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ECOLOGY AND POTENTIAL FOR FISHERY OF THE SMALL BARBS (CYPRINIDAE, TELEOSTEI) OF LAKE TANA, ETHIOPIA

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To Neter Alemu (my mother) and

Dejen Dresilign (my father)

Contents

Chapter 1

Introduction

1.1 General introduction

1.1.1 Importance of small pelagics for fisheries

The fishery on small pelagics is often commercially important for small-scale or artisanal inland fisheries (see Marshall (1984) for a review). Small-scale fisheries in the tropical regions compose of almost half of the total annual fish catch, provide twenty-fold more employment opportunities than the industrial fisheries, and have a low-capital intensity (Laggis, 1993). Moreover, artisanal fisheries supply fish and fisheries products cheaper to the final consumer even in remote and isolated localities. No record of commercial exploitation of small pelagics exists in Ethiopia.

Introduction of small pelagic fish species in African lakes and reservoirs has in most cases considerably improved fisheries productivity. In the thirteen largest natural lakes in Africa, amounting to a surface area of around 176,000 km^2, the estimated total sardine yield is 0.9-1.3 million tons (roughly equivalent to US$ 1 billion) (Pitcher, 1995). The success of *Limnothrissa miodon* introduction is evidenced by the observation that the introduction of this species alone was responsible for doubling the total fish yield over a period of 17 years (Pitcher, 1995). When this species was transferred from Lake Tanganyika to Lake Kivu during 1958-1960, the total yield increased from a few hundred tons per annum to about 4300 tons per annum (Marshall, 1995). In Lake Kariba, after the introduction of *Limnothrissa*, the pelagic fishery, consisting almost entirely of this species, now produces nearly ten times as much as the conventional inshore fishery.

1.1.2 Zooplankton and zooplanktivorous fish in the food web of tropical waterbodies

Zooplankton is a key element in the functioning of many freshwater ecosystems. It often controls the algal growth via grazing and guarantees a food source for the survival of the youngest stages of most freshwater fish species. Zooplankton also sustains the pelagic fish production as realised by obligatory zooplanktivores, facultative zooplanktivores and the piscivores relying on them.

In the temperate region, zooplanktivorous fish generally dominate the pelagic zones of lakes and reservoirs and play an important role in the food chain. In tropical freshwater ecosystems, however, this is not always the case. Often zooplanktivorous fish are poorly represented, and generally only play a minor role in the food web. The zooplankton produced in these waterbodies is generally utilised to a small extent. There are two possible reasons for this. Firstly, the pelagic fishes inhabiting tropical reservoirs and recently formed tropical lakes are generally of riverine origin and often not fully adapted to lacustrine food conditions. Therefore, they are often not capable of using the available food resources effectively. Secondly, small-bodied zooplankton species dominate the zooplankton community in tropical lacustrine environments (Fernando, 1994; Amarasinghe *et al.*, 1997; Wudneh, 1998) and because of this the small particle size cannot be utilized efficiently by most zooplanktivorous fish species.

However, within the group of obligate zooplanktivores inhabiting tropical lacustrine environments there are still a few species that seem to have well adapted to the lacustrine environment. They are small in size, have a short life cycle and are characterised by a high individual growth rate, a high reproductive rate, and an early age of first reproduction (Duncan, 1999). Most of these small pelagics from the tropical region are freshwater sardines (*Clupeidae*) whose ancestors originally came from marine environments, but some are cyprinids from riverine origin. In Lake Tanganyika freshwater sardines are represented by two species, *Stolothrissa tanganicae*, *Limnothrissa miodon*, in man made Lake Kariba by *L. miodon* (introduced from L. Tanganyika), in Cahora Bassa Reservoir by *L. miodon* (migrated from Lake Kariba), and in the man-made Lake Volta by *Pellonula afzelius* (Duncan, 1999). Lake Victoria and Lake Tana are somewhat exceptional as not a clupeid but a small cyprinid, *Rastrineobola argentae* and a small barb (*B. tanapelagius*), respectively, dominate the fish fauna in terms of numbers and production (Wanink (1998); this thesis).

1.1.3 Lake Tana and its environment

Ethiopia located in East Africa covers a total surface area of 1.1 million square kilometres. In 1992, the country became a land locked depending only on inland water resources for the supply of fish as a cheap protein source. Water bodies cover only 0.7 % of the area of the country and comprises of 10 lakes. Most of them are located in the Rift Valley, and together they have a total surface area of 7,500 km^2. By far the largest water body is Lake Tana (50 % of the total lakes area) located outside the Rift Valley on the north-western plateau. Fish consumption in Ethiopia is low and concentrated in the big cities, mainly Addis Ababa and its surroundings. Lake Tana due to its distance from the capital city (500 km) is amongst the least exploited lakes.

The climate of Lake Tana is characterised by a major rainy season with heavy rains, during June-October, and sometimes a minor rainy season during February-March. Average annual rainfall in the lake area over 1997-2000 was 1418 mm. The water level of the lake fluctuates with rainfall up to 1 m. Maximum water temperature, as a monthly average, ranged between 21 and 26 °C over 1997-2000. Water temperatures varied between narrow limits, with lowest values in January, a sharp increase in February, peak values in May and sharp decline with the big rains in June-July.

Lake Tana is an oligo-mesotrophic shallow lake (average depth 8.9 m, maximum 14 m) and is well mixed; therefore a thermocline is lacking. It is located at an altitude of 1830 m and is the source of the Blue Nile River. It is the largest lake in Ethiopia with a surface area of 3,150 km^2, a maximum length and width of 78 and 68 km respectively. A bathymetric map produced by Morandini (1940) and redrawn by Rzóska (1976) (Fig. 1.1) shows a gentle slope of the saucer shaped lake bottom, which is covered with soft sediments. The shallow littoral zone (depth 0-4 m) is relatively small, *ca.* 10 % of the total surface area of the lake. The sublittoral zone contains no macrophytes and occupies *ca.* 20 % of the lake area (depth 4-8 m), whereas the pelagic zone is 70 % of the lake surface area and relatively deep (depth 8-14 m).

The lake has been isolated from the lower Blue Nile basin by 40 m high falls, 30 km downstream from the Blue Nile outflow. The catchement area of the Lake (16,500 km^2) has a dendritic type of drainage network. Four major permanent rivers, the largest of which is Gelgel Abbay (Little Blue Nile) feed the lake. Annual soil loss in the Lake Tana catchement area ranges from 31 to 50 tons per hectare and

Figure 1.1: Bathymetric map of Lake Tana taken from Rzóska (1976). The depth contours are in meters.

shows a substantial increase during recent years (Teshale *et al.*, 2001). The inflowing rivers carry a heavy silt load into the lake during the rainy season that increases the turbidity of the lake water considerably during this period.

1.1.4 Lake Tana and its fish community

Greenwood (1976) described the Lake Tana fish community as very truncated, i.e. very poor in species and families. There is one cichlid, *Oreochromis niloticus* (Nile tilapia), which is the most widespread tilapia species in Africa. This species is predominantly a herbivore, feeding on macrophytes, algae and detritus (Getachew and Fernando, 1989; Piet *et al.*, 1999). The catfish family (Clariidae) is also presented by one species, *Clarias gariepinus* (African catfish), which is the most common member of its genus (Teugels, 1986). This species is a facultative piscivore and benthivore. The largest fish family in the lake is the Cyprinidae, represented by three genera: *Barbus*, *Garra* and *Varicorhinus*. Boulenger (1907, 1911) mentions two species of *Garra* for Lake Tana, but Nagelkerke (1997) found that the descriptions are inconsistent and concluded that the taxonomic position of the *Garra* spp. is still unclear. More recently, Getahun (2000) described four species of *Garra* for Lake Tana, but this is being researched. *Garra* spp. are obligate herbivores, feeding on algae, macrophytes and detritus (Driessen, 2002), they are widespread in the rivers and lakes of the Ethiopian highlands. *Varicorhinus beso* is a very distinct large cyprinid as described by Rüppell (1836). Like the *Garra* spp., this species is common and generally distributed in the rivers and lakes of the Ethiopian highlands. It feeds mainly on scrapping algae and detritus (Driessen, 2002).

Recently 15 large barb morphotypes have been described as species composing a world unique species flock of endemic cyprinid fish (Nagelkerke, 1997; Nagelkerke and Sibbing, 1996). Evidence for their species status came from segregation in spawning (Nagelkerke and Sibbing, 1996) and molecular genetic data (Dixon *et al.*, 1996). The 15 large barbs are hexaploid and well diversified in their distribution and feeding ecology (Nagelkerke *et al.*, 1994; Nagelkerke, 1997; Sibbing and Nagelkerke, 2001; de Graaf, 2003). On the basis of gut content data, Nagelkerke (1997) distinguished five trophic groups. A conspicuous number of species (eight) feed on fish. Small barbs are said to be almost the only prey species of the piscivorous large barbs. They may not be optimally equipped for catching fish, but this is compensated by the high abundance of prey and profitability of eating it, especially since there is no competition from specialised non-barb piscivores (Nagelkerke, 1997). One species of large barb, *B. macrophtalmus*, feeds on a mixed diet of macrofauna and fish, three species feed on benthic invertebrates (mainly insect larvae) (*B. crassibarbis*, *B. nedgia*, *B. tsanensis*), two species feed on a mixture of macrophytes and molluscs (*B. gorgorensis*, *B. surkis*) and one species (*B. brevicephalus*) feeds mainly on zooplankton (Nagelkerke *et al.*, 1994; Sibbing *et al.*, 1994).

In addition to the above mentioned large hexaploid barbs (up to 85 cm) also three diploid small barb species (<10 cm) were described: *B. trispilopleura* (Boulenger, 1902), *B. humilis* (Boulenger, 1902) and *B. pleurogramma* (Boulenger, 1902). Boulenger

(1902)'s descriptions were not adequate, most probably due to collection and preservation of his specimen by others and the low number of specimens up on which it was based. This raised the question of the validity of previous descriptions as a basis for fish biology and fisheries investigations.

These small barbs are probably the most effective zooplanktivorous fish in Lake Tana (Nagelkerke, 1997; Wudneh, 1998). In spite of their high abundance in Lake Tana, observations on their taxonomy and ecology are very scarce compared with those on the large commercially exploited fish species. Until I started my study nothing was known about their abundance, distribution, feeding, growth and reproduction. There was only one other report about the occurrence of small diploid barbs from Ethiopia. Golubtsov and Krysanov (1993) reported about small barbs from rivers in the Rift Valley areas. In general, small sized fish species (such as small barbs), which are not currently commercially important, don't receive much attention.

