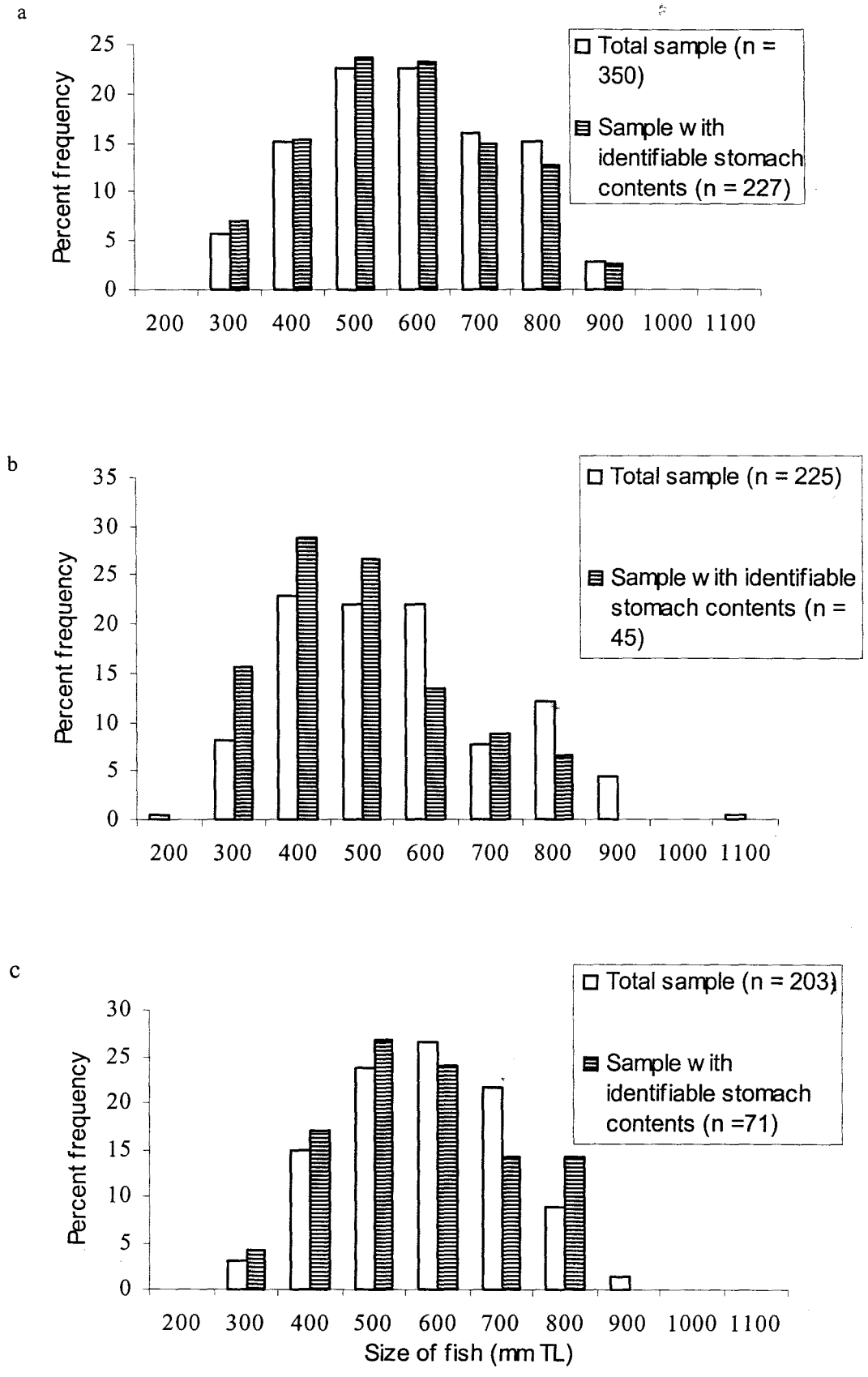


Figure 5.2. Size distribution of total sample of *Bathyclarias nyassensis* and sample that had identifiable stomach contents in (a) CD (cold-dry), (b)WW (warm-wet) and (c) WD (warm-dry seasons).

Table 5.1. Number of *Bathyclarias nyasensis* in different size classes (TL, mm) that were analysed for stomach contents.

Size class (mm)	200-299	300-399	400-499	500-599	600-699	700-865	TOTAL
No. of fish	22	62	82	76	51	50	343

Table 5.2. Number of *Bathyclarias nyasensis* that were analysed for stomach contents in different seasons.

Season	Size 1 (200-399 mm, TL)	Size 2 (400-865 mm, TL)
CD (cold-dry)	102	125
WW (warm-wet)	32	13
WD (warm-dry)	31	39

To examine possible diet changes with depth, fish in two size groups (200 – 399 mm and 401 - 865 mm TL) were placed in three depth categories: SH = shallow (10-40 m), IN = intermediate (40-60 m) and DE = deep waters (60-86 m)(Table 5.3). Size distribution of fish that were examined and those that were analysed for stomach contents per depth category are presented in Figures 5.3a, b and c.

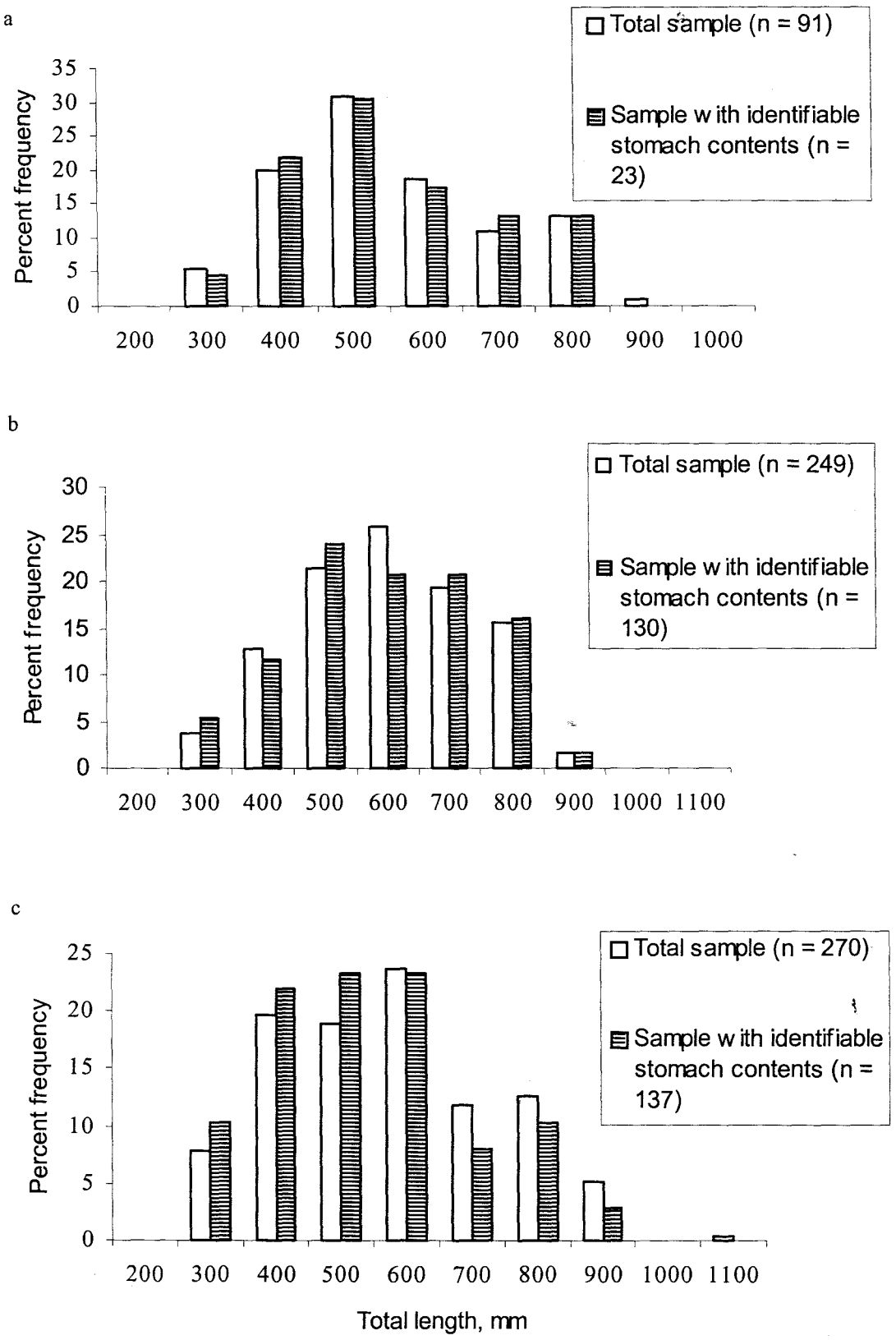


Figure 5.3. Size distribution of total sample of *Bathyclarias nyassensis* and sample that had identifiable stomach contents from (a) SH (shallow), (b) INT (intermediate) and (c) DE (deep) water.

5.2.1 Data analysis

Differences in occurrence of major prey categories were determined using contingency-table analyses (as suggested by Cortès 1997). The first step was to determine whether there was

Table 5.3. Number of *Bathyclarias nyasensis* that were analysed for stomach contents in different water depths.

Depth (m)	Size 1(200 – 399 mm TL)	Size 2 (400 – 865 mm TL)
Shallow (10-40)	11	12
Intermediate (41-60)	52	78
Deep (61-86)	74	63

significant interaction in occurrence of prey category with: a) size of fish, b) depth, and c) season in which fish were caught. Two separate (size *x* season; size *x* depth) three-way contingency tables (log-linear) of the form 7 *x* 2 *x* 3 were used to test the interactions, where:

7 = number of prey types: (1) fish remains, (2) zooplankton, (3) insects, (4) molluscs, (5) algae, (6) amorphous digested material, and (7) miscellaneous (fish larvae, fish eggs flatworms, crabs and sand or stone pebbles);

2 = the size categories of fish (200 – 399 and 400 – 865 mm TL);

3 = the number of categories of depths (S, I and D) or seasons (CD, WW and WD), respectively.

Post-hoc contingency tests were carried out to determine the sources of variation in the interactions that were significant at $p < 0.001$. The columns (food types) and/or rows (size of fish, depth range and season) were eliminated until non-significant χ^2 (chi-square) were achieved (Zar 1984).

5.3 RESULTS

Seven major prey categories were found in stomachs of *B. nyasensis*. These were fish remains, zooplankton, insects, algae, molluscs, amorphous digested material and miscellaneous material. The miscellaneous group included prey items that were identifiable but only found in small quantities, viz. fish larvae and eggs, algae, flatworms, higher plants and small portions of sand plus small stone pebbles that may have been taken together with other prey items. Table 5.4 provides the detail of the prey categories and the stage of digestion in which they were found.

Overall, results show that zooplankton formed the greatest proportion (%IRI=75.4) of the diet of *B. nyasensis.* The next major prey category was fish with %IRI of 10. It could be presumed that the amorphous digested material could be from either zooplankton or fish. Other prey categories formed a proportion of the diet. Insects, algae and molluscs had %IRI values of 0.6, 0.1 and 0.07, respectively. These results are shown in Table 5.5 and Figure 5.4.

Distinct changes in %IRI of different prey types were noted with fish size (Table 5.6, Figure 5.5). The relative importance of zooplankton increased from about 10% in small fish (200 – 299 mm TL), to 91.9% in large fish (700 – 865 mm TL). Conversely fish remains decreased in importance from 29.1% in small catfish (200 – 299 mm TL) to 2.6% in large catfish (700 – 865 mm TL). The relative importance of insects also decreased from 16.7% in the small fish (200 – 299 mm, TL) to less than 1% in the large fish (700 – 865 mm TL). However, the importance of all prey items in the small size category (200 – 299 mm TL) may have been masked by the high portion of amorphous

digested material (47.7%). The amount of this material decreased to 5.5% in large fish (700 – 865 mm TL).

Table 5.4. Details of the prey categories and the state of digestion in which they were found.

Prey category	Family/Species	State of digestion in which prey were usually found	Importance in each relation to other prey types in each category
Fish remains	*Diplotaxodon* spp.	partially digested, few occasions when identifiable to species level	
	Lethrinops spp.	partially digested, few occasions when identifiable to species level	
Zooplankton	*Mesocyclops aequatorialis aequatorials*	almost intact, easily identifiable	dominant, commonly found
	Tropodiaptomus cunningtoni	almost intact, easily identifiable	dominant, commonly found
	Bosmina longirostris	almost intact, easily identifiable	commonly found but in small quantities
	Diaphanosoma excisum	almost intact, easily identifiable	rarely found and in small quantities
	Thermocyclops neglectus	almost intact, easily identifiable	rarely found and in small quantities
Insects	Acriidae	partly digested, only parts found	
Algae	*Moagentia* sp.	almost intact, easily identifiable	commonly found
	Cynophyta (blue-green algae)	easily identifiable	rarely found
Molluscs	*Bellamya* spp.	mostly digested, only parts were found	
Amorphous Digested material		fully digested difficult to identify	
Miscellaneous	fish larvae	almost intact	commonly found
	fish eggs	almost intact	commonly found
	flatworms	almost intact	rarely found
	crabs	highly digested, only parts	rarely found

Table 5.5. Categories of prey found in stomach contents of *Bathyclarias nyasensis* (n = 343). The numbers are occurrence, % frequency of occurrence (%F), percent volume (%V), Index of Relative Importance (IRI) and % IRI of prey items.

Prey category	Occurrence	% F	%V	IRI	%IRI
Fish remains	83	24.63	21.42	527.43	10.10
Zooplankton	259	76.85	51.24	3937.81	75.40
Insects	29	8.61	3.64	31.36	0.60
Algae	14	4.15	1.25	5.20	0.10
Molluscs	7	2.08	1.72	3.58	0.07
Digested amorphous material	133	39.47	17.98	709.48	13.58
Miscellaneous	29	8.61	2.75	7.95	0.15

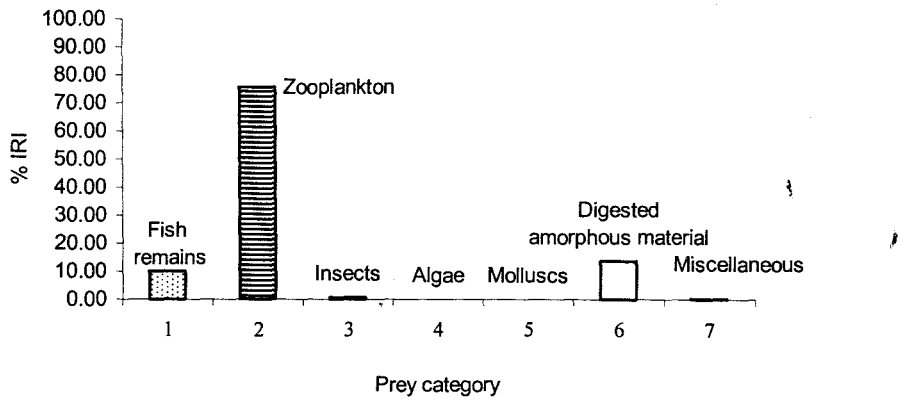


Figure 5.4. Percent IRI of dietary categories in the stomachs of *Bathyclarias nyasensis* (n = 343).

Table 5.6. Categories of prey found in stomach contents of *Bathyclarias nyasensis* per size class. Values denote occurrence (O), percent frequency of occurrence (% F), percent volume (% V), Index of Relative Importance (IRI) and % IRI of pre categories.