1.1.5 Initiation and objectives of the research

Lake Tana fishery remained completely subsistent involving ca. 1000 persons, until a fisheries development project assisted by Dutch Non Governmental Organisation (ISSE, Urk and ICCO, Zeist) was launched in the mid 1980s. Fishery is mainly confined to the southern gulf (Bahir Dar, the largest town in the region). The traditional subsistence fishery using papyrus reed boats exploits the inshore fish community (Nile tilapia, *Oreochromis niloticus* and large barb, *Barbus intermedius*). The other type of fishery, motorised boat fishery, exploits a wider lake area including the open water fish community of the large piscivorous *Barbus* species and African catfish, *Clarias gariepinus*. The commercial fishery mainly targets the river spawning large *Barbus* species in the river mouths during their breeding period (July-October). The introduction of motorised fishery resulted in an increase of annual fish catch (from 500 tonnes in 1988 to 1,300 tonnes in 1997) and consumption during the first 10 years (Wudneh, 1998).

The research program described in this thesis is part of a collaborative project between Wageningen University and the Ethiopian Government, which started in 1989 and deals with Lake Tana's fish community. The overall applied objective of this program is to assess the fish stocks in relation to fisheries and to develop management strategies. It is apparent that in depth knowledge of spatial and temporal variation of the abiotic and biotic factors of the Lake Tana ecosystem must be obtained because only such a framework of knowledge and insight will provide the basis for long term management policy. Previous studies focused on the commercially important fish stocks (Nagelkerke, 1997; Wudneh, 1998; de Graaf *et al.*, 2000b). de Graaf *et al.* (2000b) reported serious decline of the endemic stocks of large barbs in Lake Tana as the result of recruitment overfishing of the spawning aggregations. The decreasing densities of piscivorous large barbs will probably cause changes at the lower trophic levels and will finally disturbs the dynamic balance of the lake's ecosystem as a whole. It is therefore crucial to look for an alternative; *i.e.* to divert the fishing pressure from the large barbs to some other targets, possibly the unutilised small barbs. Prior to starting experimental fisheries (testing gear and fishing techniques) on these small barbs, their use of resources and the resource base, reproduction characteristics and annual biological production need to be investigated to asses their potential sustainable yield without negative effects on the current fisheries of the larger fish species. In spite of their abundance and their presumed ecological importance, the small barbs of Lake Tana have hardly been investigated.

The following research questions were addressed in this thesis:

1. Which species of small barbs of Lake Tana exist and how diverse are they morphologically and ecologically?

2. Are the small *Barbus* species of Lake Tana efficient zooplankton feeders and are they the dominant zooplanktivores within the guild of zooplankton feeding fish? What competitors are there?

3. Which key features in structure, functioning, behaviour and ecology make these small barbs such successful zooplanktivores? How do these compare to other zooplanktivorous species in Lake Tana?

4. Are the small *Barbus* species of Lake Tana characterised by a relatively high growth rate, fecundity and productivity? To what extent is growth and reproduction affected by cestode infection?

5. Are the differences in the habitat occupation of the small *Barbus* species of Lake Tana and the larger commercial fish species high enough to enable a fishery on small barbs without negative effect on the current fisheries on larger fish species?

6. Are the small barbs in terms of biological production key species of the fish community in Lake Tana?
7. Is the biomass and production of small barbs in Lake Tana large enough to ensure a sustainable yield that is high enough to make it interesting for the commercial fishermen to start a subsidiary fishery on small barbs?
8. What are the possible ecological effects of such a fishery on the structure of the Lake Tana food web?

My predecessor researchers on Lake Tana (Leo Nagelkerke and Tesfaye Wudneh) and my counterpart Martin de Graaf focused on the top-down approach, *i.e.*, from the fishermen to the piscivorous fish to their diversified prey. This thesis follows the bottom-up approach from zooplankton to zooplanktivorous fish. The study of the above research questions required an intensive sampling programme in the field. It was executed in close co-operation with a similar 2 years sampling programme of the large barbs across the same stations and habitats (Martin de Graaf, PhD thesis that will appear on the same day of my defence). This allows comparison and interactions of predators and preys. This programme provided detailed information on the spatial and temporal distribution of zooplankton and the small barb species, providing data also on the reproduction, growth and food composition of the small barbs, and with information about the habitat and diet segregation of the small barb species and their potential competitors.

1.1.6 Sampling Programme

The sampling was done in the Southern Gulf of Lake Tana (*ca.* 10 % of the lake area) from October 1999 to November 2001. The shallow littoral zone (depth 0-4 m) has macrophytes and open areas and is relatively small, *ca.* 10 % of the total lake area. The sublittoral zone (depth 4-8 m) contains no macrophytes and covers *ca.* 20 % of the lake area, whereas the pelagic zone is 70 % of the lake area and relatively deep (depth 8-14 m). A total of 17 sampling stations were selected representing these three macrohabitats. The littoral habitat was represented by nine stations, sublittoral by four and pelagic also by four stations. The littoral habitat was varied in substrate type (rocky/sandy and muddy) and border (vegetation/agricultural land). Therefore, there were relatively more sampling stations in the littoral than in the other two macrohabitats. Multi-mesh monofilament gillnets (type Norden from Lundgrens, Stockholm; 5, 6.25, 8, 10 and 12.5 mm bar mesh) were used. The size of a single mesh panel was 3 x 1.5 m. Three multimesh nets were combined as one set. The sampling programme with gillnets was carried out two times per month (day and night in the same week). At the shallow stations only a bottom-net was set. At deep stations both bottom and surface-nets were set. Nets were set between 06.00 and 09.00 for day-time sampling and between 18.00 and 21.00 for night-time sampling. Bottom trawl was used at the non-rocky stations during dusk and dawn. Trawling speed was 1.0 m s^{-1} and trawl hauls lasted for 15 minutes each. The mouth opening of the trawl (3 m wide and 1 m high) was kept open with a 3 m beam. The bar-mesh in the cod-end is 5 mm. Species composition, catch (number and weight) and length-frequency distribution were recorded from gillnet and trawl catches. From each sampling station monthly 30-40 fish (if available) were randomly selected for detailed analysis. Length, weight, sex and maturity stages were recorded from the fresh sample immediately after each catch. Fork length (FL) was measured to the nearest mm and total weight to the nearest 0.1 gram. Fish were carefully inspected for the presence of cestode larvae, *Ligula intestinalis*, in the body cavities. Gut contents of fish were analysed and measurements were also taken on morphological characters. Environmental measurements on temperature, conductivity, pH and dissolved oxygen were taken with a portable probe. Total dissolved solids were measured with a TDS meter, turbidity with a portable turbidometer and chlorophyll-a content with a spectrophotometer. Environmental variables were collected monthly at three stations. Zooplankton samples were collected every 1-2 month at six stations using a 3.5 l Friedinger type volume sampler, species composition and numerical abundance were recorded. Detailed measurements of many external and internal morphological characters and their ratios were determined to construct hypotheses about trophic specializations of the small barb species. Indoor and outdoor tanks were used to studies of growth and predation upon these small fish. Details are found in the chapters.

1.2 Introduction to the various chapters

In this section I will discuss the subsequent chapters and present their major conclusions within the framework of the project. The two main questions were: (1) what is the role of the small barbs in the food web, and (2) is it advisable to start a subsidiary fishery on the small barbs?

1.2.1 Chapter 2; Taxonomy of small barbs

In the absence of detailed revisions, the taxonomy of African Cyprinidae attributed to the genus *Barbus* remains confused. Nevertheless, external morphological characters can be used to distinguish at least two groups (Agnese *et al.*, 1990). These are the 'large' barbs characterised by their scales with many parallel striae, by their dorsal fin with nine to eleven branched rays and by the last hard ray with no denticles, and which are sometimes longer than 50 cm; the 'small' barbs, have scales with a small number of divergent striae, whose dorsal fin has seven or eight branched rays, and which are rarely longer than 10 cm (Berrebi *et al.*, 1990). In the absence of a comprehensive examination, and considering the many species that have probably not yet been described, it can be estimated that there are about 200 to 250 species of small barbs and 60 to 80 species of large barbs in Africa (Berrebi *et al.*, 1990). In Ethiopia, the genus *Barbus* is the largest with 22 species and accounts for 24 % of the total fish species ($n = 92$, Froese and Pauly (2001)). Lake Tana, home to the unique endemic large *Barbus* species flock harbours 15 large barbs. The taxonomic status of Lake Tana small barbs (*Enteromius*) species is unclear and not well researched. It is therefore essential to revise their taxonomy prior to starting detailed ecological and biological studies.

In this chapter we addressed the hypothesis that *Barbus humilis* (Boulenger, 1902) and *Barbus trispilopleura* (Boulenger, 1902) are not really a separate, but constitute a single species. Three species of small barbs (*Barbus*, subgenus *Enteromius* Cope, 1869) are known from Lake Tana: *B. humilis*, *B. trispilopleura*, *B. pleurogramma* (all Boulenger (1902)). In our study based on 32 morphometric characters using cluster analysis *B. humilis* and *B. trispilopleura* significantly differ from *B. pleurogramma* in up to 36 characters. However, *B. humilis* and *B. trispilopleura* cannot be distinguished from each other by morphometric analysis, neither by other characters. Our conclusion is that *B. trispilopleura* is a synonym of *B. humilis.*

1.2.2 Chapter 3; *Barbus tanapelagius*, a new small barb species from Lake Tana

The largest fish family in Lake Tana is Cyprinidae, represented by 3 genera, *Barbus*, *Garra* and *Varicorhinus.* The endemic cyprinid species flock in Lake Tana consists of 15 large hexaploid barbs. Additionally, Boulenger (1902) mentioned 3 diploid small barb species (< 10 cm FL), which are not only distinct from the large barbs (up to

85 cm FL) by their size, but also by their morphology. The small *Barbus* species can without difficulty be separated from juvenile large *Barbus* species by a weakly developed first dorsal spine and radiating striae on the scales.

In this chapter we described the discovery of a new small barb species in Lake Tana. Next to the three species reported by Boulenger (1902): *Barbus humilis*, *B. trispilopleura* and *B. pleurogramma*, we found a fourth previously unknown small barb in large numbers (up to 500 individuals in a single 15 minute trawl) predominantly in the unexplored offshore, deep waters of the lake. We have compared its characters with the species described by Boulenger (1902) and concluded that one more species of small *Barbus* is abundant in the lake. This chapter provides a description of the morphology and ecology of the new species, *Barbus tanapelagius* and briefly discusses some possible consequences of its discovery for existing hypotheses of the food web of Lake Tana.