	Size category (total length, mm)														
Prey category	**200 - 299 (n = 22)**					**300 - 399 (n = 62)**					**400 - 499 (n = 82)**				
	O	**% F**	**% V**	**IRI**	**% IRI**	**O**	**% F**	**% V**	**IRI**	**% IRI**	**O**	**% F**	**% V**	**IRI**	**% IRI**
Fish remains	8	36.4	31.7	1153.0	29.1	18	29.0	26.8	778.0	19.2	25	30.5	26.9	819.0	15.6
Zooplantkon	9	40.9	9.7	398.0	10.0	41	66.1	36.0	2382	58.7	63	76.8	48.6	3732	70.9
Insects	10	45.6	14.6	622.0	16.7	8	12.9	8.3	107.0	2.6	5	6.1	3.3	20.2	0.4
Algae	0	0.0	0.0	0.0	0.0	2	3.2	1.5	4.9	0.1	4	4.9	1.6	7.6	0.1
Molluscs	2	9.1	6.5	58.9	1.5	3	4.9	4.2	20.3	0.5	2	2.4	2.3	5.6	0.1
Miscellaneous	1	4.8	0.2	0.8	0.02	8	12.9	3.1	19.4	0.4	3	3.6	1.1	2.7	0.1
Amorphous digested material	10	45.6	37.3	1694.0	42.7	23	37.1	20.1	744.0	18.3	34	41.5	16.3	677.0	12.9
	500 - 599 (n = 76)					600 - 699 (n = 51)					700 - 865 (n= 50)				
Fish remains	16	21.1	18.8	401.4	7.8	9	17.6	13.2	233.0	3.6	7	14	13.7	191	2.6
Zooplantkon	56	73.7	54.5	4070.4	78.9	43	84.3	65.8	5546	85.5	47	94	72.9	6852	91.9
Insects	1	1.3	0.3	0.4	0.01	3	5.9	2.2	12.7	0.2	2	4	0.1	0.5	0.01
Algae	4	5.3	1.2	6.5	0.13	3	5.9	1.1	6.3	0.1	1	2	1.2	2.4	0.03
Molluscs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Miscellaneous	13	17.2	7.4	43.6	0.8	4	7.9	1.9	7.7	0.1	0	0	0	0	0
Amorphous digested material	27	35.5	17.7	639	12.4	22	43.1	15.8	683.0	10.5	17	34	12.1	412	5.5

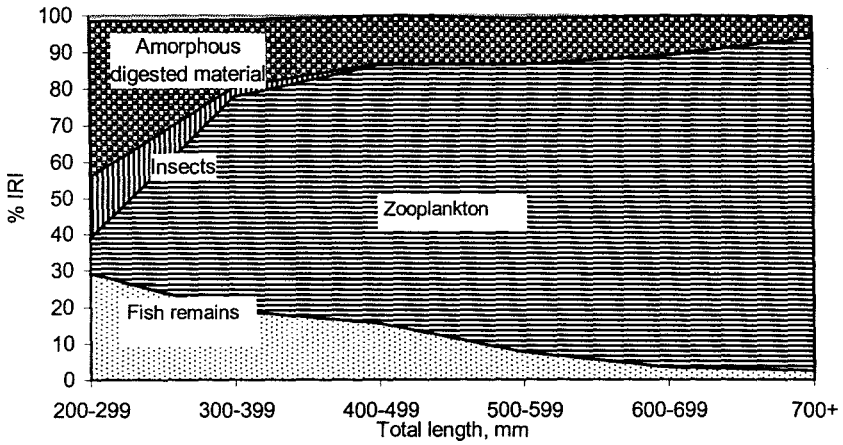


Figure 5.5. Relative importance (%IRI) of principal prey items of *Bathyclarias nyasensis* of different fish sizes (n=343). Note that only prey categories that formed a significant proportion of the diet are shown.

The contingency table analyses showed significant interactions ($p<0.001$) in occurrences of prey items in fish size *x* food type, water depth *x* food type and season *x* food type (Table 5.7). This implies that fish size, season and depth had significant effects on the prey types that were ingested.

Contingency-table and *post-hoc* analysis of variation in diet in relation to fish size are shown in Tables 5.8a and 5.8b. Non-significant values of χ^2 in the contingency-table analysis was achieved only after columns of zooplankton, fish remains, miscellaneous material and insects were deleted (Table 5.8b) - suggesting that these prey-item categories accounted for the significant variation in the diet of fish of different sizes. Amorphous digested material did not appear to account for significant variation in diet.

Table 5.7. Results from three-way contingency table (log-linear) analysis testing interactions between fish size, depth, season and prey type.

Interaction	Likelihood ratio χ_2 static	Df	P
	Model 1 (7 * 2 * 3 contingency)		
Size x prey type	224.8	24	<0.001
Depth x prey type	39.5	18	<0.001
	Model 2 (7 * 2 * 3 contingency)		
Size x prey type	314.7	28	< 0.001
Season x prey type	66.6	21	< 0.001

By examining Table 4.8a, it is evident that zooplankton occurred less frequently than previously expected in the diet of fish ranging between 200 and 399 mm TL. In fish between 500 and 865 mm TL, zooplankton became more important than expected. In contrast, fish items occurred more frequently than expected in catfish between 300 and 499 mm TL, and occurred less frequently than expected in larger fish (500 - 865 mm TL). Insects occurred more frequently than expected in small size fish (200 - 299 mm TL). The occurrence of miscellaneous food items was variable among the different size classes of fish. These results indicate that fish and insects are important food items for smaller fish (200 – 299 mm TL for insects, and 300 - 499 mm TL for fish), while zooplankton are important to larger fish (500 – 865 mm TL).

5.3.1 Seasonal changes in diet

The %IRI indicate that zooplankton formed the largest proportion of diet in both smaller (200 – 399 mm TL) and larger (400 – 865 mm TL) fish during the cold-dry and the warm-dry seasons. During the warm-wet season fish prey formed a large proportion (%IRI = 73.9) of the diet of large fish (400 – 865 mm TL) (Table 5.9, Figure 5.6).

Table 5.8a. Contingency table showing variation of seven prey categories found in stomachs of *Bathyclarias nyasensis* of various sizes. "Obs" = observed and "Exp" = expected occurrence of prey categories. The χ^2 is highly significant (*** $p < 0.001$).

Size of fish (TL, mm)	Prey category															
	Fish remains		Zooplankton		Insect		Algae		Molluscs		Amorphous digested material		Miscellaneous		N_i	χ^2_i
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp		
200 - 299	8	6	9	19	10	2	0	1	2	1	10	10	1	2	40	41.58
300 - 399	18	15	41	48	8	5	2	3	3	1	23	25	8	5	103	6.49
400 - 499	25	20	63	63	5	7	4	3	2	2	34	33	3	7	136	4.26
500 - 599	16	17	56	54	1	6	4	3	0	1	27	28	13	6	117	14.06
600 - 699	13	13	43	39	3	4	3	2	0	1	22	20	4	4	84	3.45
700 - 865	7	11	47	34	2	4	1	2	0	1	17	18	0	4	74	12.1
N_j	83		259		29		14		7		133		133		554	
χ^2_j	2.38		0.43		37.38		4.8		10		11		16			81.94***

Table 5.8b. Results on *post-hoc* analysis of variation in prey items found in stomachs of *Bathyclarias nyasensis* of different sizes.

Row(s) or columns eliminated	Significance of X statistic	Sample size
Zooplankton	p<0.001	295
Zooplankton, Fish remains	p< 0.001	202
Zooplankton, Fish remains, Miscellaneous	p <0.001	183
Zooplankton, Fish remains, Miscellaneous and Insects	Non significant	154

Table 5.9. Diet of *Bathyclarias nyasensis* per size class and season. Values denote occurrence (O), percent frequency of occurrence (% F), percent volume (% V), Index of Relative Importance (IRI) and % IRI of prey items.

Prey category	Season														
	Cold-dry (July – October)					Warm-wet (November – March)					Warm-dry (April – June)				
	200- 399 mm TL(n = 102)					*200- 399 mm TL(n = 32)*					*200- 399 mm TL(n = 31)*				
	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI
Fish remains	25	24.5	22.6	554.4	12.9	13	40.6	31.3	1270	27.3	13	41.9	38.5	1627	32.5
Zooplankton	68	66.7	44.5	2966.0	68.9	23	71.9	23.5	1690	36.4	22	71	33.9	2406	48
Insects	15	14.7	5.7	84.4	2	7	21.9	12.9	283	6.1	1	3.2	3.2	10.3	0.2
Algae	6	5.9	2.1	12.6	0.3	0	0	0	0	0	0	0	0	0	0
Molluscs	6	5.9	5.3	30.9	0.7	1	3.2	1.9	5.8	0.1	1	3.2	2.7	8.8	0.2
Miscellaneous	7	6.9	1.3	7.8	0.2	3	9.4	2.9	17.8	0.4	2	6.4	1.7	5.6	0.1
Amorphous digested material	36	35.2	18.4	649.7	15.1	16	50	27.5	1376	29.6	15	48.4	19.6	951	19
	400 – 865 mm TL (n = 125)					*400 – 865 mm TL (n = 13)*					*400 – 865 mm TL (n = 39)*				
	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI
Fish remains	16	12.8	10.9	139.5	2	8	61.5	53.4	3284	73.9	8	20.5	18.5	379	7.3
Zooplankton	112	89.6	68.3	6120.4	86.9	5	39.5	24.1	925	20.8	29	74.4	59.2	4403	84.9
Insects	4	3.2	0.3	1.1	0.02	1	7.7	7.2	55.6	1.3	1	2.6	0.1	0.2	0.0
Algae	8	6.4	1.7	10.6	0.2	0	0	0	0	0	0	0	0	0	0
Molluscs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Miscellaneous	5	4.0	1.2	2.6	0.03	5	38.5	8.0	123	0.1	7	18	10.2	93.2	1.8
Amorphous digested material	55	44.0	17.6	772.3	11.0	1	7.7	7.4	56.7	1.3	10	25.6	12.1	310	6

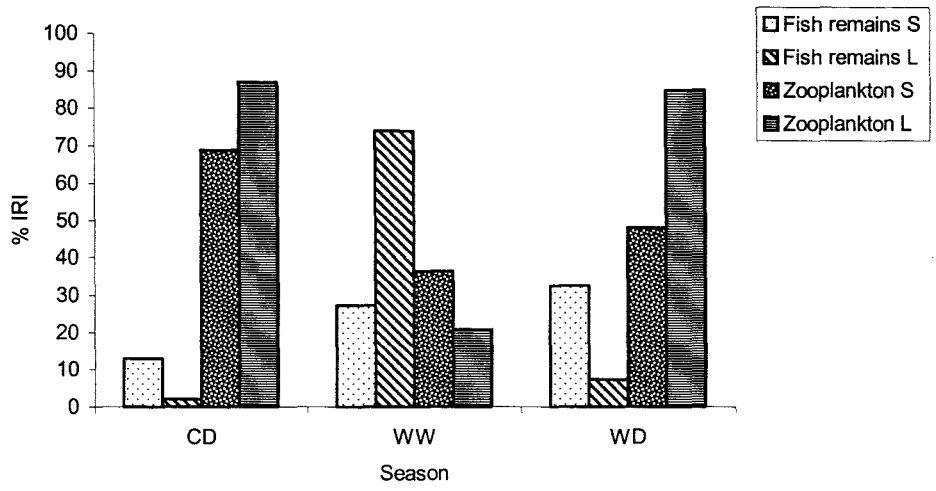


Figure 5.6. % IRI of prey items in small (S) and large (L) sizes of *Bathyclarias nyasensis* in cold-dry (CD), warm-wet (WW) and warm dry (WD) seasons (n = 342). S = 200 - 399 and L = 400 - 865 mm TL. CD = July–October, WW = November–March and WD = April–June. Note that only prey items with high % IRI are shown.

Results from contingency-table analysis also show significant ($p<0.001$) seasonal variation in the occurrence of prey items (Table 5.10a). From Table 5.10b, non-significant values for χ^2 was achieved when the column fish remains was deleted, and the warm-wet and cold-dry seasons were excluded. From Table 5.10a it is apparent that 'fish remains' occurred more frequently than 'expected' during the warm-wet (November-March) season, but less frequently than 'expected' during the cold-dry (July-October) season. In the warm-wet (November-March) season, 'zooplankton' occurred less than expected, while 'insects' and 'miscellaneous' prey items occurred more frequently than expected. In the cold-dry season (July-October), 'fish remains' were found less frequently than 'expected', while 'zooplankton', 'algae' and 'amorphous digested material' occurred more frequently than expected. 'Miscellaneous' prey types appeared less frequently than 'expected'. These results are comparable with those obtained using

IRI, and indicate a particular dietary switch in large fish (400 – 865 mm TL) from zooplanktivory to piscivory in the warm-wet season.

Table 5.10a. Contingency table analysis of prey variation in *Bathyclarias nyasensis* per seasons. "Obs" = observed and "Exp" = expected occurrence of the prey items. The χ^2 is highly significant (*** $p < 0.001$).

	Prey category															
	Fish remains		Zooplankton		Insect		Algae		Molluscs		Amorphous digested material		Miscellaneous		N_i	χ^2_i
Season	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp		
Cold-dry	41	54	180	169	19	19	14	9	6	5	91	87	12	19	363	9.33
Warm-wet	21	12	28	39	8	4	0	2	1	2	17	19	8	4	83	17.6
Warm-dry	21	16	51	51	2	7	0	3	1	2	25	26	9	6	109	8.68
N_j	83		259		29		14		8		133		29		555	
χ^2_j	7.04		0.65		5.49		10.55		0.35		3.64		7.57			35.66***

Table 5.10b. Results of *post-hoc* analysis of the seasonal variation of prey categories in *Bathyclarias nyasensis* per season.

Row(s) or columns eliminated	Significance of χ^2 statistic	Sample size
Fish remains	non-significant	472
Zooplankton	p <0.001	422
November - March	non-significant	472
April- June	p <0.001	446
July-October	non-significant	192

5.3.2 Diet changes with depth

Fish that were caught from intermediate (IN) and deep (DE) water (>40 m), consumed a higher proportion of zooplankton than fish from shallower water (<40 m). Conversely, fish from shallow water had ingested higher proportions of fish than fish from deep water (Table 5.11, Figure 5.7).

It can also be noted from Table 5.9 and Figure 5.11 that at all three depths, larger fish (400 - 865 mm TL) had generally taken a higher proportion of zooplankton than smaller fish (200-399 mm TL), and 'fish remains' occurred less frequently in larger fish than in smaller fish. The variations in the IRI value for various prey items were also noted from contingency-table analyses (Tables 5.12a and 5.12b).

In Table 5.12b a non-significant value for χ^2 was achieved when either the column of fish remains or row of '10-39 m' was excluded. From Table 5.12a fish remains and 'amorphous digested material' occurred more frequently than 'expected' at a depth of 10 - 39 m, and less frequently than 'expected' at a depth of 40 - 60 m. In the row '10 - 39 m', zooplankton occurred less than was 'expected'. The results confirm the importance of small fish as food items in shallow water.

Table 5.11. Prey items in stomach contents of *Bathyclarias nyasensis* per size class, per depth interval. Values denote occurrence (O), percent frequency of occurrence (%F), percent volume (%V), Index of Relative Importance (IRI) and % IRI of prey categories.

	Water depth														
	Shallow water (10 – 40m)					Intermediate water (41 – 60m)					Deep water (61- 86 m)				
	200- 399 mm TL (n = 11)					200- 399 mm TL (n = 52)					200- 399 mm TL (n = 74)				
Prey category	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI
Fish remains	7	63.6	75	3748.8	72.2	10	19.2	17.6	339	7.3	17	23	21.7	499	10.5
Zooplankton	5	45.4	21	954.6	19.1	33	63.5	45.5	2889	62.2	56	75.7	44.3	3400	70.9
Insects	1	9.1	9.1	82.6	1.7	6	11.5	6.2	71	1.5	13	17.6	6.5	114	2.4
Algae	0	0	0	0	0	0	0	0	0	0	6	8.1	3	24.5	0.5
Molluscs	0	0	0	0	0	4	7.7	6.6	50.9	1.1	2	2.7	2.2	5.8	0.1
Miscellaneous	0	0	0	0	0	1	1.9	0.04	0.1	0.01	7	9.5	1.91	15.4	0.3
Amorphous digested material	2	18.8	11	200	4	28	53.8	24	1293	27.9	26	35.1	20.4	717	15.2
	400 - 865 mm TL (n = 12)					400 - 865 mm TL (n = 78)					400 - 865 mm TL (n = 63)				
	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI	O	% F	% V	IRI	% IRI
Fish remains	7	58.3	50.8	2960.4	57.8	8	10.3	8	82	1.1	8	12.7	11	140	2.2
Zooplankton	7	58.3	32.2	1874	36.6	72	92.3	75.5	6967	89.5	55	87.3	63.5	5542	86
Insects	0	0	0	0	0	1	1.3	0.01	0.02	0	5	7.9	2.2	17.1	0.3
Algae	0	0	0	0	0	3	3.8	0.5	2	0.03	5	7.9	2.6	20.6	0.3
Molluscs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Miscellaneous	2	16.6	8.4	140.2	2.74	1	1.3	1.3	1.7	0.02	4	6.4	0	0.1	0
Amorphous digested material	2	16.6	8.7	145	2.8	39	50	14.7	734	9.4	22	34.9	20.7	723	11.2

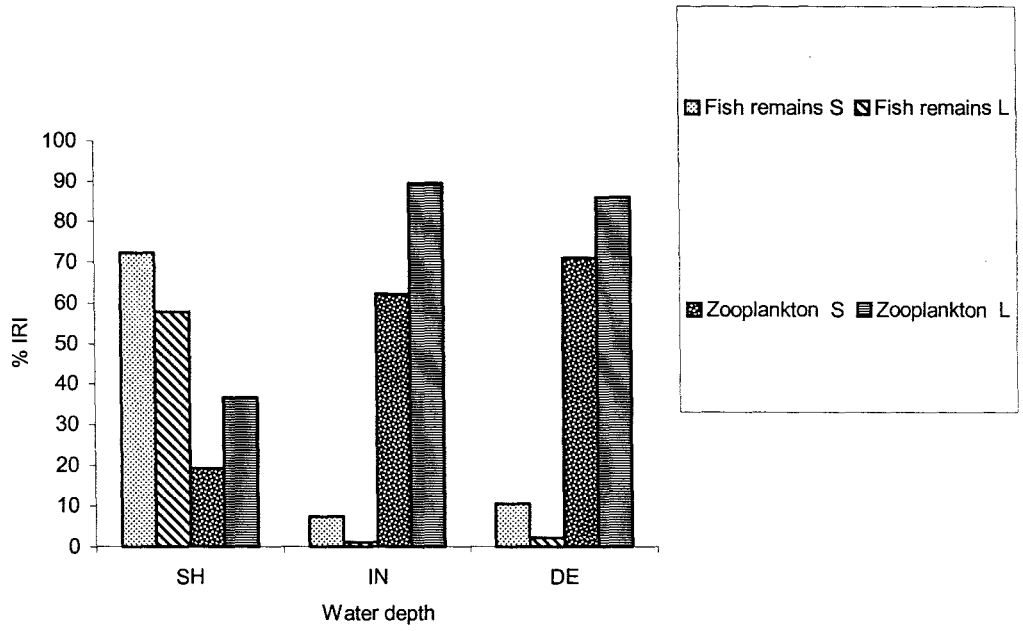


Figure 5.7. % IRI of prey categories of small (S) and large (L) sizes of *Bathyclarias nyasensis* caught from different water depths (n = 343). S = 200 - 400 mm TL and L= 400 – 865 mm TL. SH = shallow (10- 40 m), IN = intermediate (41- 60 m) and DE = deep water (61- 86 m). Note that only prey items with high % IRI are shown.

Table 5.12a. Contingency-table analysis of prey variation in *Bathyclarias nyasensis* per depth. "Obs" = observed and "Exp" = expected occurrence of the prey categories. The χ^2 value is highly significant (*** $p < 0.001$).

	Prey category															
	Fish remains		Zooplankton		Insects		Algae		Molluscs		Amorphous digested material		Miscellaneous		N_i	$\chi 2_i$
Water depth(m)	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp		
10 – 39	14	4	12	16	1	2	0	1	0	0	4	8	2	1	33	30.55
40 – 60	18	25	105	101	7	12	3	6	4	3	67	53	2	7	206	13.46
61 – 82	25	27	111	111	18	13	11	7	2	3	48	58	11	7	226	8.98
N_j	57		228		26		14		6		119		15		465	
χ^2_j	5.23		7.88		4.44		26.84		1.39		1.24		5.96			52.98***

Table 5.12b. Results of *post-hoc* analysis of prey variation in *Bathyclarias nyasensis* per depth interval.

Row(s) or columns eliminated	Significance of χ^2 statistic	Sample size
Fish remains	non-significant	408
Digested food	$p<0.001$	346
Depth: 10 - 39 m	non-significant	432
Depth: 20 - 40 m	$p < 0.001$	259

5.4 DISCUSSION

Results of diet study obtained using two approaches, the IRI approach and a contingency-table analysis were congruent. This suggests that the observed ontogenetic, seasonal and dietary changes at different water depths among different sizes of *B. nyasensis* are significant. Furthermore, the results clearly show the importance of analysing gut contents per size class, season and water depth. Omitting those data would have led to the erroneous and misleading conclusion that *B. nyasensis* is a generalist. The following is a summary of the findings:

- *B. nyasensis* feeds predominantly on zooplankton and fish while other prey types of both plant and animal origin form a smaller proportion of the diet.
- The diet of *B. nyasensis* changes with body size, being principally piscivorous between 300 and 500 mm TL and almost exclusively zooplanktivorous at larger sizes.
- Seasonal diet change overrides the ontogenetic diet changes, particularly during the warm-wet season (November-March) when large fish become piscivorous.
- Piscivorous behaviour is confined to shallow water while zooplanktivory occurs mainly in deep water (>40 m).

The food and feeding habits that were predicted from previous studies (Chapters 3 & 4) were corroborated in this study (Table 5.13). These results permit the conclusion that morphological features may be reliable indicators of the diet of a species. Therefore, the hypothesis that the observed morphological changes in buccal-cavity volume and filtering area (see Chapter 4) are reliable indicators of ontogenetic dietary changes in *B. nyasensis* can be accepted.

Table 5.13. Predicted (from previous chapters) and observed (from this study) food and feeding habits of *Bathyclarias nyasensis.*

Predicted food and feeding habits:	Study:	Accept/Reject :
Diet change with size of fish	Chapter 2	Accept
Diet changes 500 - 600 mm TL related to buccal-cavity volume and filtering area	Chapter 3	Accept
Omnivorous	Chapter 3	Accept
May include fish in diet	Chapter 3	Accept
Less inclination to fish diet	Chapter 3	Accept
High propensity to invertebrate prey	Chapter 3	Accept
Diet includes molluscs	Chapter 3	Accept

The scope of a fish's diet may vary due to, among many factors, habitat productivity or prey availability (Hughes 1980). It seems unlikely that the diet change in large *B. nyasensis*, from zooplanktivory to piscivory, during the warm-wet season is due to a scarcity of zooplankton. The maximum zooplankton production occurs between July and December, while minimum production occurs between February and May (Allison *et al.* 1995). This diet shift may be due to migration of the large fish to shallow water as explained below.

If the hypothesis that large *B. nyasensis* migrate to shallow water for breeding is correct, this would occur during the warm-wet season see (Chapter 3), as this is the established breeding period (Chapter 3). Coincidentally, this is the same season when large fish switch from zooplanktivory to piscivory. The results show that piscivory appears

confined to shallow water; therefore, fish caught during this season in shallow water would likely contain a high proportion of fish prey.

The observed ontogenetic changes in both habitat and diet is a case of size-specific habitat use, wherein smaller fish in their first year (Chapter 3) are mostly found inshore and are piscivorous, while the large fish move to offshore regions where they become zooplanktivorous. Mittlebach (1983) observed that a switch to piscivory as fish grow results in an accelerated growth rate because consumption of large prey is more cost effective. Feeding on small-sized prey is more energy demanding and, therefore, more costly than feeding on larger prey (Juanes & Conover 1994). Thus, it could be concluded that the high and slow growth rate of small and large *B. nyasensis*, respectively, is due to a change from a fish diet to a zooplankton diet. Bruton (1979) reported similar observations regarding *C. gariepinus* in Lake Sibaya. Bruton (*op. cit.*) noted that fish prey was largely confined to shallow water and was ingested by small fish that grew faster, while larger *C. gariepinus* in deep water relied on a low standing crop of zooplankton and had a lower growth rate.

One question that immediately presents itself from these findings is, "what drives this size-structured community set-up and/or ontogenetic habitat shift?" Ecological theory that explains interactions in such size-structured communities is essentially lacking (Crowder 1986). However, two lines of thought explaining ontogenetic habitat shifts are discernible from the literature. One is the theory of optimal habitat (Werner & Gilliam 1984), which states that juvenile fish maximise their fitness by staying in a habitat where mortality risk is minimal. This theory is supported by the findings of Mittlebach and Chesson (1987), He and Kitchell (1990) and Langeland *et al.* (1998). These authors have demonstrated that ontogenetic changes in diet or habitat are predator-mediated.

Furthermore, Langeland *et al.* (1998) demonstrated that in the Arctic charr, an ontogenetic shift from the epibenthic to pelagic region was not genetically, but environmentally determined.

The second school of thought relates to intraspecific competition (and by inference, resource partitioning) and factors other than predation (Matthews 1998). Traditional interpretations on this have focussed on the fact that by using different foods, often in different habitats, fish at different life stages ameliorate intraspecific competition. However, other explanations for segregation of size-classes is possible. For example, Matthews (1985) demonstrated that juveniles of *Etheostoma flabellare* segregated from adults across current speed gradients.

Examples of segregation due to intraspecific resource partitioning are available. Tallman and Gee (1982) observed that *Semotilus margarita* of different age classes were segregated into different habitats, yet converged for common use of deep pools in winter. This segregation into different habitats appeared due to food availability. Tallman and Gee (*op. cit.*) concluded that by being dietary specialists in microhabitats, the species facilitated intraspecific resource partitioning.

Haraldstand and Johnson (1983) found that younger *Salmo trutta* that occurred mostly in the littoral zone, and the older fish in the offshore region, preyed on similar types of prey. Haraldstand and Johnson (*op. cit.*) explained that the ontogenetic advance of individuals from the littoral to deeper or more pelagic habitats acted as a mechanism to open up the littoral habitats for the next cohort, and thereby contributing to stable populations.

While the habitat shift and high growth rate of young *B. nyasensis* may be explained by the optimal habitat theory of Werner and Gilliam (1984), the findings of this study cannot prove that these ontogenetic habitat changes are predator-mediated. On the other hand, changes in morphological features relating to buccal-cavity volume and filtering area (see Chapter 4) may in part, support the hypothesis by Tallman and Gee (1982). These features synchronously change with habitat shift, which may suggest their evolution as an adaptation for large *B. nyasensis* to effectively filter zooplankton in the pelagic region, thus would reducing competition for food resources in inshore areas. The circumstantial evidence that large *B. nyasensis* are capable of utilising the same prey items in shallow water as do small fish, further supports this hypothesis. Results indicate this occurred during the breeding (warm-wet) season (November-March) and the interaction seem to have been asymmetrical, favouring larger fishes. Small catfish had relatively lower fish intake than in other seasons (Figure 5.6). Given that larger fish move into deeper water during other seasons other than the breeding period suggests that diet shifts in *B. nyasensis* occur to ameliorate intraspecific competition, opening the inshore habitat to the new recruits, thereby maintaining a stable population.

Overall, the current findings suggest that *B. nyasensis* play different ecological roles depending on habitat (being piscivorous when inshore and zooplantivorous in offshore regions). Studies to determine the trophic status of *B. nyasensis* in inshore regions are underway (Darwall pers. comm.). The pelagic food web has been recently studied (see Menz 1995), therefore inferences on the trophic status of *B. nyasensis* in this zone can be made.

While Thompson *et al.* (1996) observed that *B. nyasensis* formed part of the pelagic system, there were no data to include the species in the ECOPATH model of Allison *et*

al. (1995). Given the results presented in the present study, it becomes possible to reconstruct the pelagic food web proposed by Allison *et al.* (1995) (Figure 5.8).

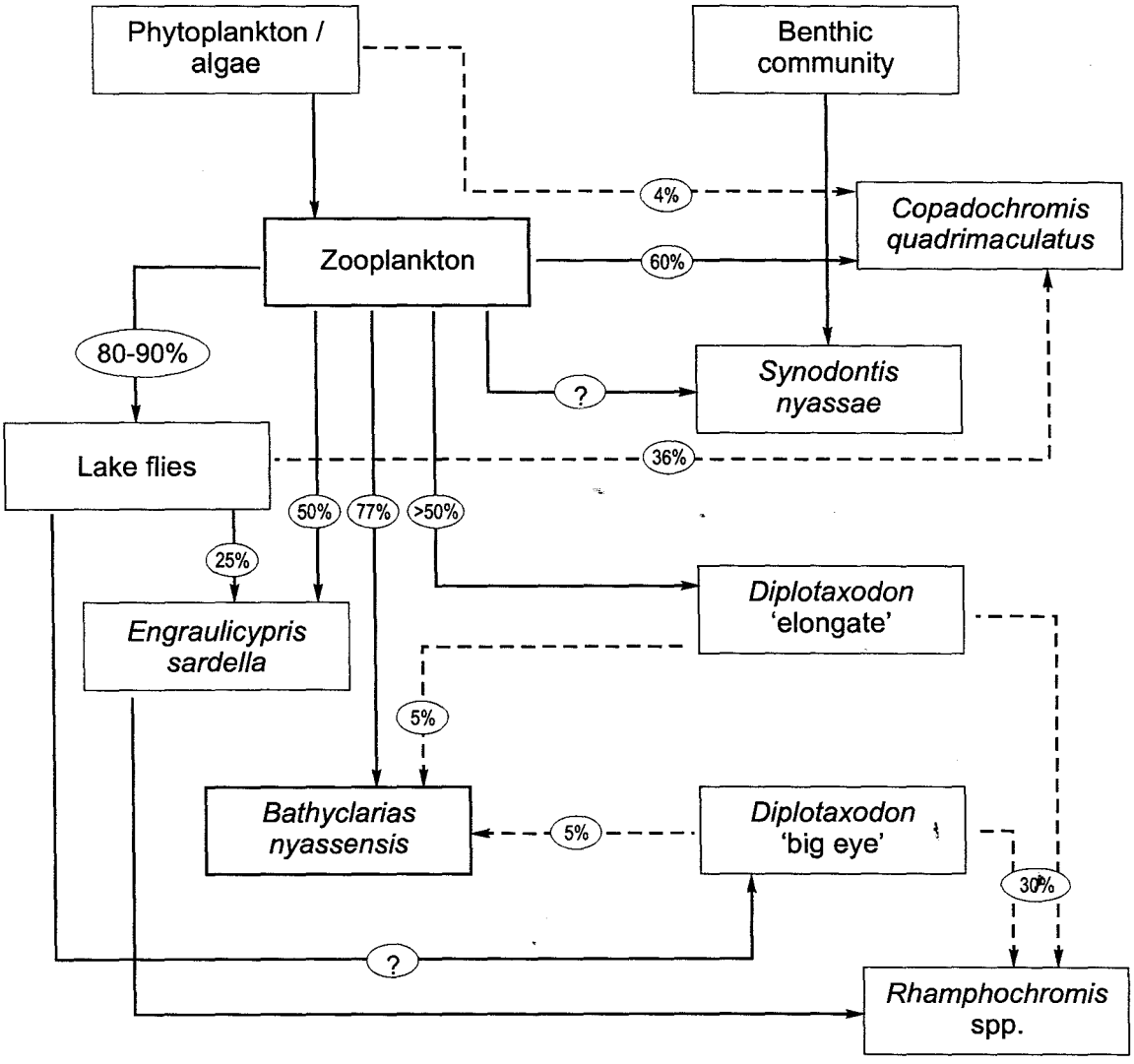


Figure 5.8. The pelagic food web of Lake Malawi (Allison *et al.* 1995) reconstructed using data from this study and Menz (1995). The numbers indicate the approximate percent Index of Relative Importance of the particular prey in the diet of the predator. Question marks indicate that data are not available.