The morphological difference in cluster analysis, difference in feeding habits and habitat occupation of *B. humilis* and *B. tanapelagius*, suggest that *B. humilis* and *B. tanapelagius* belong to different species, but most recent molecular analysis (de Graaf, 2003) suggest that *B. humilis* and *B. tanapelagius* are very closely related species that probably diverged in evolution after formation of Lake Tana, or its latest desiccation.

1.2.3 Chapter 4; Zooplankton composition and distribution in relation to environmental factors

In Lake Tana, microcrustacean zooplankton constitutes a major component of the food chain. It is an important link between primary production and planktivorous fish, mainly two small barbs, *Barbus tanapelagius* and *B. humilis.* As prey-fish for top-predators, these small barbs provides the basis for the commercial fish production. In addition, all larval and most small juveniles of all fish species more or less exclusively utilise zooplankton for growth (Post and Kitchell, 1997). Recently Wudneh (1998) conducted the first preliminary study about the zooplankton species composition and distribution in Lake Tana, but his study did not include an analysis of the effects of environmental factors and food (chlorophyll-a) on the zooplankton distribution. In this chapter we described the relation between environmental factors and the temporal and spatial distribution of microcrustacean zooplankton in a shallow turbid tropical lake, addressing the hypothesis that turbidity is the most important factor regulating zooplankton community structure over seasons and space. This study provides a baseline for future studies since the Lake Tana catchement is under alarming threat from increased human activities (*e.g.* deforestation), soil erosion and climate change (*e.g.* erratic rainfall). Canonical Correspondence Analysis (CCA) was used to estimate the influence of abiotic factors and chlorophyll-a content in structuring the zooplankton assemblage. Among the environmental factors, zooplankton abundance correlated most strongly with turbidity. Turbidity was negatively correlated with species abundance, especially for *Daphnia* spp. and to a lesser extent for *Diaphanosoma* spp. We also observed significant temporal differences in zooplankton abundance, the highest densities occurring during the dry season (November-April) when the turbidity is low compared to the rainy season. Consistent identification of zooplankton species is essential for assessing the long-term status and trends in taxonomic structures of the assemblages. Our investigations showed four species of cladocerans (*Diaphanosoma sarsi*, *Daphnia hyalina*, *Daphnia lumholzi* and *Moina micrura*) that were not reported earlier for Lake Tana.

1.2.4 Chapter 5; Resource partitioning

An important condition for improving the rational management of the Lake Tana ecosystem is the understanding of the dynamic interactions among fish stocks and their environment (Sibbing *et al.*, 1994). Partitioning of resources or interaction between organisms can occur along three resource dimensions (trophic, spatial and temporal), which in it self are mutually interconnected. The importance of these dimensions is often difficult to establish. Firstly, it is unclear what variables can be used to characterise the occupation of this resource dimension, and secondly in what ways can interrelation between the various resources dimension occur (Piet *et al.*, 1999).

In this chapter we described resource use (habitat and food) of five taxa of obligate and facultative zooplanktivores: the small barbs, the large barb *B. brevicephalus* and juvenile large barbs. Our result suggests that habitat use differed along the littoral-pelagic gradient; *B. pleurogramma*, *B. humilis* and juvenile large barbs preferred the littoral shallow habitats, whereas *B. tanapelagius* and *B. brevicephalus* predominantly occupied sublittoral and pelagic habitats. Gut content analysis revealed that zooplankton constitutes the major component of the diet for *B. tanapelagius*, *B. humilis* and *B. brevicephalus.* Niche overlap and niche breadth are considered measures indicating potential competition for resources between populations and their capacity to avoid it. Based on the niche occupation along the trophic and spatial dimensions, the measure of niche breadth and niche overlap was calculated for the five fish taxa. In Lake Tana the trophic resource dimension was equally as important as the spatial dimension for segregating species.

By sampling gut contents of fish it is possible to get an impression of trophic resource partitioning as it is at the moment, but this method has no predictive value on how interactions will shift, once circumstances change (under human and environmental influence) (Sibbing and Nagelkerke, 2001). The ecomorphological paradigm states that the morphology of an organism holds essential information about its ecological functioning, *e.g.* the structure and functioning of the feeding apparatus determines how an organism feeds, and what challenges, imposed by food items, can it meet effectively (Nagelkerke, 1997; Sibbing and Nagelkerke, 2001). The previously developed food-fish model (Sibbing and Nagelkerke, 2001) was used as a newly available tool to generate hypotheses based on a long series of morphological characters and mechanical requirements for different food types and resource use of the different species. These were tested from the gut content collected in the field. We measured the functional morphology of each fish species to predict its potential food niches and to subsequently tested them for their actual diets. Morphologically, *B. tanapelagius*, *B. pleurogramma* and *B. brevicephalus* showed a high degree of specialisation, whereas *B. humilis* was a very generalised opportunistic feeder. The potential feeding niche of *B. humilis*, *B. pleurogramma* and juvenile large barbs, as deduced from their morphology and confirmed by their gut contents analysis, are broad and fit to littoral and benthic areas with diversified food types. In contrast *B. tanapelagius* and *B. brevicephalus* are specialised on few food types, and adapted to their pelagic habitat with a low diversity of potential food. This approach confirmed the prediction value of the earlier developed food-fish model and therefore substantiates the importance of this approach.

1.2.5 Chapter 6; Reproductive strategies

The reproductive biology of a fish species in a lake provides vital information required in preparing and designing fisheries management policy. It provides essential information on size of maturity, spawning period and breeding place to set the minimum allowable fish size in the catch and also to advise when and where fishing must be restricted. Although the small barbs are not currently exploited, the proposed fishery on small barbs in Lake Tana is only possible when information on their reproductive biology is available.

Small pelagic species generally have a short life cycle and are characterised by a high individual growth rate, a high reproductive rate, and an early age at first reproduction (Miller, 1996). In this chapter we described the reproductive biology of the two small barbs and compare their reproductive traits with other small cyprinids and clupeids in Africa. In view of Lake Tana's evolution and exploitation, the reproductive strategies of the bentho-littoral *B. humilis* and the pelagic *B. tanapelagius* were investigated for their adaptive traits. The breeding period of both species is protracted (six months) and peak in March (high water temperatures) and August (big rains). The differences in the reproductive strategies between the two small barbs, *B. humilis* and *B. tanapelagius* of Lake Tana, were attributed to interacting biotic factors: parasite infection rate, availability and partitioning of food and predation risk. *Barbus tanapelagius* reproduction traits were most adapted to relatively new lacustrine conditions. The low relative fecundity, compared with small lacustrine cyprinids and clupeids from other African lakes, can probably be explained by the meso-oligotrophic state of Lake Tana.

1.2.6 Chapter 7; Parasitism and its effect on small barbs

Most fish face a wide range of different enemies including competitors, predators and parasites. Parasites may induce shifts in species densities, size composition and affect commercially interesting stocks. They can also alter the size-specific schedules of reproduction and mortality of their hosts. This may depend on vulnerability of species, habitats and seasonal factors. Ligulids are important cestode parasites of cyprinid fish in lakes and reservoirs throughout the world (Dick and Choudhury, 1995). In Africa, infection by cestode larvae has been reported from fish of the Nile in Egypt and the Sudan and from the East African lakes (Paperna, 1980).

In this chapter we described environmental factors causing fluctuations in prevalence of plerocercoid larvae of the tapeworm, *Ligula intestinalis*, and the effect of this parasite on its intermediate host, small cyprinid fish species. *Ligula intestinalis* was often found in the two small barbs *B. humilis* and *B. tanapelagius*, but not in *B. pleurogramma* and the three *Garra* species. Zooplankton (intermediate host) availability and water temperature are correlated with parasite prevalence. In all infected species

L. intestinalis caused retardation in gonad development, small size at maturity and reduced absolute fecundity, thus affecting their life history strategies. The differences in habitat and trophic position were found as major reasons for difference in parasite prevalence within and between species. Infection rate, averaged over all habitats, was significantly higher in *B. tanapelagius* (10 %) than in *B. humilis* (6 %). The high infection rate in *B. tanapelagius* is explained by its specialised zooplanktivory, ingesting more copepods infected with tapeworm than *B. humilis*, a polyphagous bentho-littoral species.

1.2.7 Chapter 8; Estimation of biomass and production of the small barbs and potential for fishery

Studies on growth and mortality of fish are vital components in understanding the pattern of population dynamics of the stock. These estimations are used to characterise the state of the population and are also used as input variables to estimate biomass and potential yield of the stock (Sparre and Venema, 1998).

This chapter deals with the population dynamics and production biology of the two small barbs. This information is then used to estimate the potential sustainable yield. Recommendations for a sustainable fishery on *B. tanapelagius* based on the annual maximum sustainable yield and production potential are discussed. Growth and mortality of the two small barbs (*Barbus humilis* and *B. tanapelagius*) were investigated from length-frequency data using FiSAT II (FAO-ICLARM Stock Assessment Tools) computer package (Gayanilo *et al.*, 2002). The annual maximum sustainable yield of *B. tanapelagius* was 3,850 ton. This study has shown the potential to start a subsidiary fishery for *B. tanapelagius* in the pelagic habitat. However, it must also be noted that this study considered only biological factors. Ideally, proposal for promoting the sustainable use of fishery resources should be based on biological and environmental investigations, as well as the economic and social aspects. It is therefore recommend to further investigate the viability, the magnitude, the fishing methods (night-fishery, lift net, trawl, gillnet), operation time and management for such a fishery.

Chapter 2

The ‘small barbs’ *Barbus humilis* and *B. trispilopleura* of Lake Tana (Ethiopia): are they ecotypes of the same species?[1]

Four species of ‘small barbs’ (*Barbus*, subgenus *Enteromius* Cope, 1869) are known from Lake Tana, isolated in the Ethiopian highlands: *B. humilis*, *B. trispilopleura*, *B. pleurogramma* (all Boulenger (1902)) and *B. tanapelagius* de Graaf *et al.* (2000a). However, only three species appear valid from cluster analysis using 32 morphometric characters and taking specimens from different locations in the southern Gulf of Lake Tana during August-October 1999. *B. humilis* and *B. trispilopleura* significantly differ from *B. tanapelagius* and *B. pleurogramma* in up to 36 characters. However, *B. humilis* and *B. trispilopleura* cannot be distinguished from each other by morphometric analysis or by gut contents. Specimens from clear, shallow rocky areas with vegetation have a darker back, will be more susceptible to birds, have significantly higher infection by cestodes, smaller size at first reproduction, lower fecundity, and correspond most to the *B. trispilopleura* phenotype. Specimens in turbid deeper water without vegetation are most similar to the *B. humilis* phenotype. We conclude that both species actually are extremes (ecotypes) of a continuum, belonging to a single biological species. The observed variation may well be induced by habitat-dependent predation pressure by birds. The high frequency (57 %) of spot numbers intermediate between Boulenger’s number for *B. trispilopleura* (3) and for *B. humilis* (0) demonstrates the continuum best. Pigment spots and colour change in response to aquarium conditions and are in this case no valid taxonomic characters. Both characters may reduce the risk of predation. It is concluded that *B. trispilopleura* is a synonym of *B. humilis*. For future research we recommend to use the most appropriate name, *B. humilis*, for both types.