From Figure 5.8 it is apparent that apart from the lake fly *Chaoborus edulis*, *B. nyasensis* is the only other major predator that relies heavily on zooplankton. However, it should be noted that this does not indicate the impact of *B. nyasensis* on zooplankton. The impact can only be established when estimates of fish biomass and food consumption rate are integrated with the diet data of this study (this is done in Chapter 7). Despite the fact that zooplankton is not very abundant in Lake Malawi (Allison *et al.* 1995), many predators including *B. nyasensis* rely on it. Therefore, the question of whether or not interspecific competition and resource partitioning is the organising force of the Lake Malawi pelagic fish community needs to be addressed.

After the works of Hutchinson (1957) and MacArthur (1958), the paradigm of interspecific competition (and its collary resource partitioning) as a driving force in communities was initially accepted without question. During that time, fish communities were studied from the perspective that communities are typically relatively stable (or at least predictable) entities, and that over the course of evolutionary or ecological time, co-evolution resulted in members of a community segregating along important resource axes, permitting similar (but not ecologically identical) species to coexist (Matthews 1998).

With time, other views began to emerge that emphasized the notion that competition might not be pervasive under all conditions, since other variables such as abiotic stress and periods of scarce resources also played a substantial role in structuring communities. Wiens (1977) suggested that interspecific competition might be a major factor in community structure only during periods of resource shortages.

The difficulty of accepting competition as the most important factor regulating communities was emphasized by Connell's (1980) admonition of the unproven "ghost of the past" - that a lack of observable competition in communities could be due to past coevolutionary mechanisms that allowed coexisting species to diverge in resource use as they evolved separately. Finally, the neutral models of Connor and Simberloff (1979) (1984) suggested random structure in many communities and further eroded confidence that there was strong deterministic structuring of animal communities.

Nevertheless, most published studies show that species in fish assemblages differ along axes of food, habitat, or activity time (Ross 1986) and that resource overlap does occur between or among species (Matthews 1998). However, this does not mean that (1) there is highly regular, competitively mediated resource sharing or (2) that competition is the dominant factor imposing structure or function of fish communities. Elucidating the factors that regulate community organization requires a combination of experimental manipulations of biotic interactions and long-term studies of resource availability, trophic interactions and population dynamics (Grossman 1982, Moyle *et al.* 1982, Schlosser & Toth 1984).

Hence, the zooplankton resource overlap that is evident by the diets of several pelagic species in Lake Malawi cannot be interpreted to indicate that competition is or is not occurring. However, Matthews (1998) suggests that based on the abundance of resource, some inferences may be made regarding competition and resource partitioning. At moderate levels of resource availability, species may diverge on the resource spectrum, with each specializing on that part for which it is optimally adapted. When abundant all species may use the resource opportunistically, whereas in times that it is scarce, all species may converge to use almost identical resources (e.g., if nothing else is available).

Since Lake Malawi is a food-limited system (Chapter 2), given the number of species that prey on zooplankton, it is reasonable to assume that the resource may be under intense predation, and competition and resource partitioning probably occurs, influencing the present fish community structure. It is suggested that *B. nyasensis*, unlike *C. gariepinus* (see Chapter 4), has adopted an efficient filtering mechanism, particularly at a size when it begins to rely on the pelagic ecosystem and so begins to compete with other species for scarce food resources.

In summary, the findings of the present study allow us to accept the hypotheses regarding life-history traits and feeding habits that emerged in previous chapters. In particular, we can accept the hypothesis that morphological features may be used as an accurate predictor of the food and feeding habits of this species. Comparisons with other well-studied species may facilitate those predictions. We can also accept the hypothesis that *B. nyasensis* utilise different resources when in the inshore and off shore regions. The ontogenetic diet and habitat shift seems to be a mechanism allowing juveniles to utilise highly "profitable" fish prey. In offshore areas *B. nyasensis* uses a resource that is dilute, and which is shared by other predators and competition and resource partitioning probably occurs. The results and conclusions of this study contribute to the long-term debate regarding the introduction of new species to the Lake Malawi pelagic system (Allison *et al.* 1995). The study results also raise questions as to whether or not trophic cascade effects would manifest in the face of changes to the Lake Malawi pelagic fish community structure that otherwise seems to be stable. These issues are discussed in the final chapter.

CHAPTER 6

Food assimilation in *Bathyclarias nyasensis* using carbon isotope ratios

6.1 INTRODUCTION

Fish diet is generally determined by examination of gut content (Elliot & Persson 1978, Hyslop 1980) (see also Chapter 5). However, the gut content only reflects food intake during the last few hours of feeding and such single estimates may not provide time-integrated assimilation measurements of diet. Therefore, it would be useful to have access to a method that provides insight into the food or dietary items that have been assimilated by fish over a longer time period. A possible tool is the determination of naturally occurring stable isotopes in fish tissue that accumulate from the diet over a long period (Fry & Sherr 1984).

The elements C, N, S, H and O have more than one isotope, and the isotopic composition of natural material can be measured with great precision using a mass spectrometer (Peterson & Fry 1987). Combinations of C, N, S are often complementary (Peterson & Fry 1987) and are frequently used (DeNiro & Epstein 1978, Fry & Sherr 1984, Lilyestrom & Romaire 1987, Persson & Hansson 1998). Isotopic compositions change in predictable ways from one trophic level to the other, hence stable isotope measurements can provide crucial information on energy flow in an ecosystem.

Most ecological feeding studies express isotopic compositions in terms of ∂ values, as a part per thousand difference from a standard:

$$\partial X = [(R_{sample}/R_{standard}) - 1] \times 10^3 \qquad \text{Equation 6.1} \quad \text{(Peterson \& Fry 1987)}$$

where X is ^{13}C, ^{15}N or ^{34}S, and R is the corresponding ratio $^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$. The values are measures of the amounts of heavy and light isotopes in a sample. Increases in these values denote increases in the amount of the heavy isotope components. Conversely, decreases in ∂ values denote decreases in the heavy isotope content, and a reciprocal increase in the light isotope component. Standard reference materials are the Pee Dee limestone, nitrogen gas in the atmosphere and sulphur from the Canyon Diablo meteorite.

Carbon isotope ratios, expressed as $\partial^{13}C$, have been used to trace metabolic pathways in freshwater ecosystems (Fry & Sherr 1984), estuaries (Murphy & Abrajano 1994, Paterson & Whitfield 1997) and in aquaculture (Shroeder 1983, Lilyestrom & Romaire 1987). This is possible because during photosynthesis plants utilise ^{13}C and ^{12}C at different rates and this difference is reflected in their $\partial^{13}C$ values. Hence, higher plants fall into two categories, *viz.* those employing conventional photosynthetic processes (C_3 plants) such as legumes, alfalfa, cotton, and algae with lower $\partial\ ^{13}C$ values (-24 to -34) and C_4 plants with higher $\partial^{13}C$ values (-10 to -18) (Mohr & Schopfer 1995). Once animals assimilate these sources of carbon, the carbon isotope ratio of an animal will indicate its primary food source regardless of the trophic pathway it was derived from (DeNiro & Epstein 1978). However, problems arise when identifying the relative contribution of two or more diets to isotopic composition of the animal when these diets are not isotopically distinct (DeNiro & Epstein 1978).

Other problems in interpreting isotope values include enrichment and turnover rate of tissues. Enrichment, which is an increase in the $^{13}C/^{12}C$ ratio, may occur between different trophic levels due to isotopic fractionation (alteration of the ratio of heavy to light isotopes) during assimilation and respiration (DeNiro & Epstein 1978, Fry & Sherry 1984). Enrichment occurs because of a greater loss of light carbon (^{12}C) during respiration, and preference for ^{13}C when food is assimilated and/or mechanisms of enzyme-mediated biochemical reactions (Rau *et al.* 1983, Spiro *et al.* 1986). This enrichment ranges between 0 - 2 ‰ per trophic level (DeNiro & Epstein 1978, Fry & Sherry 1984, Peterson & Fry 1987). Tissue turnover complicates the interpretation of results for animals that switch diets, because as the newly assimilated carbon gradually replaces the original carbon of the tissue from previous diet, the isotope value is an intermediate between the previous and the newly assimilated diet (Tieszen *et al.* 1983). This is of particular relevance in this study in view of the change in diet of *B. nyasensis* between 500 - 600 mm TL (see Chapter 5).

Despite the stated limitations, carbon isotope ($\partial^{13}C$) values have been successfully used in determining dietary sources in cases where, gut contents for example, are not easily identified (Shroeder 1983). In the previous chapter it was shown that the diet of juvenile catfish (<300 mm TL) consisted of a high proportion of amorphous material, which could not be identified. The use of $\partial^{13}C$ therefore may help to reveal the origin of this material.

The aim of this investigation is to test the hypothesis that the findings of the dietary investigations (Chapter 5) are a realistic reflection of the long-term food preference of *B. nyasensis* and also to validate the findings that a major dietary shift occurs in the species between 500 - 600 mm TL.

A complimentary study was undertaken in which *B. nyasensis* in earthen ponds were fed on fishmeal and maize bran based diets. The objective of the complimentary study is to test whether/or not the $\partial^{13}C$ values obtained could accurately reflect the diet of the fish.

6.2. MATERIALS AND METHODS

A sample of 12 fish ranging from 370 to 730 mm TL were collected from the south-east arm of Lake Malawi in June 1998. Muscle tissue for $\partial^{13}C$ analysis was taken from the anterior flank of the fish (Figure 6.1).

Principal prey items (fish and zooplankton) of *B. nyasensis*, as identified in Chapter 4, were collected from Lake Malawi in November 1998. This included samples of prey fish, *Lethrinops* sp., and zooplankton. Zooplankton was collected from approximately 30 – 50 m offshore at Monkey Bay (Figure 2.1) using a 85 *u*m plankton net that was slowly towed near the water surface. After collection, all debris was removed from the samples. Approximately 98% of the sample was found to consist of *Mesocyclops aequatorialis aequatorialis*, and the remainder *Tropodiaptomus cunningtoni* (which were the principal zooplankton components in the diet of *B. nyasensis* in Chapter 5). Samples of the muscle tissues of *B. nyasensis* and *Lethrinops* sp. were sundried and sent to Quaternary Dating Research Unit, CSIR laboratories in South Africa for analysis. The material was defatted using organic solvent (chloroform/methanol/water 1:1:0.8) and subsequently vacuum dried. Thereafter, the samples were combusted in a circulating oxygen gas stream in a CuO oven system (600^0C). Combustion in the circulating CuO oven system purified the CO_2 gas. The $^{13}C/^{12}C$ ratio of the CO_2 gas was measured on a SIRA-mass spectrometer.

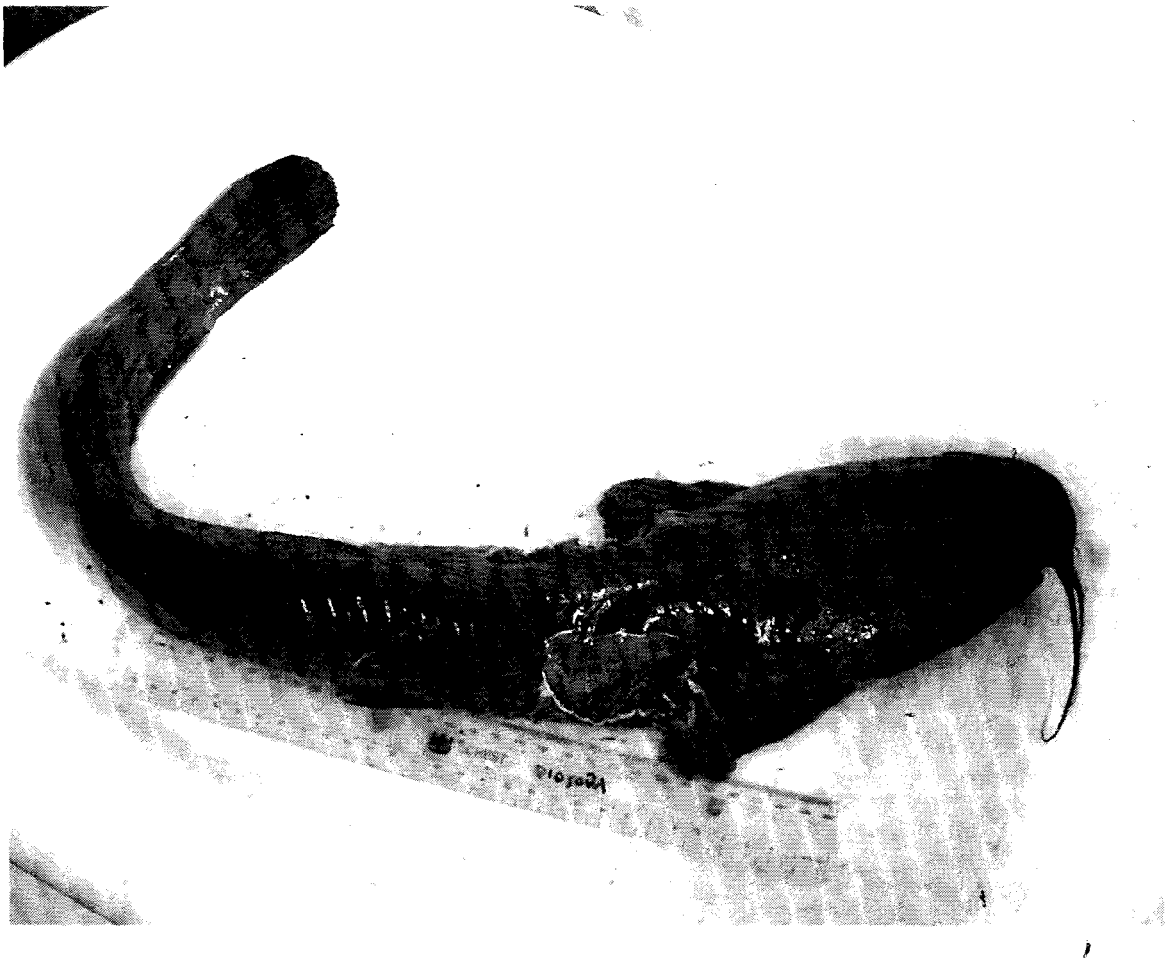


Figure 6.1. The lateral region where tissue of *Bathyclarias nyasensis* were taken for $\partial^{13}C$ analysis.

Ratios of the stable carbon isotope were reflected relative to the Pee Dee Belenmite (PDB) and were reported in ‰:

$$\partial^{13}C = \frac{^{13}C/^{12}C_{sample} - ^{13}C/^{12}C_{standard}}{^{13}C/^{12}C_{standard}}$$ Equation 6.2

The pond experiment was carried out for a period of 16 months. Fish were collected from the study area (Figure 2.1) in June 1997 and were brought to Bunda College farm where they were stocked into four 200m^2 by 1m deep ponds. Sixteen fish were stocked into each pond. The mean weight of fish at stocking was (850 ± 100 g). During the 16-month period, fish were fed on two dietary formulations in duplicate. Diet A was formulated to contain 42% crude protein and comprised of 30 % fishmeal, 26% roasted soybean, 21% maize meal and 21% maize bran. Diet B contained maize bran as the sole ingredient with a crude protein content of 11%. Feed was administered once daily at 09h00, at 5% body weight/day. In October 1998, tissue from four fish, or two from each treatment, were collected, and sun-dried. Together with the diets and diet ingredients these were sent to the CSIR laboratories in South Africa to be analysed for $\partial^{13}C$ as described above.