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[1] **Dejen, E., Rutjes, H.A., de Graaf, M., Nagelkerke, L.A.J., Osse, J.W.M., Sibbing, F.A. (2002). *Env. Biol. Fish.* 65, 373-386.**

2.1 Introduction

As a part of the analysis of the community structure and dynamics of the Lake Tana ecosystem, its production and its evolution, the status of its 'small barbs' must be assessed. In spite of their abundance and their presumed ecological importance, they have hardly been investigated (Boulenger, 1902, 1911; Nagelkerke, 1997; de Graaf *et al.*, 2000a). Recent research on Lake Tana has focused on the peculiar species flock of 'large barbs' and its evolution (Nagelkerke *et al.*, 1994; Mina *et al.*, 1996a,b; Nagelkerke, 1997; Nagelkerke and Sibbing, 2000; Wudneh, 1998; de Graaf *et al.*, 2000b). The commercial importance of the many top predators among them created the need for studying their prey fish, the 'small barbs', in order to understand the potential of the resource at that level of the food chain. Small barbs form a main link in the food chain between primary consumers (zooplankton) and top-predators, and therefore in commercial fish production (Nagelkerke, 1997; de Graaf *et al.*, 2000a).

Barbs (genus *Barbus*) form a complex polyphyletic group of Old World Cyprinidae that provide an attractive model for studying evolutionary phenomena in freshwater fish (Berrebi *et al.*, 1996). It is estimated that there are about 200-250 species of 'small barb' and 60-80 species of 'large barb' in Africa (Berrebi *et al.*, 1990). 'Small barbs' are considered to belong to the *Barbus* subgenus *Enteromius* Cope, 1869, by Bini (1940) and to '*Barbus* sensu lato' by Howes (1987). 'Small barbs' are evolutionary diploid ($2n = 50$) characterised by an adult size of < 10 cm standard length, and by diverging striae on the exposed part of their scales. This is in contrast with the 'large barbs', subgenus *Labeobarbus* Ruppell, 1836, which are evolutionary hexaploid ($2n = 150$), have parallel striae and a larger dorsal spine (Golubtsov and Krysanov, 1993). The genus *Barbus* accounts for more than 50 % of the Cyprinidae family (Howes, 1991). In Ethiopia, 93 species of freshwater fish are reported (Getahun and Stiassny, 1998; Froese and Pauly, 2001), of which 44 species are cyprinids.

In Lake Tana, the largest freshwater basin of Ethiopia (*ca.* 3150 km^2), an endemic flock of 15 large *Barbus* species has been found and studied (Nagelkerke *et al.*, 1994; Nagelkerke, 1997; Nagelkerke and Sibbing, 2000). Recently, also a new 'small barb' species has been decribed for Lake Tana (de Graaf *et al.*, 2000a). Apart from the endemic subspecies *Oreochromis niloticus tana* (Seyoum and Kornfield, 1992) (Cichlidae), also the cyprinid genus *Garra* may include some endemic species (Getahun, 2000). The other fish species found in Lake Tana are widespread in the rivers and lakes of the Ethiopian highlands: *Clarias gariepinus* (Clariidae) and the cyprinid

Varicorhinus beso.

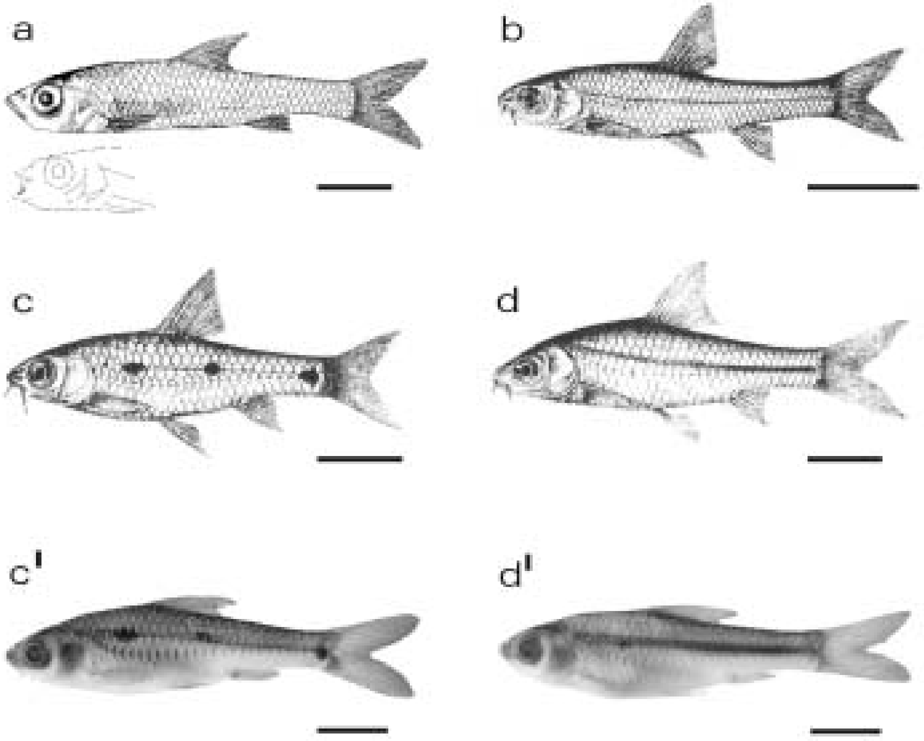

Figure 2.1: The small barbs of Lake Tana according to the original illustrations of preserved specimens: a - *Barbus tanapelagius* de Graaf *et al.* (2000a); b - *B. pleurogramma* (Boulenger, 1907); c - *B. trispilopleura* (Boulenger, 1907); d - *B. humilis* (Boulenger, 1911). c′ and d′ are pictures of the fresh specimens that we collected for present study. Scales equal 10 mm.

Boulenger (1902) described three species of 'small barbs': *B. pleurogramma*, *B. humilis* and *B. trispilopleura* (Fig. 2.1). The recently found fourth species *B. tanapelagius* (de Graaf *et al.*, 2000a) is abundant in the surface layers of the deeper open water (4-14 m), far from the shore. It differs from the other species by its small barbels, its large eye diameter, its prominent and hooked lower jaw contour, and by its slender silvery-white body. *B. pleurogramma* is distinct by its copper-brown colour, its small scales and its conspicuously serrated dorsal spine. It occurs mainly between shore vegetation and in floodplains shallower than 1 meter. *B. humilis* and *B. trispilopleura* are distinct from the previous two species. However, during sampling serious doubts developed about Boulenger's distinction between *B. humilis* and *B. trispilopleura*. Boulenger (1902) descriptions are not adequate, most probably due to collection and preservation of his specimens by others, and due to the low number of specimens (3 for *B. trispilopleura*, 10 for *B. humilis*). The hypothesis of the present paper is that *B. humilis* and *B. trispilopleura* are not separate, but a single species.

2.2 Materials and methods

2.2.1 Sampling sites and collection

Fish were sampled from August to December 1999 in five different mostly turbid habitats, replicated in 17 sampling stations (Fig. 2.2, Table 2.1): (a) shallow (ca. 2 m deep) littoral zone with rocky bottom; (b) shallow littoral zone with muddy/sandy bottom, some stations bordering temporary floodplains with submerged vegetation, others exposed to agricultural crop land; (c) sub-littoral zone, *ca.* 6 m deep, with sandy/muddy bottom, sampled at surface and bottom; (d) open, *ca.* 10 m deep water with sandy/muddy bottom, sampled at surface and bottom; (e) shallow but clear water habitat with much vegetation and rocky bottom, close to trees and houses of Bahar Dar town. Habitats a-d are grouped as turbid areas with no conspicuous vegetation (TNV), habitat e is clear and rocky with *Ceratophyllum* vegetation (CRV). Multi-mesh monofilament gillnets (type Norden from Lundgrens, Stockholm; 5, 6.25, 8, 10 and 12.5 mm bar mesh) were used at all sites. Trawling (cod-end 5 mm bar mesh) was done at the non-rocky sites and 15 minutes at speed 1 m s^{-1} yielded about 400-800 small fish. Scoop and lifts nets were used in habitat e.

2.2.2 Identification of species

Barbus pleurogramma (copper-brown with serrated dorsal spine) and *B. tanapelagius* (silvery, with large eye and hooked lower jaw) are easy to identify. The initial identification of fresh *B. humilis* and *B. trispilopleura* followed Boulenger's description (Fig. 2.1, Table 2.2), using body colour and spot patterns as key characters. This means that of *B. trispilopleura* only specimens with three clear spots on the side and blue-brown back were included in the morphometric analysis (Table 2.3), and that

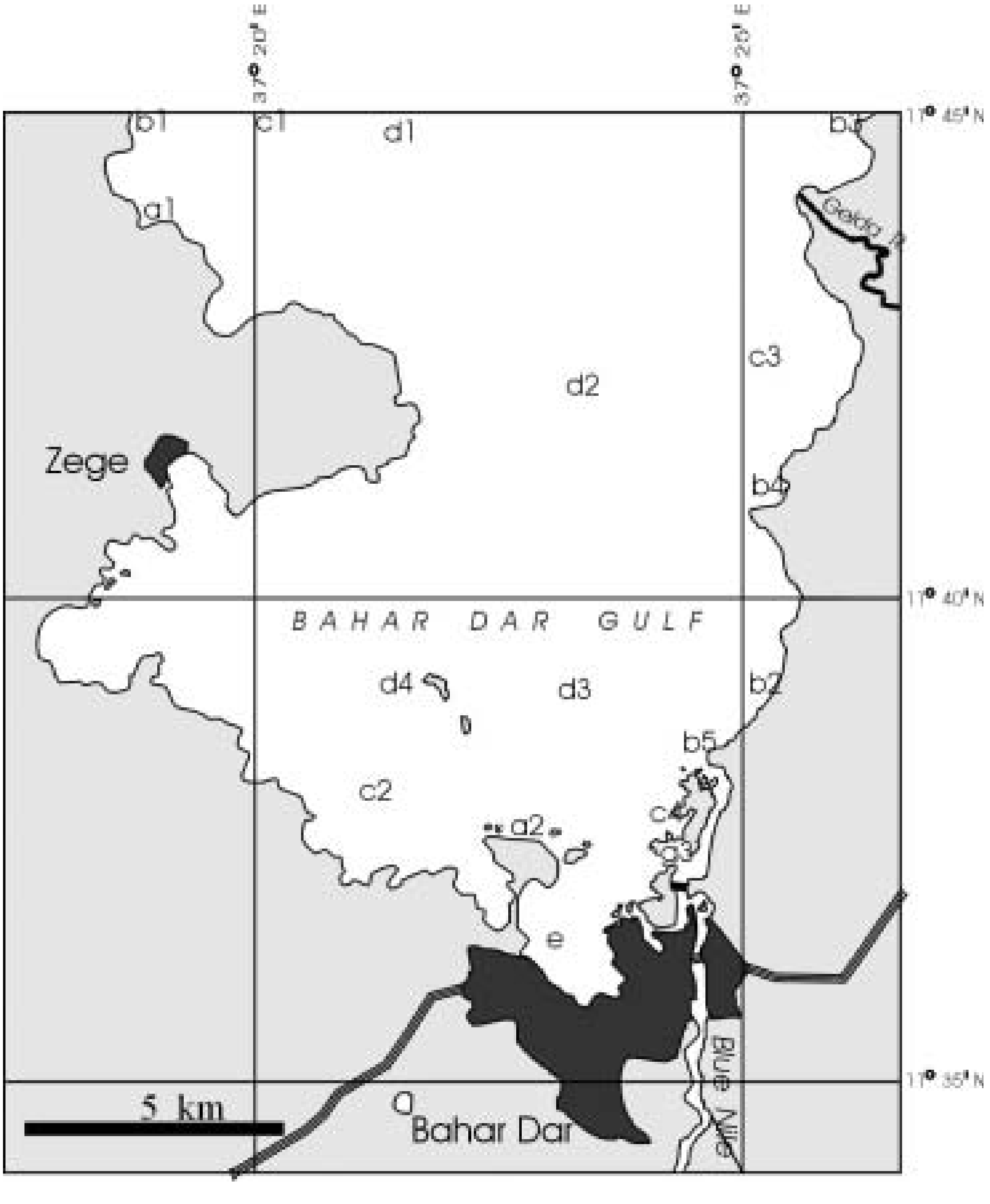

Figure 2.2: Sampling stations in the Bahar Dar Gulf, the southern part of Lake Tana: a1, a2, a3 = sampling stations in littoral zone with rocky bottom (*ca.* 2 m deep); b1, b2, b3, b4, b5 = stations in littoral zone with muddy/sandy bottom, bordered by papyrus, grass or agricultural land (*ca.* 2 m deep); c1, c2, c3,c4 = stations in sub-littoral zone with sandy/muddy bottom (*ca.* 6 m deep); d1, d2, d3,d4 = open water stations with sandy/muddy substrate (*ca.* 10 m deep); e = shallow station (*ca.* 2 m deep), close to the city of Bahar Dar, clear, rocky and with floating vegetation (*Ceratophyllum*). For a map of Lake Tana and its main in- and out-flowing rivers, see Nagelkerke and Sibbing (1996).

Table 2.1: Sampling stations in the southern bay of Lake Tana (*cf.* Fig. 2.2): their local name, depth, substrate (m = mud; r = rock; s = sand), area border (fp = flood plain, temporary submerged vegetation; p = papyrus; t = tree; al = agricultural crop land; h = houses; ow = open water) and co-ordinates (each minute 1.8 km). The larger the depth at which a Secchi-disc can still be seen (Secchi-depth), the clearer the water. Secchi-depth range indicates change over seasons. Note that only station 'e' has large amounts of floating vegetation (mainly *Ceratophyllum*)

Station	Local name	Depth (m)	Sub-strate	Border	Secchi-depth range (cm)	Co-ordinates	
						Lat.	Long.
a1	Mushe	1.5-3	r	p	40 - 70	11°, 44′	37°, 19′
a2	Gerima	1.5-3	r	p	45 - 80	11°, 37′	37°, 23′
a3	Blue Nile	1.5-3	r	r/t	60 - 75	11°, 37′	37°, 24′
b1	Menkir Dingaye	1.5-3	m	p	35 - 70	11°, 46′	37°, 19′
b2	Yigashu	1.5-3	m/s	fp	30 - 60	11°, 39′	37°, 25′
b3	Bosit	1.5-3	m/s	r/al	25 - 75	11°, 45′	37°, 26′
b4	Mebra	1.5-3	m/s	r/al	35 - 75	11°, 41′	37°, 25′
b5	Guma Tirs	1.5-3	m	fp	30 - 50	11°, 39′	37°, 25′
c1	East of Ambo	4-7	m	ow	45 - 65	11°, 45′	37°, 20′
c2	Airport	4-7	m	ow	45 - 75	11°, 38′	37°, 21′
c3	Boled	4-7	m	ow	30 - 60	11°, 43′	37°, 25′
c4	Debre Mariam	4-5	m/s	ow	40 - 75	11°, 38′	37°, 24′
d1	Mid Gulf	10-14	m/s	ow	50 - 75	11°, 45′	37°, 22′
d2	Mehale Zege	10-13	m	ow	40 - 70	11°, 42′	37°, 23′
d3	Kentefami	8-10	m/s	ow	45 - 65	11°, 39′	37°, 23′
d4	Kibran	8-10	m	ow	40 - 70	11°, 39′	37°, 21′
e	Bahar Dar town	0.5-3	r	p/t/h	70 - 145	11°, 36′	37°, 23′

of *B. humilis* only spotless individuals with pale brown back and lateral pigmented band were used. More than half of the fresh specimens did not fully match these criteria and was discarded for morphometrics, however, included in the analysis of spot patterns and population parameters.

2.2.3 Measurements and observations

Meristic and morphometric measurements (58 parameters; Table 2.3) followed Nagelkerke and Sibbing (2000). The only type specimens deposited, described by Boulenger

Table 2.2: Characteristics of *B. trispilopleura* and *B. humilis* by Boulenger (1902) compared with matching specimens collected in 1999. Between the two species no conspicuous and consistent distinction was found, except for colour and spot patterns, the criteria used for selecting matching specimens. Differences between Boulenger's and our specimens are probably due to preserved instead of fresh specimens and/or to different ways of measuring. The maximum length recorded refers to thousands of specimens caught over 1999 and 2000. TL = total length, HL = head length.

	B. trispilopleura		*B. humilis*	
	Boulenger (1902)	Present study	Boulenger (1902)	Present study
Colouration	Brownish above, silvery on the sides and below	In fresh specimens also a slightly blue tint all over	Silvery brownish on the back, and a distinctive dark lateral band	Same
	Fins greyish	Same	Fins whitish	Same
Spots	Three round black spots on each side, first and second above lateral line, third on lateral line at caudal finbase		No spots	
Number of specimens	3	15	6	15
Mean length (range)	49 mm (46-51)	52 mm (46-95)	64 mm (49-74)	51 mm (49-88)
Max. length		113 mm		110 mm
Body depth	$3^{1}/_{2}$ times in TL	4.7 times in TL	$3^{1}/_{3}$ to $3^{3}/_{4}$ times in TL	4.9 times in TL
Head length	$3^{1}/_{2}$ times in TL	4.8 times in TL	$3\ ^{2}/_{3}$ - 4 times in TL	4.9 times in TL
Eye diameter	3 times in HL	3.1 times in HL	3-$3^{1}/_{2}$ times in HL	3.0 times in HL
Caudal peduncle	$1^{1}/_{2}$-$1^{2}/_{3}$ as long as deep	2.5 times as long as deep	Nearly twice as long as deep	2.8 times as long as deep
Scales	Radial striae, 27-28 on lateral line, $4^{1}/_{2}/4^{1}/_{2}$ at dorsal and ventral fin, 2 between lateral line and anal fin; 12 around caudal peduncle	Radial striae, 28-32 on lateral line, $4^{1}/_{2}/3$ at dorsal and ventral fin, 3 between lateral line and anal fin; 12-14 around caudal peduncle	Radial striae, 29-31 on lateral line, $4^{1}/_{2}/4^{1}/_{2}$ at dorsal and ventral fin, 2 between lateral line and anal fin; 12-14 around caudal peduncle	Radial striae, 29-31 on lateral line, $4^{1}/_{2}/3$ at dorsal and ventral fin, 3 between lateral line and anal fin; 12-14 around caudal peduncle

(1902), were measured as well: three syntypes of *B. trispilopleura* (BMNH 1902.12.13: 350, 351 and 352) and ten syntypes of *B. humilis* (BMNH 1902.12.13: 340-349). For measuring digital callipers and a stereo microscope with a measuring grid at 20-40 times magnification were used. All measurements were taken from fresh fish (except Boulenger's preserved material); those infected by tapeworms were discarded. Differences between the mean character values of the three species were tested for statistical significance using a Mann-Whitney U-test for two samples (Sokal and Rohlf, 1995), since the distributions of most character values were non-normal. The significance level (α) was adjusted for multiple comparisons with the Dunn-Šidák method (Sokal and Rohlf, 1995), which uses the adjusted significance level $\alpha' = 1 - (1 - \alpha)^{1/k}$, where k is the number of comparisons (in this case $k = 3$). This results in $\alpha'= 0.017$ for $\alpha = 0.05$, $\alpha' = 0.0033$ for $\alpha = 0.01$, and $\alpha' = 0.00033$ for $\alpha = 0.001$.

To analyse the spot pattern distribution among the whole population, including intermediates, 201 random fish were analysed. In the shallow clear area with rocks and vegetation (CRV; habitat e in Fig. 2.2 and Table 2.1) 91 specimens (*B. trispilopleura* and *B. trispilopleura*-likes) were checked for the number of spots (Table 2.4). In the turbid water without vegetation (TNV; habitat a, b, c and d in Fig. 2.2) 110 specimens (*B. humilis* and *B. humilis*-likes) were checked. To investigate preservation effects on the spot pattern (*cf.* Farm (2001)), *B. humilis*-like specimens from one catch site have been preserved in formalin and the spots were recorded again after six weeks. In addition, preliminary data were collected from these two habitat-groups on length-weight relationships, length at maturity, fecundity, prevalence of cestode parasites and gut contents.