In order to determine ingestion of natural and supplemental diets in ponds, stomach contents were analysed from 45 fish in October 1998, (see Methods used in Chapter 5) Finally, growth and specific growth rates of fish raised according to two treatments was determined and compared using a one-way analysis of variance (ANOVA).

6.3 RESULTS

6.3.1 Carbon ($\partial^{13}C$) values of *Bathyclarias nyasensis* from Lake Malawi

The $\partial^{13}C$ values of tissues ranged from -21 to -17.8 ‰, and the values for zooplankton and *Lethrinops* were -23.6 and -21.1 ‰, respectively (Table 6.1).

Table 6.1. Carbon isotope ($\partial^{13}C$) values of tissues from *Bathyclarias nyasensis* and prey items from Lake Malawi.

Sample	Total length (mm)	Weight of fish (g)	($\partial^{13}C$) ‰
Bathyclarias nyasensis (n=12)	355	350	- 21.0
	355	350	- 21.1
	370	400	- 21.0
	589	1500	- 20.3
	590	1600	- 19.9
	595	1600	- 18.0
	662	2500	- 19.7
	663	2500	- 20.1
	670	2500	- 19.8
	688	2600	- 19.9
	730	3300	- 21.0
	730	3300	- 20.6
Lethrinops species (Chisawasawa)			- 21.1
Zooplankton			- 23.6

It is evident from Table 6.1 that the $\partial^{13}C$ values changed with the size of fish. A second-order polynomial equation was fitted to the data (Figure 6.2), to formulate the following equation:

$$\partial^{13}C = -33.188 + 0.4997L - 0.0045L^2 \quad (r^2 = 0.598, n = 12, p=0.022) \qquad \text{Equation 6.3}$$

where: L = total length of fish in mm.

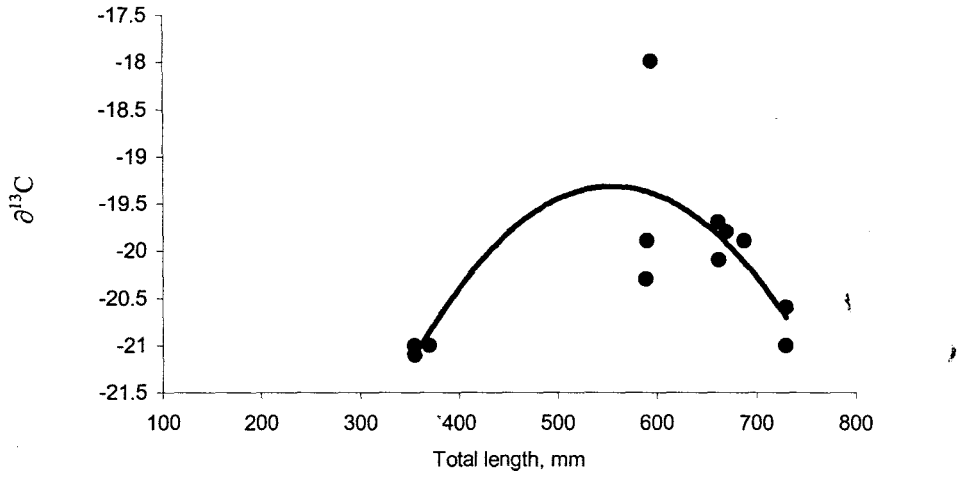


Figure 6.2. $\partial^{13}C$ values in *Bathyclarias nyasensis* from Lake Malawi. The fitted second order polynomial is provided in the text.

The $\partial^{13}C$ value changed from light" or "more negative" in small fish (approximately -21‰) to heavy" or "less negative" in medium-size fish (-19.5 ‰) and to light" or more negative in large fish (-20.7 ‰) (Figure 6.2). This reflects the findings of Chapters

4 and 5 where results indicated a significant change in buccal cavity volume/filtering area (Figures 4.11, 4.12, 4.13) and diet shift (Figure 5.5) in fish between 500 – 600 mm TL.

6.3.2 Carbon ($\partial^{13}C$) values of *Bathyclarias nyasensis* from pond experiments

The $\partial^{13}C$ values of the dietary ingredients ranged from –11.1 ‰ (maize meal) to –27 ‰ (soybean meal) (Table 6.2) in catfish raised in ponds over a 16 month period. Maize and soybean are considered C_4 and C_3 plants, respectively (Mohr & Schopfer 1995), and this was reflected by the relatively $\partial^{13}C$ values. Fish in Treatment A had a more negative value (-19.85 ± 0.07 ‰) than those fed diet B (-16.55 ± 0.92 ‰), indicating that $\partial^{13}C$ provided a reliable indicator of diet composition.

Table 6.2. Carbon isotope ($\partial^{13}C$) values of the feed ingredients in two diets fed to fish reared in ponds.

Treatment/Diets	∂^{13} C (‰)
Feed ingredients	
Maize meal	-1.1
Soya bean (roasted)	-27.0
Fish meal (dried *Engraulicypris sardella*)	-21.1
Diets	
Diet A (formulated)	-22.4
Diet B (maize bran)	-11.5
Fish samples from different treatments	
Treatment A (40 % Crude Protein)	-19.9
Treatment A (40 % Crude Protein)	-19.8
Treatment B (maize bran)	-15.9
Treatment B (Maize bran)	-17.2

Stomach content analysis showed that, in fish from ponds 1, 2 and 4 feed constituted a high proportion of fish's diet (Table 6.3) confirming supplemented feed was ingested. Hence, the $\partial^{13}C$ values of fish tissue were a reflection of the supplemented feeds.

Table 6.3. Mean percent index of relative importance (%IRI, ± SD) of stomach contents of pond fish.

Prey item	Pond 1 (diet A) n=9	Pond 2 (diet B) N=7	Pond 3 (diet A) n=9	Pond 4 (diet B) n=10
Fish feed	61.8±4.5	89.3 ±6.4	18.5 ±2.1	62.1±37.1
Zooplankton	33.4±6.4	7.7 ±10.7	68.5 ±16.3	21.8 ±15.6
Fish remains	0	0	0	3.1± 1.6
Insects	4.8 ±1.8	0.2 ±0.07	0.5 ±0.7	0.2 ±0.3
Algae	0	0.6 ±0.8	0	0.3 ±0.4
Higher plants	0	2.4±3.3	15.0±21	12.7 ±37.1

Results of the growth studies show that fish reared on Diet A had significantly higher growth and specific growth rates ($p<0.05$) than fish fed Diet B (Table 6.4) implying that the supplied feed affected growth of fish in varying way as reflected in $\partial^{13}C$ values.

Table 6.4. Initial and final weight, weight gain and specific growth rates of fish fed on Diet A (formulated diet) or Diet B (maize bran) in fish ponds at Bunda College.

Diet (Treatment)	Mean initial weight (g) ± SD	Mean final weight (g) ± SD	Average weight gain (g)/day	Specific growth rate (% body weight/day)
A	872±120	1578±119	1.5[a]	0.12[a]
B	852±90	1062±74	0.4[b]	0.05[b]

Numbers with different letters are significantly different ($p<0.005$)

6.4 DISCUSSION

A prerequisite for the use of the stable isotope technique in food-chain studies is the understanding of the amount of $\partial^{13}C$ fractionation (either enrichment or depletion) normally occurs between the food source and consumer (DeNiro & Epstein 1979). Generally, it is assumed that there is an enrichment of approximately 0 – 1 ‰ (Peterson & Fry 1987), or 2 ‰ (following DeNiro & Epstein 1979) from one trophic level to the next. Rounick and Hicks (1985) found an enrichment of approximately 1.7 ‰ in rainbow trout. In this study, an enrichment factor of 1-2 ‰ was assumed.

Within the animal's body, $\partial^{13}C$ values vary among the different tissues; the choice of tissue sampled may influence conclusions about diet. Tieszen *et al.* (1983) demonstrated that $\partial^{13}C$ values in liver, muscle and brain were reliable indicators of the diet of gerbils. In some studies, however, whole animals are used, while in others, analyses of muscle or protein fractions have proven adequate indicators of diet (Peterson & Fry 1987). Rounick & Hicks (1985) found white muscle to be a good indicator of diet in rainbow trout. Due to the large body size of *Bathyclarias* and the absence of freeze-drying facilities in Malawi, muscle tissue from the antero-lateral region proved easiest to collect and prepare

for carbon isotope analyses; the results indicate the tissue is a reliable indicator of dietary composition.

The ontogenetic changes in $\partial^{13}C$ values, as observed in this study, have also been reported in Malaysian prawn, *Macrobrachium rosenbergii* (Lilyestrom & Romaire 1987), and brown shrimp (Fry 1982). Temporal changes in $\partial^{13}C$ have also been observed in the channel catfish *Ictalurus punctatus* (Lilyestrom & Romaire 1987). In those cases, changes were attributed to changes in food habits and/or habitat of the animals.

While the ontogenetic changes in $\partial^{13}C$ values recorded for *B. nyasensis* reflect and indeed confirm a change in food habits (see Chapter 5), it is often difficult to isolate the relative contribution of each prey item in animals that change diet. As noted earlier, each tissue type in such animals may be expected to have an isotopic "memory" (Tieszen *et al.* 1983). This means that the isotope value obtained may be a function of the $^{13}C/^{12}C$ ratio in the food at the time of synthesis, the $^{13}C/^{12}C$ ratio of subsequent food stuffs, and the biochemical turnover rate of the carbon in the tissue in question (Tieszen *et al.* 1983). Hence, Tieszen *et al.* (1983) demonstrated that carbon from a wheat diet replaced the carbon of the liver in the gerbils that had consumed corn and subsequently wheat over 84 days. During this replacement time, the $\partial^{13}C$ of the gerbils' liver tissue reflected the intermediate values of corn and wheat. Thus, in a situation where an animal periodically changes from one isotopically distinct food source to another, stable isotope ratios may provide only limited information concerning the relative importance of the two carbon sources, due to complications introduced by the carbon turnover.

Another problem in determining sources of carbon arises when the ingested foods are not isotopically distinct such as allochthonous and autochthonous material, or C_3 and C_4

plants (DeNiro & Epstein 1978, Rounick & Hicks 1985). Where the $\partial^{13}C$ values of a diet source is not sufficiently different, the overlap of the $\partial^{13}C$ values does not permit the determination of the contribution of each source to the animal's diet (DeNiro & Epstein 1978).

Given the stated limitations of interpreting $\partial^{13}C$ values, the interpretation of ontogenetic changes in $\partial^{13}C$ values as noted in this study can be made only with respect to the stomach-content data obtained in Chapter 5. Assuming an enrichment of 1 - 2 ‰, smaller fish (<350 mm TL) with a $\partial^{13}C$ value of -21 ‰ (Figure 6.2), are likely to have consumed prey with $\partial^{13}C$ values of -22 to -23 ‰. In this size group, the major component of the gut content was amorphous material and prey fish with %IRI values of 43 and 29.1, respectively. The $\partial^{13}C$ value of fish prey was -21 ‰, which discounts fish as the main contributor to the tissue carbon of *B. nyasensis* in this size range. Based on the fact that the $\partial^{13}C$ value of zooplankton was -23.6 ‰, the amorphous material seems to represent digested zooplankton.

It is interesting to note that the $\partial^{13}C$ value of the medium-size *B. nyasensis* (400 - 600 mm TL) shifted to -19.5 ‰. Again, assuming an enrichment factor of between 1-2 ‰, this indicates a shift towards prey with a $\partial^{13}C$ value of between -20.5 and -21.5, which corresponds to the value obtained for *Lethrinops* (-21 ‰). This confirms the findings in Chapter 5, which suggest that fish become the principal prey item of *B. nyasensis* at sizes between 300 - 500 mm TL.

The most interesting result was the obscured shift in $\partial^{13}C$ values among the largest fish. The shift from a $\partial^{13}C$ value of -19.5 to -21.0 is indicative of a diet shift from prey fish

back to zooplankton. In Chapter 4, results show a significant increase in buccal cavity volume in fish between 500 - 600 mm TL, suggesting a switch in diet. This is confirmed by the feeding study (Chapter 5) in which a shift from prey fish to zooplankton was observed in catfish of this size range. The "lag" in changes of $\partial^{13}C$ values is most likely a reflection of the low tissue turnover rate. Results presented in Chapter 3 suggest a high growth rate during the first two years, with a concomitant higher turnover rate of tissue carbon. Hence, the $\partial^{13}C$ value may reflect the diet assimilated at a particular time. Conversely, the low growth rate of fish that had reached 500 mm TL may reflect low tissue turnover, confirmed by the lag in the $\partial^{13}C$ values observed here.

From the combined results of this study and those in Chapters 4 and 5, it is evident that the diet of *B. nyasensis* changes from zooplankton during the juvenile stage to prey fish in the subadult stage and back to zooplankton during the adult phase.

The $\partial^{13}C$ values in tissues of fish fed on Diet A (formulated feed with 40% CP) had $\partial^{13}C$ of -19.85 ± 0.07 ‰ while those fed on diet B (maize bran) had a mean $\partial^{13}C$ value of -16.55 ± 0.92 ‰. The effect of diet on $\partial^{13}C$ of animals in aquaculture has been noted in fish and prawn (Shroeder 1983, Lilyestrom & Romaire 1987), and such data can be used to determine the relative contribution of different formulated feeds and natural food to the growth of fish or prawns in aquaculture. However, the experiment undertaken here was designed as a means to test whether or not the technique provides a reliable predictor of change in diet. The results clearly indicate that the $\partial^{13}C$ values can reflect diet of fish, and from this, an inference can be made that the $\partial^{13}C$ values of *B. nyasensis* in Lake Malawi provide a reliable indication of the shift in diet as otherwise observed.

The findings of three independent methods (morphology, gut content and stable isotope analysis) provide adequate evidence that *B. nyasensis* in Lake Malawi display a clear ontogenetic dietary shift from zooplankton during the juvenile phase, to prey fish in the subadult phase, reverting to zooplanktivory in the adult phase.

CHAPTER 7

Estimates of daily food consumption rates under natural conditions

7.1. INTRODUCTION

Estimates of daily food consumption rates (daily ration) have been used to investigate the relationship between ration size and growth (Walsh *et al.* 1988, Boisclair & Leggett 1989a), seasonal food limitations (Ensign *et al.* 1990), as well as interspecific competition and resource partitioning (Parrish & Margraf 1990). Recently, such estimates have also been used to test if laboratory-derived variables (as functions of temperature and mass) as used in bioenergetic models can approximate field values (Wahl & Stein 1991). In addition, estimates of daily food consumption rates have been used as input parameters into multispecies fisheries management models such as ECOPATH (Allison *et al.* 1995), since such estimates allow for calculating predation-mortality at various trophic levels.

The relationship between ration size and growth has been studied since Winberg's (1956) description of fish growth as a balanced energy equation. Using Winberg's equation, it has been implicitly accepted that the growth of fish in natural populations is strongly regulated by the quantity of food consumed (ration size) per day. Laboratory studies have supported this view by demonstrating a positive relationship between food consumption and growth (Elliot 1979, Wootton 1990). However, recent evidence has suggested that this may not always be correct. Boisclair and Leggett (1989a, 1989b, 1989c, 1989d), in a series of papers, showed a lack of correlation between field estimates of food consumption and relative growth rates in yellow perch in 12 lake populations. In

subsequent studies, Boisclair and Leggett (1989d, 1990, and 1991) demonstrated that differential activity costs, such as energy costs associated with feeding, rather than food consumption rate, led to the differences in interpopulation growth rates.