2.2.4 Cluster analysis

For the cluster analysis 13 *B. pleurogramma*, 14 *B. tanapelagius*, 14 *B. humilis*, and 17 *B. trispilopleura* were used, collected in August 1999. In the first analysis, 32 metric and angular variables (indicated by C in Table 2.3), were measured for all 58 specimens. The type specimens of *B. humilis* and *B. trispilopleura* were not included, since many measurements could not be taken from these alcohol-preserved specimens. Data were log-transformed (natural logarithm), and then standardised by subtracting the mean value and dividing by the standard deviation of the variable. The data set contained no missing values. Pearson's product-moment correlation between specimens was calculated, and used for cluster analysis by the unweighted pair-group method, using the arithmetic average (UPGMA: Rohlf[2]. The resulting dendrogram was bootstrapped using 1000 resamplings.

Similarly, we performed a cluster analysis of *B. humilis*, *B. tanapelagius*, and *B. trispilopleura*, this time including the type material, however, limited to the 10 metric variables (indicated by T in Table 2.3) which could also be measured on the type specimens. Cluster analysis was performed with DGGEStat, version 1.0 (developed at the Netherlands Institute for Ecological Research, NIOO-KNAW, Nieuwersluis, The Netherlands).

2.3 Results: Identification and spatial distribution of *B. trispilopleura* and *B. humilis*

2.3.1 Comparison with Boulenger's description

Comparison of our specimens, selected by colour and spots as *B. trispilopleura* and *B. humilis*, with data as given for the type specimens by Boulenger (Table 2.2) show few morphometric differences. Some parameters such as body depth, head length and caudal peduncle shape are systematically larger than those reported by Boulenger, most probably due to a different way of measuring, since his drawings closely correspond to our specimens (Fig. 2.1). Using 15 or more specimens of each species (Boulenger measured only 3 and 6 specimens respectively), scale counts are similar for the two species, just like maximum total length recorded over two years of sampling. The comparison of *B. tanapelagius*, *B. trispilopleura* and *B. humilis* for 58 characters (Table 2.3) show minimal differences between *B. trispilopleura* and *B. humilis*, even though they were selected as extreme phenotypes.

The diagnostic character for identification in the field is the combined presence of three dark lateral spots and the dark back of *B. trispilopleura.* Specimens identified as *B. humilis* had a distinct lateral band, no spots. However, the majority of small barbs is intermediate between *B. trispilopleura* and *B. humilis* in spot patterns, not reported by Boulenger since he received few and already preserved specimens from Lake Tana in London, so he did not collect the specimens himself. We will name these not fully matching specimens *B. trispilopleura*-like (dark back and 1-2 spots;

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[2] Rohlf, F.J. 1998. NTSYS-pc. Numerical taxonomy and multivariate system. Version 2.0. Exeter Software, Applied Biostatistics Inc., Setauket, New York.

Table 2.3: Morphometric and meristic data on three small Lake Tana barb species. All specimens fully match Boulenger (1902)'s description. Measurements are according to Nagelkerke and Sibbing (2000). Significant differences (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) between *B. humilis*, *B. trispilopleura* and *B. pleurogramma* are listed. The second column indicates the parameters (C) used for overall cluster analysis (Fig. 2.3) and those (marked T) also used for cluster analysis including the type specimens (Fig. 2.4). *Sd* = standard deviation.

		B. humilis					*B. pleurogramma*				
		Mean	*Sd*	Min	Max	*n*	Mean	*Sd*	Min	Max	*n*
Meristic measures											
Dors. fin rays (simple)		3.0	0.0	3	3	16	3.0	0.0	3	3	15
Dors. fin rays (branched)		9.0	0.0	9	9	16	7.9	0.4	7	8	15
Anal fin rays (simple)		3.0	0.0	3	3	16	2.9	0.4	2	3	15
Anal fin rays (branched)		6.0	0.0	6	6	16	6.3	0.5	6	7	15
Pect. fin rays (total)		15.0	0.0	15	15	16	13.9	0.9	12	15	15
Vent. fin rays (total)		8.0	0.0	8	8	16	8.4	0.6	7	9	15
Scales on lateral line (total)		29.3	0.6	29	31	16	34.9	1.1	32	36	15
Predorsal scales		10.1	0.3	10	11	16	14.3	0.9	13	16	15
Scales from dorsal fin to lateral line		4.5	0.0	4.5	4.5	16	6.4	0.5	5	8	15
Scales from anal fin to lateral line		2.9	0.2	3	3	16	3.4	0.5	3	4	15
Scales from ventral fin to lateral line		2.8	0.3	2.5	3	16	4.4	0.5	4	6	15
Circumpeduncular scales		12.1	0.5	12	14	16	15.8	0.6	14	16	15
Circumference scales		21.2	0.8	20	22	16	27.7	0.6	26	28	15
Raker nr. inner side		8.9	0.5	8	10	11	8.4	0.5	8	9	16
Raker nr. outer side		9.8	0.4	9	10	11	9.4	0.5	9	10	16
Morphometric measures in % of standard length											
Head length	CT	25.1	2.3	18.8	29.9	26	18.2	3.3	15.9	27.2	15
Body depth	CT	25.9	2.5	21.0	31.6	26	19.4	3.9	16.0	28.2	15
Body width	CT	14.6	0.9	12.4	16.2	26	11.2	1.4	9.6	15.3	15
Caudal peduncle length	C	31.7	1.9	24.9	35.3	26	29.3	3.4	18.4	32.8	15
Caudal peduncle depth	CT	12.2	1.1	9.6	14.0	26	7.9	1.0	7.1	11.4	15
Predorsal length	C	46.6	2.8	35.7	49.9	25	49.2	1.9	45.2	52.1	15
Preanal length	C	67.9	3.1	54.4	71.0	26	70.8	1.4	67.5	73.5	15
Preventral length	C	45.7	4.6	26.6	50.0	26	49.7	1.5	47.5	52.1	15
Pect.-vent. length	C	22.0	1.5	18.6	24.4	25	23.2	1.4	21.1	26.2	15
Vent.-anal length	C	22.7	1.8	18.0	26.8	26	21.4	1.6	19.7	24.5	15
Dorsal spine length		21.6	5.8	13.4	29.0	22	18.3	3.9	12.7	23.1	15
Dorsal fin base length	C	17.5	7.2	10.6	30.5	23	8.7	1.4	7.2	13.3	15

		B. trispilopleura					Differences		
		Mean	*Sd*	Min	Max	*n*	H-P	H-T	P-T
Meristic measures									
Dors. fin rays (simple)		2.9	0.2	2	3	18			
Dors. fin rays (branched)		9.0	0.0	9	9	18	***		***
Anal fin rays (simple)		3.0	0.0	3	3	18			
Anal fin rays (branched)		6.0	0.0	6	6	18			
Pect. fin rays (total)		14.0	1.3	10	15	18	***	**	
Vent. fin rays (total)		8.1	0.5	7	9	18	*		
Scales on lateral line (total)		29.7	0.8	28	32	18	***		***
Predorsal scales		9.8	0.4	9	10	18	***		***
Scales from dorsal fin to lateral line		4.5	0.0	4.5	4.5	18	***		***
Scales from anal fin to lateral line		2.8	0.3	2	3	18	**		**
Scales from ventral fin to lateral line		2.9	0.2	2.5	3	18	***		***
Circumpeduncular scales		12.2	0.6	12	14	18	***		***
Circumference scales		20.3	1.0	18	22	18	***	*	***
Raker nr. inner side		9.0	0.8	8	11	10			
Raker nr. outer side		9.9	0.9	9	12	10			
Morphometric measures in % of standard length									
Head length	*CT*	25.1	1.6	22.5	29.0	21	***		***
Body depth	*CT*	26.9	1.9	23.6	30.9	21	***		***
Body width	*CT*	14.5	1.5	11.8	17.3	21	***		***
Caudal peduncle length	*C*	32.2	3.0	28.6	44.4	21	**		**
Caudal peduncle depth	*CT*	11.9	1.1	10.4	14.9	21	***		***
Predorsal length	*C*	46.5	1.9	43.3	49.3	21	**		**
Preanal length	*C*	69.2	1.7	65.8	72.5	21	***		*
Preventral length	*C*	47.6	1.1	45.4	49.9	21	***		***
Pect.-vent. length	*C*	22.2	1.6	18.4	25.0	21			
Vent.-anal length	*C*	22.4	1.5	19.3	25.9	21			
Dorsal spine length		24.1	1.6	21.3	28.7	19			***
Dorsal fin base length	*C*	13.8	3.0	11.9	24.2	18	***		***

Continued from previous page.

		Mean	*Sd*	Min	Max	*n*	Mean	*Sd*	Min	Max	*n*
Anal fin length	*C*	15.4	1.7	11.5	17.3	16	11.0	1.9	9.2	17.2	15
Anal fin base length	*C*	7.2	0.5	6.4	8.1	16	5.8	1.2	4.1	9.2	15
Pectoral fin length	*C*	19.0	1.4	15.3	20.9	26	11.5	1.8	10.3	17.7	15
Vent. fin length	*C*	18.0	1.6	14.3	20.6	26	10.5	1.7	9.1	15.8	15
Upper caudal fin lobe length		29.7	2.5	24.3	33.9	13	18.0	2.8	15.6	24.0	15
Lower caudal fin lobe length		30.0	3.0	23.1	35.5	17	18.3	3.2	15.0	24.5	15
Gut length		111.0	11.0	92.7	141.9	27	110.6	7.6	94.6	127.3	22
Morphometric measures in % of head length											
Head depth at occiput	*CT*	75.9	3.5	68.0	81.6	26	73.0	10.2	50.0	84.1	15
Head width	*CT*	56.2	2.8	49.3	61.4	26	55.4	9.2	35.7	74.1	15
Snout length	*CT*	20.5	1.0	18.2	22.0	26	20.5	3.2	13.3	25.0	15
Snout width	*C*	36.4	3.4	25.3	41.8	26	37.5	6.9	23.5	53.2	15
Eye diameter	*CT*	32.1	2.1	27.6	35.3	26	26.0	5.6	17.3	42.9	15
Orbit diameter	*C*	35.4	3.5	30.8	50.7	26	28.6	6.4	18.4	44.4	15
Postorb. length	*CT*	44.4	2.5	40.0	48.9	26	51.5	9.2	31.6	71.4	15
Interorb. width	*CT*	33.7	4.1	24.4	42.3	26	53.7	6.4	37.8	60.4	15
Operculum depth	*C*	37.2	3.4	30.6	45.1	26	45.6	11.4	26.1	68.3	15
Ant. barbel length	*C*	12.9	2.4	7.4	18.4	16	19.2	4.5	7.8	25.4	15
Upper jaw length	*C*	23.9	2.7	20.2	30.8	26	26.2	6.8	15.5	39.7	15
Lower jaw length	*C*	35.3	2.8	30.3	40.9	26	41.4	11.6	21.2	64.5	15
Ceratobranchial length		31.3	2.8	29.0	38.2	12	28.7	2.4	23.9	32.6	16
Angular measures											
Dors. head inclination	*C*	28.8	2.6	25	35	16	26.1	3.3	20	31	14
Gape inclination	*C*	37.8	4.9	29	44	16	43.7	5.3	30	48	14
Coded qualitative measures											
Head profile		2.0	0.0	2	2	15	2.1	0.3	2	3	15
Nuchal hump development		1.0	0.0	1	1	15	1.0	0.0	1	1	15
Upper lip development		1.0	0.0	1	1	15	1.1	0.3	1	2	15
Lower lip development		2.0	0.0	2	2	15	1.8	0.4	1	2	15
Ant. extension of lower jaw		2.0	0.0	2	2	15	2.1	0.3	2	3	15
Protrusion measures in % of head length											
Protrusion length		33.2	5.4	26.6	41.8	10	34.0	7.5	24.7	57.3	14
Horizontal oral gape	*C*	27.1	3.2	20.0	31.0	16	34.4	7.2	22.6	48.4	15
Vertical oral gape	*C*	34.6	2.9	29.1	39.8	16	42.4	10.7	22.6	58.4	14
Protrusion angle (°)	*C*	18.9	3.6	14	24	16	15.0	2.8	11	20	14