Many fisheries are now assessed within the context of the overall ecosystem that supports them, using trophic interaction models such as the ECOPATH (Moreau 1995, Allison *et al.* 1995, Pauly *et al.* 1998). Fish population food consumption rates expressed as annual consumption per unit biomass (Q/B) are among the input parameters required in these models. When daily food consumption rates are expressed relative to fish body weight, they become estimates of consumption (Q) to biomass (B) ratios (Q/B) (per day) (Ngatunga & Allison 1996). These estimates are combined with estimates of prey consumption and total fish biomass by species. The estimates can then be integrated with estimates of production and biomass at each trophic level to summarise the trophic structure of an ecosystem (Allison *et al.* 1995).

Food consumption rate is affected by many factors, such as motivational state of hunger and appetite, rate of gastric evacuation, temperature, fish body weight and physiological state of fish (Pandian & Vivekanandan 1985, Wootton 1990,). Hunger (the propensity to feed) and appetite (the quantity of food consumed before the fish ceases to feed voluntarily) are motivated by systemic demand generated by metabolic and digestive requirements (Wootton 1990).

The rate of gastric evacuation depends on temperature and food value. The rate increases with temperature and reaches a maximum at an optimum temperature. Food with low-energy content is evacuated faster than food with high-energy content (Jobling 1980). At low temperatures fish may cease to feed and may reduce their consumption rates if temperature increases or decreases beyond the optimal ranges (Wootton 1990).

Fish body weight and physiological state of fish also affect food consumption rate in various ways. Generally, as fish grow, the weight of food consumed relative to body weight decreases. When fish become reproductively active, feeding rate decreases in some species while in others it ceases (Wootton *op cit.)*.

Sainsbury (1986) summarised a number of methods that are used to estimate the daily food consumption rates of fishes. These are: measure food consumed by fish under laboratory conditions that simulate natural conditions; estimate of food intake using bioenergetic models; or estimate daily food consumption from quantity of food present in the stomach in relation to stomach evacuation rates (method of Elliot & Persson 1978). The latter method has been used successfully in several studies (see review by Heroux & Magnan 1996, Cortès 1997). However, the problem with these methods is that they require confinement of the fish, which becomes impractical for fish that are difficult to handle. Moreover, in certain cases the gastric evacuation rates may be underestimated as a consequence of confinement. Since digestion rates vary considerably as a result of prey type (Wootton 1990), prey size (Jobling 1980) and diel variation in water temperature (Windell 1966), estimation of daily ration from *in situ* diel studies provide more accurate values (Matthews 1998).

Sainsbury (1986) suggested a method to be used for *in situ* diel studies. The method estimates daily ration of fish from a set of parameters including ingestion and evacuation rates, and the beginning and end of a feeding period from a feeding cycle of arbitrary length. Based on the work of Sainsbury (*op. cit.*), Jarre *et al.* (1990) developed an iterative software program, MAXIMS that allows the estimation of daily food consumption rates in fish, for up to two feeding cycles. Using the MAXIMS software,

reasonably accurate results have been obtained by various workers (De Silva *et al.* 1996, Palomares *et al.* 1997, Ngatunga & Allison 1996).

Indirect methods to estimate annual food consumption/fish biomass ratios include the empirical model derived by Pauly (1989) and Jarre *et al.* (1990). In this model, annual food consumption (Q) per unit biomass (B) of the fish population (Q/B) is estimated using the relationship between metabolism and morphological attributes of the fish.

The empirical method of Jarre *et al.* (*op. cit.*) has been used to estimate daily food consumption rates of *B. nyasensis* (Ngatunga & Allison 1996). While the methods are theoretically sound, the question remains whether the empirical results accurately reflect what occurs in nature. The aim of this study is to test the accuracy of the empirical estimates against the findings of an *in situ* diel study. If the results of the two methods are similar, then future studies on multispecies interactions and management could make use of the empirical method with a greater degree of confidence.

7.2 MATERIALS AND METHODS

Fifteen, 30-40 minute trawls using the R/V Ndunduma (trawling speed as detailed in Chapter 3) were made in the south-east arm of Lake Malawi over three days from 7 through 9 June 1997. Trawling depth ranged from 23 to 123 m, although approximately 70 % of the specimens were taken between 30 and 60 m.

After each drag the fish were gutted, stomach contents removed and immediately preserved in the onboard deep freezer at approximately –10°C. Once in the laboratory the samples were thawed and weighed to the nearest 0.0001 g. A subsample was processed

for dry-matter analysis. These subsamples were dried to a constant weight at 65°C over 48 hours. Percent dry matter (% dm) of the subsample was calculated by:

$$\% \text{ dry matter (dm)} = \frac{\text{weight of subsample}}{\text{weight of subsample after drying}} \times 100 \qquad \text{Equation 7.1}$$

and the total dry matter of each stomach content sample was calculated by:

$$\text{Total dry matter} = \frac{\% \text{ dm}}{100} \times \text{weight of whole fresh sample} \qquad \text{Equation 7.2}$$

The size and number of fish that were processed for stomach contents at the different sampling times during the 24-hour period is presented in Table 7.1.

Data analysis

Daily ration estimates are size-specific, and in situations where there are an insufficient number of fish on which to model different size groups, as was the case for this study, stomach contents are expressed as ratios of fish body weight, either on a wet-weight (Ngatunga & Allison 1996, Palomares *et al.* 1996) or a dry-weight basis (Heroux & Magnan 1996). In this study, dry weights of stomach contents are expressed as a ratio to total fish wet weight and is referred to as gut fullness (Heroux & Magnan 1996).

Table 7.1. Number and size of *Bathyclarias nyasensis* at different sampling times.

Time of sampling	N	Mean total length mm ± SD (Range)	Mean weight g ± SD (Range)
10h45	5	641 ± 96 (550 – 760)	2220 ± 1060 (1200 – 3700)
13h10	7	554 ± 159 (380 – 775)	1540 ± 1280 (200 – 3450)
17h30	4	367 ± 54 (311 – 440)	400 ± 230 (150 – 700)
20h28	8	356 ± 105 (202 – 485)	390 ± 280 (58- 850)
23h31	8	353 ± 48 (233 – 422)	340 ± 140 (90 – 500)
02h21	11	375 ± 90 (215 – 600)	400 ± 410 (55 – 1500)
Total	43		

The MAXIMS software program (Jarre *et al.* 1990) was used to estimate daily food consumption rate. MAXIMS uses two models: in Model I, a constant feeding rate is assumed; in Model II, a feeding rate inversely proportional to the weight of the stomach contents is assumed. MAXIMS can accommodate either one or two feeding cycles. A non-linear algorithm is used to vary the parameter values in question in order to minimise the sum of squared residuals. MAXIMS assumes an exponential evacuation model of the form:

$$S = S_o \exp(-E(t-t_o)) \qquad \text{(Equation 7.3)}$$

where: S = stomach content at time t;

E = the instantaneous evacuation rate (per hour);

S_o = the stomach contents at the beginning of a given period;

t_o = the time at the beginning of the period in question.

As stomach contents are continuously evacuated, the quantity of food evacuated must be subtracted from the quantity of food that is actually ingested. This change in stomach contents is given for Model I by:

$$dS/dt = J_1 - ES \qquad \text{(Equation 7.4)}$$

where: $S = S_r \exp(-E(t-t_o)) + J_1/E(1-\exp(-E(t-t_o)))$ (Equation 7.5)

and where: J_1 = the ingestion rate at the beginning of the feeding period;

S_r = the weight of the stomach content at the beginning of the feeding period.

The model assumes that during the feeding period, the stomach contents increased from S_r towards an asymptote (J_1/E), and the daily ration is computed as the integral of the ascending part of the trajectory of stomach contents, representing the feeding period. The residual sum of squares (RSS) are used as a measure of goodness fit. Further details on the MAXIMS software program may be found in Jarre *et al.* (1990).

7.3 RESULTS

The mean percent dry matter for stomach contents of fish was 21.8 ± 8.7% (n=43).

Figure 7.1 shows the gut fullness of fish at different sampling times.

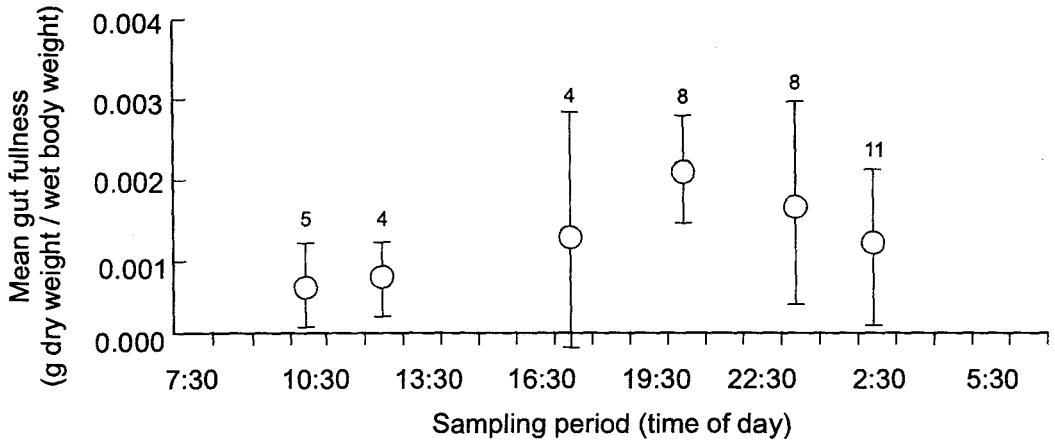


Figure 7.1. Gut fullness (g dry weight/g wet body weight of fish) of *Bathyclarias nyasensis* from Lake Malawi at different sampling times, and 95% confidence intervals for estimates. Number of observations are indicated at the top of the 95% confidence intervals.

Since MAXIMS can not handle small numbers (3 decimal places), the gut fullness data as shown in Figure 7.1 were multiplied by 100. Table 7.2 shows estimates of daily food consumption rate, ingestion, evacuation rate, time when feeding started and ended. These results are graphically presented in Figure 7.2.

Table 7.2. Estimates of daily food consumption rate and parameters of the stomach content dynamics for *Bathyclarias nyasensis* estimated using the MAXIMS software program.

Parameter	Value
Ingestion rate (hour $^{-1}$)	0.046
Evacuation rate (g hour^{-1})	0.264
Start of feeding period (hour)	9.91
End of feeding period (hour)	0.91
Daily food consumption rate (g dry wt/ g wet body wt*100)/day	0.6897
SSR (sum of squares residual)	0.0037

The estimated values of daily food consumption rate were expressed in g dry weight/g wet weight x 100/day. To allow comparison of these results with other studies, the values were expressed as percentage body weight/day on a wet-weight basis as follows:

Daily food consumption rate: 0.6897 (g dry wt/g wet body wt x100)/day
Dry ration size in g dry wt/g wet fish body weight/day = 0.006897
% dry matter content = 21.8

Daily food consumption rate in g wet wt/wet fish body weight/day = $\frac{100}{21.8}$ x 0.006897 = 0.0316

Daily food consumption rate expressed as a percentage of fish wet body weight/day = $\frac{0.0316}{1}$ x 100 = 3.16.

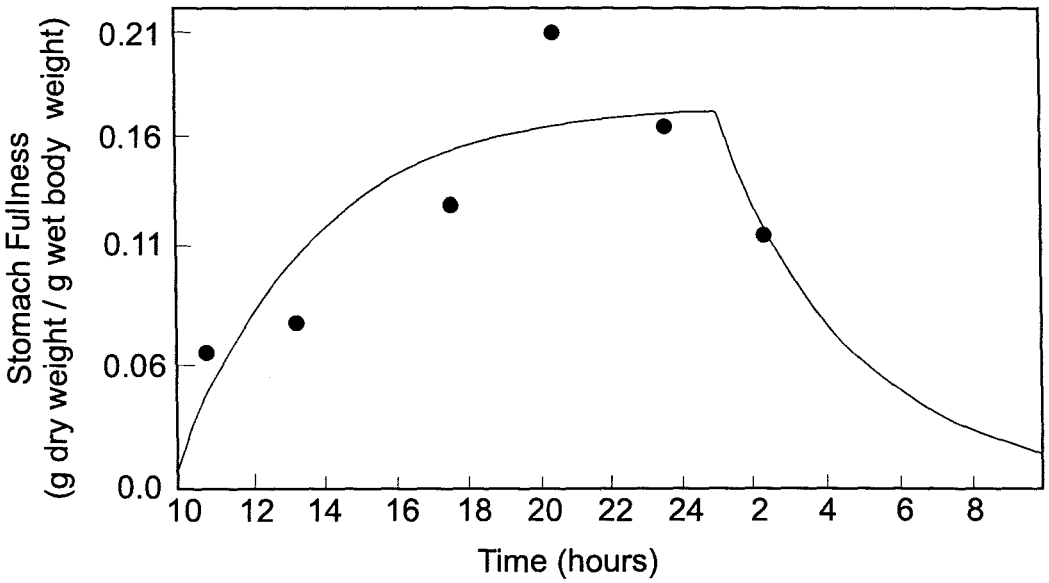


Figure 7.2. Mean dry weights of stomach contents (g) relative to predator wet body weight (g) of *Bathyclarias nyasensis* sampled from Lake Malawi over 24- hour period. The fitted curve is a model of ingestion and evacuation rate (from MAXIMS) used for calculation of the daily food consumption rate.

7.4 DISCUSSION

Since many factors affect the feeding rate of fish (e.g., food type, temperature, fish size) (Pandian and Vivekanandan 1985, Wootton 1990), estimates of daily food consumption rate must be size and locality specific. Therefore, interpretation of the results must be

made with respect to the available food, as well as the environmental and physiological condition of the fish.

In general, the feeding rate of tropical fishes is higher than for temperate fishes. Pandian and Vivekanandan (1985) plotted a semi-logarithm of feeding rate against temperature for 32 temperate and 12 tropical species, and concluded that the feeding rate for tropical fishes was about 180% higher than the mean value for temperate species. The feeding rate for tropical species ranged from 4.1 to 36.0% (mean = 16.7%) and that of temperate fishes ranged from 1.8 to 17.3% body weight per day (mean = 5.9%).

In the present study, the feeding or food consumption rate for *B. nyasensis* (3.16 % body weight/day) was lower than the minimum rate for tropical fishes as reported by Pandian and Vivekanandan (1985). However, the estimate from this study is similar to the food consumption (Q) to biomass (B) ratio (Q/B) of 3.1 ± 0.61 (Ngatunga & Allison 1996). No particular explanations can be given for the relatively low food consumption rate estimated for *B. nyasensis*. It is probable that the 12 tropical species examined by Pandian and Vivekanandan (1985) was too small to represent most tropical species. On the other hand, the relatively low food consumption rate of *B. nyasensis* may be explained by the relationship between swimming mode and metabolism (Pauly 1989).

Recent studies (Wolfgang *et al.* 1999, Daviss 2000) have shown that body undulations play a major role in fish swimming. "The fish benefits from the smooth near body flow patterns and the generation of controlled body-bound vorticity, which is propagated towards the tail, shed prior to the peduncle region and then manipulated by the caudal fish to form large-scale vortical structures with minimum waste of energy. This manipulation of body-generated vorticity and its interaction with the vorticity generated

by the oscillating caudal fin are fundamental to the propulsion and manoeuvring capabilities of fish" (Wolfgang *et al.* 1999). However, these findings do not provide a direct relationship between body shape and food consumption rate. Pauly (1989) derived empirical models for subcarangiform, carangiform and thunniform fishes (see review by Lindsay 1978 on swimming modes) that relate body shape to food consumption. These models do incorporate the findings of Wolfgang *et al.* (1999) since they include all body parts that are involved in swimming, viz. body depth, body size, depth of caudal peduncle and shape of caudal fin.