		Mean	*Sd*	Min	Max	*n*	H-P	H-T	P-T
Anal fin length	*C*	14.7	1.0	13.2	16.8	17	***		***
Anal fin base length	*C*	7.8	2.0	6.6	15.6	18	***		***
Pectoral fin length	*C*	18.0	2.7	14.9	27.5	21	***	*	***
Ventral fin length	*C*	17.2	2.0	14.0	21.0	21	***		***
Upper caudal fin lobe length		27.8	1.5	25.8	31.4	18	***	*	***
Lower caudal fin lobe length		28.2	1.8	26.1	32.6	18	***	*	***
Gut length		108.9	11.5	90.0	135.5	28			
Morphometric measures in % of head length									
Head depth at occiput	*CT*	77.7	4.8	68.1	85.3	21			
Head width	*CT*	57.8	3.9	52.4	67.3	21			
Snout length	*CT*	22.2	2.1	17.7	26.5	21		**	
Snout width	*C*	38.3	4.7	29.4	47.5	21			
Eye diameter	*CT*	31.7	3.2	19.8	36.0	21	***		***
Orbit diameter	*C*	34.3	3.8	21.0	41.0	21	***		**
Postorbital length	*CT*	44.1	2.7	38.7	51.6	21	***		**
Interorbital width	*CT*	36.6	6.8	26.8	59.0	21	***		***
Operculum depth	*C*	38.2	6.0	31.9	56.6	21	**		*
Ant. barbel length	*C*	13.3	2.3	8.6	17.8	18	***		***
Upper jaw length	*C*	26.0	2.4	21.1	30.4	21		*	
Lower jaw length	*C*	35.5	3.2	28.4	41.8	21			
Ceratobranchial length		30.0	6.0	23.7	33.9	10			
Angular measures									
Dorsal head inclination	*C*	30.2	5.6	19	47	18			*
Gape inclination	*C*	41.9	3.5	32	47	18	**	*	
Coded qualitative measures									
Head profile		1.0	0.0	1	1	18	***		***
Nuchal hump development		1.0	0.0	1	1	18			
Upper lip development		1.0	0.0	1	1	18			
Lower lip development		1.1	0.2	1	2	18	***		***
Anterior extension of lower jaw		2.0	0.0	2	2	18			
Protrusion measures in % of head length									
Protrusion length		34.5	3.4	28.3	42.9	18			
Horizontal oral gape	*C*	27.7	2.8	22.8	33.8	18	**		**
Vertical oral gape	*C*	33.9	4.1	26.5	41.3	18	*		*
Protrusion angle (°)	*C*	23.8	5.0	18	34	18	*	*	***

only caught at the CRV-station e) and *B. humilis*-like (pale brown back and 1-2 spots; only caught at TNV-stations a-d).

2.3.2 *B. trispilopleura*

B. trispilopleura Boulenger, 1902, having three spots, was only found in the clear and vegetated rocky areas in the shallow shore ($<$ 3 m depth), close to the city of Bahar Dar (Fig. 2.2, CRV station e). The rich vegetation is mainly composed of *Ceratophyllum* sp. growing both on rocky and sandy substrate until 3 m depth. Sheltered bay areas like the most southern station (e in Fig. 2.2) often remain clearer (Secchi-depth or transparency up to 1.45 m) than others (as low as 0.25 m) due to less mixing with sediment loaded river and lake water and reduced effect of the wind. The maximum total length among thousands of *B. trispilopleura* recorded over 1999 and 2000 is 113 mm. This species was observed to swim in schools of few to several hundreds of fish composed of many size classes (ranging around 30-100 mm FL) (personal observation). The large specimens always swim at the bottom of the school. *B. trispilopleura* may occur at other clear-rocky-vegetated (CRV) habitats in the lake, but has not been found yet distant from Bahar Dar, the only big city along lake Tana's coastline.

2.3.3 *B. humilis*

B. humilis Boulenger, 1902, dominates in shallow and intermediately deep areas (0-8 m) without vegetation, over both rocky and sandy/muddy substrate, with much lower transparency ($<$ 0.7 m) than the shore area: turbid non-vegetated (TNV) areas. This species is widely distributed in the lake, but decreases sharply in abundance with increasing depth and distance from the shore in favour of the recently discovered *B. tanapelagius* which dominates the offshore deep waters de Graaf *et al.* (2000a). At intermediate depths (4-8 m) *B. tanapelagius* dominates the upper and *B. humilis* the lower half of the water column. The maximum total length recorded for *B. humilis* over 1999 and 2000 is 110 mm. When preserved in formalin the back remains lightly pigmented and the rest of the body turns white. The pigmented band above the lateral line becomes even more conspicuous after preservation.

Table 2.4: a - Lateral spot patterns in the small Lake Tana barb species (30-100 mm FL) caught in clear shallow water with rocks and vegetation (CRV = station e in Fig. 2.2) and in turbid shallow-deep areas without vegetation (TNV = stations a, b, c, d in Fig. 2.2). Note that most (57 %) among 201 fish have between 0 (32 %) and 3 (11 %) spots, making the distinction between *B. trispilopleura* and *B. humilis* according to Boulenger's description impossible. *B. trispilopleura* with three spots are not found in the TNV area, where *B. humilis* with zero spots dominate (55 %). In the CRV area only 24 % have three spots, whereas two-spotted barbs dominate. b - Among the barbs from the TNV area, the number of spots at different sampling stations significantly differs (Chi-square test, α 0.05). After preserving specimens their number of spots more than doubled. b2, c2 and c4 refer to the sampling stations in Fig. 2.2.

	Spots (%)				Mean number of spots per specimen	*n*
	0	1	2	3		
a.						
Clear - rocky - vegetation	5	9	62	24	2.05	91
Turbid - no vegetation	55	21	24	0	0.69	110
b.						
Airport (c2)	62	32	6	0	0.44	34
Airport preserved	24	44	32	0	1.08	34
Debre-Mariam (c4)	14	24	62	0	1.48	29
Yigashu (b2)	80	11	9	0	0.29	45

2.3.4 Spots and body colour

The fresh fishes identified as *B. trispilopleura* by their dark brown-blue back, had spots located as described by Boulenger: first spot between head and dorsal spine just above the lateral line, the second at half total body length, and the third at caudal fin base on the lateral line (Fig. 2.1, c and c$'$). In clear, shallow areas with rocks and vegetation (CRV; Fig. 2.2, station e), small barbs look like *B. trispilopleura* in colour and pigmentation, but only 24 % had the maximum of three spots and were identified as *B. trispilopleura*. Most fish were *B. trispilopleura*-like: they had two distinct to vague spots (62 %) and some only one spot (9 %), which was always the caudal spot. Spots were absent in 5 % of the specimens (Table 2.4a).

Most fish caught in turbid, shallow or deeper areas without vegetation (TNV; Fig. 2.2, stations a, b, c, d) looked like *B. humilis* in colour and pigmentation. However, only 55 % had no spots; 45 % still had one or two distinct or vague spots. No fish had three spots. So there is a conspicuous difference in spot-pattern between *B. trispilopleura* and *B. humilis*, however, not as absolute (0 versus 3) as reported by Boulenger.

Spot patterns in catches of *B. humilis*-likes caught at different stations, significantly differ (Table 2.4b). At Debre Mariam (Fig. 2.2, station c4) the mean number of spots per specimen was by far the highest, five times as high as at Yigashu (Fig. 2.2, station b2). Debre Mariam is closest to the clear rocky vegetated area of shoreline where *B. trispilopleura* and fish eating birds are abundant (station e). From our studies on growth and maturation in the small barbs, it appears that spot patterns are not related to size classes (3-10 cm FL), sex or sexual stage.

The visibility of the spots varied from barely visible grey to black. It seemed that the fishes with more spots also had darker spots, but this was not tested. When preserved in formalin, the back of the fish remained strongly pigmented brown-grey and spots turned black. Some fish without spots in fresh condition (including some identified as *B. humilis*) appeared to develop spots after up to 3 months of preservation, rendering spots fully inappropriate for identification. The mean number of spots per specimen (0.44) in the catch at 'Airport' (station c2 in Fig. 2.2) more than doubled after preservation (1.08).

2.3.5 Cluster analysis

Among the four small Lake Tana *Barbus* species, the morphology of *B. tanapelagius* (33 parameter values in de de Graaf *et al.* (2000a)) is most distinct, indicated by its homogeneous clustering and the very high bootstrap value (98.8 %; Fig. 2.3). *B. pleurogramma* also has a homogeneous cluster (except for the inclusion of *B. trispilopleura* Tr18), but a lower bootstrap value (44.0 %). However, morphologically it is very distinct by its serrated dorsal spine and its small scales, which are not included in the cluster analysis (*cf.* Table 2.3). *B. humilis* and *B. trispilopleura* cluster randomly with a very low bootstrap value (3.9 %) and cannot be distinguished by the measured variables.