Pauly (*op. cit.*) observed that 'specialised cruisers' have a deep, forked or lunate caudal fin with a high aspect ratio (A), a narrow caudal peduncle (P) and an intermediate ratio of maximum body depth to body length (D). They also have high gill surface areas, supplying high quantities of oxygen to large masses of red muscle working aerobically. They have high energy intake and therefore a high food consumption to biomass (Q/B) ratio. Conversely, the muscle mass of 'specialised accelerators' is concentrated nearer the caudal fin than it is in 'cruisers', and the depth of the caudal fin is relatively greater (high P value). The muscles of specialised accelerators work anaerobically. They have a low overall metabolic level and, hence, a low relative food consumption (Q/B) ratio. This group includes predators that stalk their prey, e.g., *Esox lucius*. In 'manoeuvring' fishes, such as some coral reef fish, the caudal fins are rounded with a low aspect ratio (A); they have a short body and high value for the depth ratio (D). Table 7.3 provides a summary of relationships between body shape and food consumption rates.

As a basis on which to relate the swimming mode to the food consumption rate in *B. nyasensis*, the body shape and Q/B ratios of some fishes from the pelagic zone in Lake Malawi are compared in Table 7.4.

Table 7.3. Relationships between swimming schemes in subcarangiform, carangiform and thunniform fishes, and body shape and food consumption as proposed by Pauly (1989).

Swimming mode	Aspect ratio (A)	Caudal peduncle (P)	Depth ratio (D)	Food consumption rate
Specialised cruisers	high	low	intermediate	high
Specialised accelerators	-	high	-	low
Manoeuvring Fish	small	-	high	-

Table 7.4. Morphometric data and estimates of Q/B values (mean, ± SD in parentheses) for common fish species from the pelagic zone of Lake Malawi obtained by empirical and diel stomach-content analysis (DSCA) (data from Ngatunga & Allison 1996, and this study).

Species	N	Size range (mm, SL)	Aspect ratio (A)	Depth ratio (D)	Peduncle ratio (P)	W_{max} (g)	Q/B values: empirical method	Q/B values: DSCA
Copadochromis quadrimaticulatus	12	131-160	2.26 (0.20)	2.81	0.34	97	5.67 (0.23)	
Diplotaxodon 'big eye'	6	78-120	3.43 (0.19)	3.11 (0.25)	0.44 (0.09)	57	6.68 (0.64)	12.79
Rhamphochromis Esox	3	176-185	2.84 (0.20)	5.83 (0.35)	0.47 (0.00)	686	5.33 (0.21)	
Rhamphochromis Ferox	11	216-414	2.74 (0.25)	4.17 (0.31)	0.36 (0.02)	1477	4.96 (0.19)	
Rhamphochromis Longiceps	41	49-300	3.28 (0.29)	4.77 (0.38)	0.45 (0.03)	107	6.75 (0.37)	11.56
Engraulicypris Sardella	13	35 - 98	3.77 (0.43)	6.96 (0.68)	0.50 (0.05)	11	9.82 (0.68)	
Synodontis Njassae	15	87-115	4.64 (0.65)	4.87 (0.52)	0.42 (0.04)	67	8.50 (0.61)	6.45
Bathyclarias nyasensis	8	389-790	1.75 (0.27)	7.66 (0.87)	0.59 (0.07)	6378	3.31 (0.61)	
Bathyclarias nyasensis (this study)	43	215-890				3700		3.16

Note: W_{max} = maximum observed live weight.

Table 7.4 shows that *B. nyasensis* has the highest P, D and W_{max} values, and the lowest A value, corresponding to a lower Q/B value. The relatively high P and low A values with lower food consumption ratios is characteristic of "specialised accelerators". As noted above, these species employ burst swimming behaviour and stalk their prey. It could be

presumed that *B. nyasensis* have this type of swimming mode, thus accounting for the low Q/B value. This seems likely, as the closely related species *Clarias gariepinus* (see Chapter 1) is also known to stalk its prey (Bruton 1979).

While the Q/B value estimated for catfish in this study, using a diel sampling program, is the same as the empirical value of Ngatunga and Allison (1996) the value estimated here must be accepted with caution due to circumstances and constraints under which this study was conducted. Firstly, the diel study was only conducted once, during the warm-dry season. Factors such as temperature, size and prey density will invariably affect feeding rate of fish (Pandian & Vivekanandan 1985, Wootton 1990). Given the seasonal temperature changes in Lake Malawi (Chapter 2) and the euryphagous nature of *B. nyassenssis* (Chapter 5), the value may not be a true representation of the annual food consumption rate of *B. nyasensis.*

The second reason for caution relates to the size range of the fish used in this study. Estimates of daily ration or food consumption are size-specific (Wootton 1990, Ngatunga & Allison 1996). To reduce the problem of size specificity stomach contents were expressed relative to fish body weight (Palomares *et al.* 1997). The standard deviation of the size of fish sampled during the day was high (Table 7.1), implying that most size classes were represented. However, the size distribution of fish that were caught after 19h00 was skewed towards small fish (Table 7.1). It seems, therefore, that the observed feeding regime during the night-time reflected the trajectory of stomach contents of fish of relatively small size.

However, as the Q/B value estimated in this study was similar to that which was obtained using empirical model (Ngatunga & Allison 1996), suggests that the value obtained in

the present study may be close to the actual Q/B value of *B. nyasensis*. Moreover, a wide size range of fish was represented by samples collected during day. Therefore, one could suggest that this value can be used in trophic studies until other *in situ* diel studies are conducted to improve on or validate it.

The size of fish caught over 24-hour period may provide some insight into the feeding habit of *B. nyasensis,* and so permit us to make suggestions on how to conduct a 24-hour sampling program in order to obtain less biased results. Anecdotal reports suggest that *B. nyasensis* undergoes vertical migration and feeds from the water surface at night (Ngatunga 1995). The fact that in the present study, larger fish did not appear in the sample at night, may, in part, support this hypothesis. Fish were not caught at night because demersal trawling gear was used (Chapter 3) when *B. nyasensis* had migrated to the upper water surface to feed. To obtain a less biased result, it is suggested *that B. nyasensis* should be fished from the upper water column during the night (following the vertical migration of zooplankton, Chapter 2) and from the demersal region only during the day.

When the Q/B value is combined with data on the diet (Chapter 5) and biomass of *B. nyasensis* (Chapter 1) an estimate of the impact of fish on prey population can be made. In the pelagic zone, *B. nyasensis* is zooplanktivorous (Chapter 5), hence, in this particular case, the consumption of zooplankton can be assessed. Table 7.5 shows steps that were followed to estimate zooplankton consumption by *B. nyasensis*.

From Table 7.5, it is apparent that consumption of zooplankton by *B. nyasensis* represents an increase of about 12% over the previously estimated total zooplankton consumption, and a probable increase of 7.8% and 33.5% over the estimated

consumption of *Tropodiaptomus cunningtoni* and *Mesocyclops aequatorialis aequatorialis,* respectively. Although these figures are specific to the study area (Chapter 1), they nevertheless show that omission of *B. nyasensis* from the trophic studies may have led to overall underestimation of the zooplankton predation in the pelagic zone of Lake Malawi.

In conclusion, it is apparent that more diel studies are required to validate the Q/B value obtained in this study. The suggested sampling program may allow collection of fish of all size classes during a 24-hour cycle. Meanwhile, it seems reasonable to suggest that the Q/B value estimated in this study may be close to the actual Q/B value of *B. nyasensis*.

Given that this value was the same as that obtained by other workers using an empirical model, it may be suggested the latter may be used for other species not requiring much research effort - atleast until a comparative diel study is conducted to validate the findings of this study (or otherwise). The estimated Q/B value permitted an estimate of the impact of *B. nyasensis* on the zooplankton resource in the pelagic zone of Lake Malawi.

The fact that zooplankton predation may have been underestimated by between 7-33% depending on the zooplankton species, entails that the available information on trophic levels of the Lake Malawi pelagic zone (Allison *et al.* 1995) needs to be revisited. In light of these findings more questions arise on the debate regarding the introduction of foreign species into the pelagic zone of Lake Malawi; this issue is discussed in Chapter 8.

Table 7.5. Steps followed in estimating zooplankton consumption by *Bathyclarias nyasensis* in the pelagic zone of Lake Malawi.

A) Biomass of *Bathyclarias nyasensis* in pelagic zone

= 5200 mt per 528 m^2 (Area C, Banda *et al.* 1995).

Therefore, total biomass of catfishes = $\frac{20x100}{5200}$ = 1040 mt

Given the assumption that *Bathyclarias* spp. = 50% of catfishes, and *Bathyclarias nyasensis* = 70% of *Bathyclarias* species (Chapter 1), weight of *Bathyclarias nyasensis* per area (g/m^2),

= (364mt x 1000 x 1000)g /538 km^2 *x* 1000 *x* 1000 m^2

= 0.67g/m^2

B) Zooplankton consumption by *Bathyclarias nyasensis*

Given the Q/B value of 3 (from this study and Ngatunga & Allison 1996) and that the proportion of zooplankton in the diet is 70% (Chapter 5), zooplankton consumption is given by:

Q/B x weight of fish/area x proportion of prey in diet (Allison *et al.* 1995)

= 3 *x* 0.7 *x* 0.67 = 1.4 g wet weight/m^2

C) Total zooplankton consumption by *Bathyclarias nyasensis* and other predators from the pelagic zone of Lake Malawi

Total zooplankton consumed (previous estimate) = 11.6 g wet weight/m^2 (Allison *et al.* 1995)

Consumption consumed by *Bathyclarias nyasensis* = 1.4 g wet weight/m^2

Total zooplankton consumed = 11.6 + 1.4 = 13 g wet weight/m^2

Percent increment over previous estimation = $\frac{1.4}{11.6}$ x 100 = 12.07%

D) Consumption of zooplankton by species (by *Bathyclarias nyasensis*)

Assuming that zooplankton consumption between the dominant species, *Tropodiaptomus cunningtoni* and *Mesocyclops aequatorialis aequatorialis* is 1:1 ratio (Chapter 4), consumption of each species is 0.7 g wet weight/m^2

For *Tropodiaptomus cunningtoni:*

Given that consumption of *Tropodiaptomus cunningtoni* = 8.42 g wet weight/m^2 (Allison *et al.* 1995), then total consumption including *Bathyclarias nyasensis* = 8.42+0.7 = 9.12 g wet weight/m^2; and percent increment = $\frac{0.7}{8.42}$ x 100 = 7.67%

For *Mesocyclops aequatorialis aequatorialis:*

Given that consumption of *Mesocyclops aequatorialis aequatorialis* = 1.39 g wet weight/m^2 (Allison *et al.* 1995), then total consumption including *Bathyclarias nyasensis* = 1.39+0.7 = 2.09 g wet weight/m^2; and percent increment = $\frac{0.7}{2.09}$ x 100 = 33.5%.

CHAPTER 8

General discussion

This study demonstrates the importance of approaching feeding studies from a life-history and morphological perspective. Not only can life history and morphological studies be used to predict, but also to explain the observed food and feeding habits of a species. Moreover, this study has provided base-line information that is fundamental for single-species stock assessment models (Chapter 3), as well as inputs for ecosystems or predator/prey management approaches (Chapters 5 & 7).

In the following section, the management needs of *Bathyclarias nyasensis* are briefly discussed in light of observed life-history parameters and strategies (Chapter 3). This is followed by a discussion on the ecological role of *B. nyasensis* in Lake Malawi. Finally, the issue of introducing new species into the pelagic zone of the Lake Malawi ecosystem (Allison *et al.* 1995) is debated in regard to the findings presented in this study.

Life history strategy of *Bathyclarias nyasensis*

Since information on life-history traits on which to relate the feeding biology of *B. nyasensis* were not available, studies on age, growth and aspects of reproductive biology of the species were undertaken (Chapter 3). Life-history theory can provide some insight into where attention might be most profitably focused interms of fisheries monitoring and research (Adams 1980, Garrod & Horwood 1984, Ware 1984). The study has demonstrated that, in comparison to other species found in Lake Malawi, *B. nyasensis* mature at a relatively large size (mean age 6 years, 500 to 650 mm TL), have a high fecundity (14,265 ± 4, 903 eggs/kg), a high growth rate in the first year (reaching approx. 400 mm TL) and reach a relatively large maximum size (up to 1,020 mm TL). Although

nothing is known of the diet of larvae and early juveniles the data show that "young-of – the-year" juveniles feed mainly on fish. It was postulated that the piscivorous habit of juveniles accounts for a rapid growth rate in the first year. Furthermore, evidence has been presented to suggest that large *B. nyasensis* migrate inshore to spawn during the warm wet season. It was also demonstrated that the r-k and altricial/precocial life history theories fail to explain the life history style of *B. nyasensis*. Rather, the life-history style of these catfish is best explained by the "periodic life-history strategy," one of the three alternative life-history strategies proposed by Winemiller and Rose (1992).

The theory of Winemiller and Rose (1992) predicts that periodic strategists exploit differences in environmental quality that occur temporally and spatially. The periodic strategy is viewed as the tactic of spreading reproductive effort over many years (or over a large area), so that high larval/juvenile survivorship during one year (or in one spatial zone) compensates for years of poor recruitment per spatial unit. Given the high fecundity and small size of the eggs of such fishes it can be assumed that larval mortality is high. According to Winemiller and Rose (1992) since "most larvae are never recruited into the adult population, it follows that spawning must proceed unimpeded each year in fairly undegraded habitats if fitness payoff is to be collected during the exceptional year". Hence, to manage long-lived periodic strategists it is pivotal to maintain some critical density of the adult stock and to protect the spawners and spawning habitats during the short reproductive period. The data provided in this thesis suggest that mature *B. nyasensis* migrate into the inshore region to spawn, and it is in this region where they are heavily overfished (Chapter 1), thus the future viability of the stock becomes threatened. On the basis of this information, it is recommended that managers need to consider options concerning how catches of *B. nyasensis* in the inshore region can be reduced during spawning.

Ecological role of *Bathyclarias nyasensis*

From the preceding chapters it is evident that *B. nyasensis* occupies two trophic levels, being piscivorous during the juvenile inshore phase and zooplanktivorous during the offshore adult phase, and reverting back to piscivory in the inshore region during the spawning season. One conclusion reached from the diel study (Chapter 7) states that *B. nyasensis* undertakes vertical feeding migration from the demersal region and feeds in the pelagic zone at night. A summary of the theoretical inshore/offshore migratory life-history cycle of *B. nyasensis* is presented in Figure 8.1.

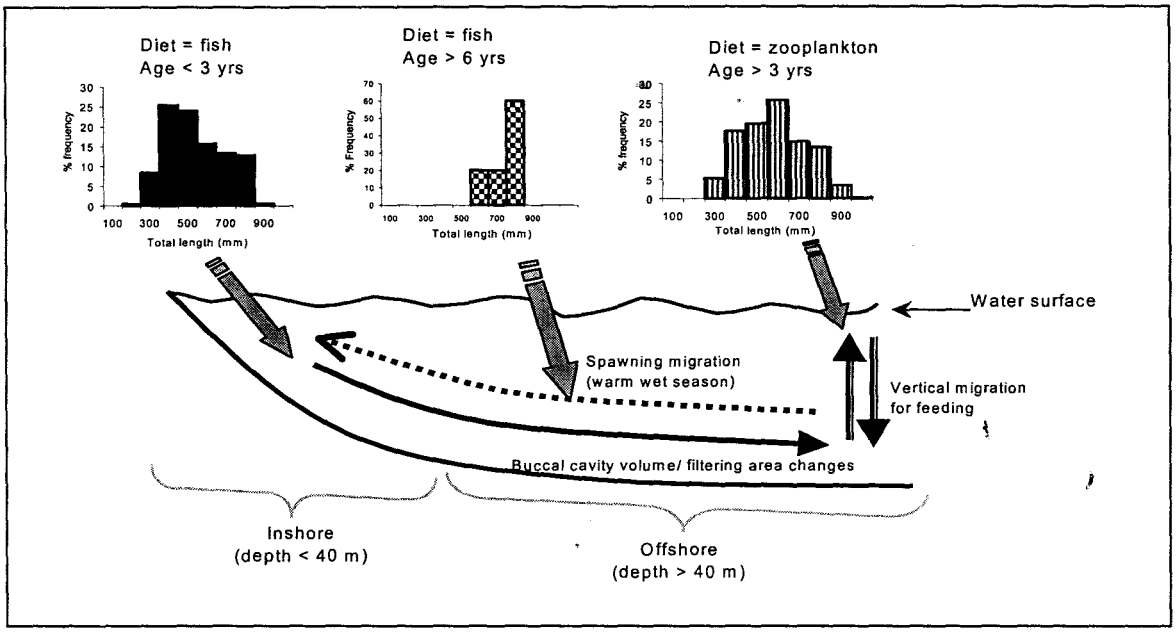


Figure 8.1. The theoretical inshore/offshore migratory life-history cycle of *Bathyclarias nyasensis* in Lake Malawi.

To appreciate the ecological role of *B. nyasensis*, theories pertaining to factors that control the food web in which it exists are discussed. Two categories of models attempt to explain the factors that govern the structure of aquatic food webs. Firstly, the "bottom

up" or resource-controlled models of trophic structure suggest that nutrient availability determines plant growth and abundance, which in turn determines zooplankton abundance, which determines the fish biomass (Currie *et al.* 1999).

The "bottom–up" model was a solution to the eutrophication debate of the 1960s and 1970s (Dillion & Rigler 1972). According to that debate, the problem was to explain what is responsible for the variation in algal biomass among lakes and through time. Using the "bottom–up" model, Dillion and Rigler (1972) suggested that nutrients might be responsible for changes in algal biomass. This was proved to be correct through experimental manipulations (Schlinder 1977, Edmonson 1991).

The second category of models, generally known as "top-down", trophic cascade or predator-controlled models (Carpenter & Kitchell 1985, 1992), emphasise the effects of predators on algal biomass and productivity at lower trophic levels. The predator-based hypothesis predicts that an increase in the abundance of piscivorous fish should reduce the abundance of planktivorous fish. This in turn would allow zooplankton biomass to increase, which then graze down the phytoplankton biomass.

The trophic cascade theory has been successfully demonstrated in experimental studies. It has been shown that adding piscivores to a planktivore-dominated lake causes extensive changes in the zooplankton community, causes increased rates of herbivory, and reduced primary production. Reversing the manipulation (i.e., removing the piscivores) reverses the effects. Simultaneous manipulations of food-web structure and nutrient loading in ecosystems dominated by piscivores and with large-bodied zooplankton will effectively limit phytoplankton biomass even at very high nutrient loads (Kitchell & Pace 1998).

Theoretically, the trophic cascade hypothesis is sound. Larger herbivores are consumed selectively by planktivorous fishes (Brooks & Dodson 1965) and this shifts the zooplankton composition toward dominance by smaller individuals. Carnivorous zooplankton feed most heavily on smaller zooplankton (Hall *et al.* 1976) and will shift zooplankton composition toward dominance by larger individuals. This occurs when planktivorous fishes are absent and predation is restricted to that by planktivorous invertebrates (Brooks & Dodson 1965, Hall *et al.* 1976). Large herbivorous zooplankton have a greater impact on phytoplankton because they consume a broad range of sizes and morphologies of algae (Bergquist *et al.* 1985). However, owing to their size, these large zooplankton have a lower mass-specific rate of nutrient excretion (Peters 1983), resulting in low algal biomass. In contrast, small-bodied zooplankton have higher rates of nutrient excretion that result in a higher rate of nutrient recycling. Thus, algal biomass and primary production can expected to be less in lakes dominated by large zooplankton than in lakes dominated by small zooplankton (Carpenter & Kitchell 1985). If fish are included in the trophic cascade theory, then the presence of piscivores (apex predators) should ultimately lead to a lower biomass of planktivorous fish, which should lead to more large-sized zooplankton and, therefore, low algal biomass.

Practically, however, larger-scale bio-manipulations have had mixed results in relation to the trophic cascade hypothesis. An aggressive salmonid stocking program in Lake Michigan was, as expected, followed by improvements in water quality (Scavia *et al.* 1986). In contrast, similar salmonid stocking in Lake Ontario did not lead to changes in chlorophyll levels (Lean *et al.* 1990). In natural aquatic systems, findings in terms of the trophic cascade hypothesis are equivocal. Currie *et al.* (1999) demonstrated that in natural aquatic systems neither algal nor zooplankton biomass is significantly related to piscivorous fish presence.

Nevertheless, the effect of planktivorous fish on the size distribution of zooplankton is unequivocal, even as reported for natural aquatic systems. Currie *et al.* (1999) observed that when piscivorous fish were present, zooplankton composition was indeed dominated by larger-sized zooplankton.

The Lake Malawi trophic system shows many characteristics of "bottom-up" control (Allison *et al.* 1995). The seasonal wind-induced cycle of mixing has a strong influence on biological production in the lake. Periods of increased mixing result in increases in nutrient availability to photosynthesising phytoplankton in the epilimnion, leading to higher primary production (Chapter 2). This in turn increases the food available to herbivorous zooplankton. Furthermore, secondary and tertiary production in the lake show marked seasonal variation (Chapter 2). However, unlike other typical "bottom-up" controlled lakes, there is evidence of damping of variability further up the food chain. Mean fish biomass at the top of the food chain does not show any seasonal variation (Allison *et al.* 1995).

In the inshore region *B. nyasensis* is an apex predator. It seems unlikely that perturbations of the *B. nyasensis* stock in this region would cascade to affect the lowest level of the food web (i.e., phytoplankton). However, interactions stemming from the apex predator may be substantial and discernible at the upper level of a food web. For example, a United States National Research Council panel review of interactions in the Bering Sea (NRC 1996) concluded that trophic cascades could be traced to the exploitation of whales. Reduction of whales allowed significant increases in prey resources such as krill, which fuelled an explosive population response by walleye pollock and, through competition-predation interactions, depressed the local herring and capelin populations.

The latter are key energy-rich prey for juvenile fur seals and sea lions and in this case, their survival and numbers declines in concert with declines in their preferred prey resources (NRC 1996, and see Kitchell & Pace 1998 for other examples of trophic cascade effects due to reduction of apex predators).

Other effects of removing apex predators are unrelated to the trophic cascade theory. In a food web, piscivores determine the species and size composition of the planktivorous fish assemblages beneath them (Tonn & Magnuson 1982). At times, exploitation of predatory fishes may relax selection pressures on the unexploited species. If this happens, the traits that evolved under previously more intensive selection are lost. This may lead to homogenising fish communities and "inhibiting the evolution of novelty and of biotic competence" (Vermeij 1978). Furthermore, predation can restrict the distribution or limit the abundance of prey species. Heck &Valentine (1995) reported that sea urchins were selectively preyed upon when inhabiting sand flats, but were less likely to be preyed upon when inhabiting sheltered seagrass beds.

From the foregoing, it is clear that apex predators play an important role in the structuring of fish communities; thus, their removal may lead to undesirable ecological, and by extension, economical consequences. It may not be easy to demonstrate the effects of removing *B. nyasensis* from the inshore region. It seems probable that the effects of overfishing in inshore areas have in the past been obscured due to the observed ontogenetic habitat shifts in an offshore region where the stock is not fished. Therefore, it may be assumed that the offshore region acts as a refuge area for *B. nyasensis*.

In the offshore region *B. nyasensis* is zooplanktivorous and its presence there could be expected to affect the community structure of the lower trophic levels in two ways.

Firstly, the presence of *B. nyasensis* may provide the right zooplankton size to other zooplanktivores such as the lakefly *Chaoborus edulis,* which has been identified as one of the most important zooplankton grazers in the lake (Turner 1982). As noted above, the presence of planktivorous fish leads to dominance of small-sized zooplankton. It is also known that the gape of *Chaoborus edulis* limits the size of zooplankton that can be ingested (Irvine 1995). Hence, it can be expected that the absence or a reduced abundance of *B. nyasensis* would lead to dominance by large zooplankton which can not be ingested by *C. edulis,* resulting in starvation-induced mortality of the latter. In turn, a reduced biomass of *C. edulis* would affect *Diplotaxodon* "elongate", as this species relies almost entirely on *C. edulis* (Allison *et al.* 1995).

Secondly, *B. nyasensis* may reduce competition for the dilute resource of the herbivorous zooplankton, *Tropodiaptomus cunningtoni*. It is known that the carnivorous zooplankton *Mesocyclops aequatorialis aequatorialis*, larval *Engraulicypris sardella* and *C. edulis* feed on *T. cunningtonii*. *B. nyasensis* feeds on both *M. a. aequatorialis* and *T. cunningtoni* (Chapter 5). The circumstances under which *B. nyasensis* take one and not the other is not known. However, it can be assumed that by eliminating *M. a. aequatorialis*, the presence of *B. nyasensis* would reduce competition between *M. a. aequatorialis*, *E. sardella* larvae and *C. edulis* for *T. cunningtoni*. The absence of *B. nyasensis*, therefore, may lead to stiff competition for *T. cunningtoni*, which may culminate in low production of *C. edulis* and *E. sardella* larvae with possible effects to the upper level of the food web.

While these predictions remain speculative, it may be possible that in the past such ecological consequences have not been noticed because the offshore region has not been intensively fished and the pelagic ecosystem was considered to be stable (Allison *et al.*

1995). The life history and feeding habit of *B. nyasensis* suggests that intensive fishing of the demersal zone would affect the pelagic ecosystem. Current there is an interest to expand demersal trawling in the offshore region of the lake (Allison *et al.* 1995). Large species often suffer from a "fishing down" syndrome (Pauly *et al.* 1998) and are selectively eliminated in a multispecies fishery (Welcomme 1999). That *B. nyasensis* is one of the larger species (cf. Table 7.4) suggests that ecological changes would rapidly manifest in the face of fishing. These predictions should therefore serve as a warning that exploitation of the offshore fisheries should proceed on the basis of the precautionary principle.

The role of *B. nyasensis* as a zooplanktivore provided an opposing dimension to the debate about the zooplanktivore efficiency of Lake Malawi, which prompted the proposition of introducing a zooplanktivorous species into the lake. From studies by Walzack (1982), Turner (1982) and Degnbol (1982), it was concluded that the consumption of zooplankton by fish was only 3-4% of that consumed by *C. edulis*. Turner (1982) and Rufli and Vitullo (1982) estimated the pelagic fish biomass to be low, ranging from 75-90 kg/ha, which appeared to make only partial use of *C. edulis* as a food resource. It was further concluded that the majority of primary production was being channelled into *C. edulis* production that was then lost to the system (Degnbol & Mapila 1982, Turner 1982, Walzack 1982). The implication was that the Lake Malawi planktivorous fish community was competitively inferior to *C. edulis*. The absence of *C. edulis* from Lake Tanganyika which supports a high biomass of clupeid zooplanktivores (Coulter 1991) was taken as good reason to suggest that the introduction of a clupeid may lead to *C. edulis* being either out-competed (Hecky 1984) or preyed upon to extinction (Turner 1982). This would then be of benefit to the pelagic fisheries in the lake. Opponents to this view argued that zooplankton biomass in the pelagic region is in fact

low (Allison *et al.* 1995), and that the fish biomass in the pelagic region may have been underestimated (Tweddle & Lewis 1990). Furthermore, the case of the introduction of *Lates niloticus* into Lake Victoria, which has resulted in ecological instability, environmental degradation and loss of species diversity, was cited as a warning against any possible introductions (Allison *et al.* 1995). These arguments are summarised in Table 8.1

Table 8.1. A summary of the arguments for and against the introduction of a planktivorous fish into the pelagic zone of Lake Malawi.

Proponents of introductions	**Opponents to introductions**
Zooplankton consumption by *Chaoborus edulis* is high, while consumption by fish is only 3-4% of the total consumed by *C. edulis*.	Overall, zooplankton consumption by *Chaoborus edulis* is low. It is only about 10-20% of the total zooplankton production.
Fish production in the pelagic zone is low and is not comparable to Lake Tanganyika. Therefore, the bulk of the primary production is channelled into *Chaoborus edulis* which is lost out of the system.	Fish production in the pelagic zone may not be as low as suspected. Yields of the pelagic fish *Engraulicypris sardella* may have been underestimated. Fish yields may well be comparable to Lake Tanganyika.
Planktivorous fish (excluding *Bathyclarias nyasensis*) are not as efficient as *Chaoborus edulis* in utilising the zooplankton resource.	Zooplankton density is low, and no other fish may be capable of utilising this dilute resource.
In Lake Tanganyika fish production is high due to a clupeid zooplanktivore and there is no *Chaoborus edulis*. A plausible option is to introduce the Lake Tanganyika clupeid zooplanktivore into Lake Malawi so that it can either out-compete or prey *Chaoborus edulis* to extinction.	Elimination of *Chaoborus edulis* will affect upper levels of the food web. Lessons should be learnt from the Lake Victoria experience, wherein introduction of *Lates niloticus* led to ecological instability, environmental degradation and loss of diversity.

Findings from the present study substantiate opposition to the idea of introducing a foreign fish species to the pelagic zone of Lake Malawi, viz:

a) Offshore demersal fish stocks, such as *B. nyasensis*, rely on the zooplankton resource. Therefore, the previously estimated "low" pelagic fish biomass that was supposed to feed on zooplankton was underestimated.
b) Zooplankton predation by fish may have been underestimated by between 7-33%, depending on the zooplankton species (Chapter 7).
c) Given points (a) and (b) planktivorous fish (now including *B. nyasensis*) may not be inferior to *C. edulis* in utilising the zooplankton resource.

It is somewhat surprising that for decades studies on Lake Malawi proceeded without due attention to *B. nyasensis,* an ecologically important species in both inshore and offshore zones of the lake's ecosystem. Several reasons may account for this. Firstly, the taxonomic debate surrounding the species (Chapter 1) may have diverted the attention of researchers to taxonomic issues. Secondly, the "slimy and ugly" appearance of *B. nyasensis* (Thompson *et al.* 1996) may have diverted the attention of researchers to the brightly coloured species of Lake Malawi. Results from this study suggest that irrespective of the taxonomic status or appearance of a species any study which uses the ECOPATH or other whole-system models must look at all species.

The findings of the present study suggest that management policies of *B. nyasensis* need to be put in place. Particularly, as a periodic strategist, overfishing of the spawner biomass in the inshore areas may lead to a collapse of the stock. It is also apparent that overfishing of the juveniles in the inshore areas would affect the pelagic fish community due to an ontogenetic habitat shift. The current interest to expand demersal trawling in the offshore zone is considered to be a threat to *B. nyasensis* stock. This zone seems to have acted as a "refuge" or reserve area for *B. nyasensis*, hence a theoretically stable

pelagic ecosystem has been maintained. Exploitation of the demersal zone, therefore, should proceed with caution and the effects must be closely monitored.

Finally, findings from this study suggest that feeding ecology studies are pivotal to discerning the rational exploitation of a fishery. Such studies lead to defining the ecological role of certain species, which in turn can lead to reconstruction of food webs. It is clear that when life-history characteristics are studied in a food web context, immediate insight into the system can be obtained. This insight can allow for predictions on the effects of current and future exploitation patterns. Furthermore, feeding studies can resolve issues of possible species introductions where such actions are considered. The importance of feeding studies in fisheries management was recognised as early as the 1960s: "the construction of a rational method of exploitation would be impossible without a knowledge of the manner in which the fish exploits its food resources, of the nature of the interrelationships between fish and others which consume the same food, and also of predators" Nikolsky (1963).

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