To focus on the distinction between *B. humilis* and *B. trispilopleura* we included their type specimens in the cluster analysis (Fig. 2.4), however, measuring less and only external characters (marked 'C' in Table 2.3) on this valuable preserved material. The dendrogram shows once more the distinctness of *B. tanapelagius* (bootstrap value of 71.9 %), but there appears no morphological distinction between *B. humilis* and *B. trispilopleura.*

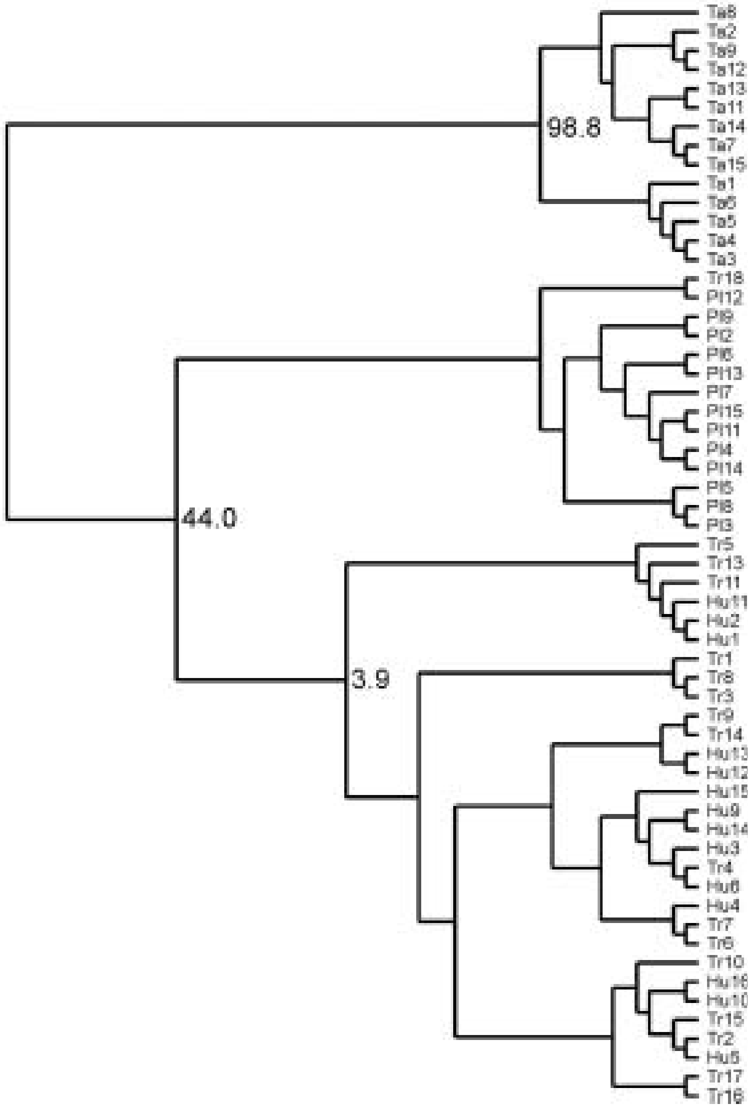

Figure 2.3: Dendrogram of 58 specimens of the four small Lake Tana *Barbus (Enteromius)* species, clustered by the unweighted pair-group method, using the arithmetic average (UPGMA: Rohlf 1998). The 32 parameters used are listed in Table 2.3. Note that *B. tanapelagius* and *B. pleurogramma* cluster as separate groups with high bootstrap-values (1000 resamplings), whereas *B. humilis* and *B. trispilopleura* (identified according to Boulenger) are mixed. *B. pleurogramma* is, however, most distinct by its serrated dorsal spine and its small scales, not included in this analysis. Hu = *B. humilis*, Pl = *B. pleurogramma*, Ta = *B. tanapelagius*, Tr = *B. trispilopleura*. Numbers specify the specimens.

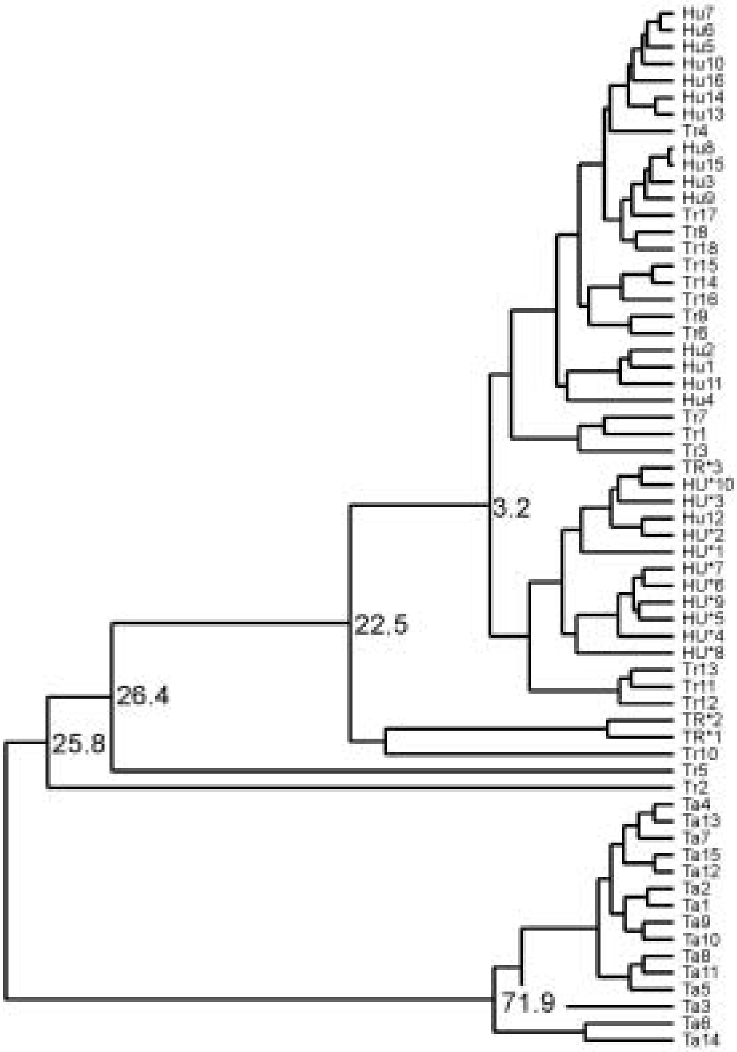

Figure 2.4: Dendrogram of 62 specimens of three Lake Tana *Barbus* (*Enteromius*) species, clustered by the unweighted pair-group method, using the arithmetic average (UPGMA: Rohlf 1998). Only the 10 parameters that could be measured from all, including Boulenger's type specimens (indicated by capitals and an asterisk), were analysed (*cf.* Table 2.3). Note that the type specimens of *B. humilis* (10) and *B. trispilopleura* (3) more or less cluster among our specimens and separate from *B. tanapelagius* with high bootstrap-values (1000 resamplings). Hu = *B. humilis*, Ta = *B. tanapelagius*, Tr = *B. trispilopleura*. HU* and TR* are Boulenger's type specimens. Numbers specify the specimens.

2.3.6 Ecology and reproduction

For the two groups distinct by habitat (possibly populations), a preliminary comparison was made (Table 2.5). The first group (TNV) was collected in all stations except station 'e' and composed of *B. humilis* and *B. humilis*-like fish. The second group (CRV) is collected exclusively at station 'e' (clear and vegetated rocky areas close to the city of Bahar Dar) and composed of *B. trispilopleura* and *B. trispilopleura*-like fish.

Length-weight relationships (FL in mm; W in gram) show that the TNV-population ($W = 1.97 * 10^{-5} FL^{2.898}$; $n = 4886$; $r^2 = 0.92$) and the CRV-population ($W = 1.67 * 10^{-5}\ FL^{2.945}$; $n = 2351$; $r^2 = 0.91$) have slightly different growth curves (95 % confidence interval of 2.874-2.921 for TNV-population and 2.907-2.982 for CRV-population). Preliminary observations on gonad maturity stage indicate that for both groups the breeding period lasts for about six months, showing peaks during March and August. The average length at maturity (L_{50}) for females is larger for TNV-group (58.8 mm FL) than for the CRV-group (51.4 mm FL). The absolute fecundity of stage-IV females ($n = 20$), expressed as the number of eggs per individual, ranges from 400-3235 (mean 1269) for the TNV-barbs and from 260-1365 (mean 656) for the CRV-barbs. Mean and maximum ova diameters are the same for the two groups (Dejen unpublished data). Prevalence of a cestode parasite (most probably *Ligula intestinalis*) revealed a significant difference between the TNV-group (3 % of observed specimens infected) and the CRV-group (10 % infected). Infection frequency increases with fish size.

Gut content analysis of the CRV- and TNV-barbs sampled from the five different habitats (a-e in Fig. 2.2) during October - December 1999 showed that both consume a significant amount of detritus and insects, or insect larvae, and a minor component of zooplankton (Dejen unpublished results). The important contribution of detritus in the gut contents of both groups (often without other food types) suggests that the two groups of 'small barbs' play a similar role in the food web. Both transfer energy from detritus to the top level of the food web, being prey-fish for the large piscivorous barbs and other predators. Benthic organisms and detritus were not found in the other 'small barb', *B. tanapelagius* whose diet is mainly zooplankton (copepods and cladocerans) (de Graaf *et al.*, 2000a).

2.4 Discussion

Phenotypic plasticity is a common type of intraspecific variation in fish (Witte *et al.*, 1997). In the present case, the variation is continuous and not linked to ontogeny, sexual dimorphy or strict geographical isolation (Dejen, unpublished results), but most probably to ecological pressure. Hybridisation between two true species or backcrossing would produce much less intermediates than actually found (57 %). A molecular genetic comparison might show a pattern of gene flow among the investigated specimens. Thus it may become clear if and how far speciation has progressed.

We hypothesise that *B. humilis* and *B. trispilopleura* are not two separate phenetic species (Boulenger, 1902), but a single biological species with continuously varied phenotypic plasticity in pigment patterns. Boulenger's descriptions fit as the two extremes of the continuum, and seem to represent two ecotypes (Mina, 1992; Ridley, 1998). Such hypothesis is supported by the present study. (1) Analysis of morphometric data on *B. tanapelagius*, *B. pleurogramma*, *B. humilis* and *B. trispilopleura* reveals the clear existence of three instead of four species of small barbs. Current specimens of *B. humilis* and *B. trispilopleura* are mixed in the cluster analysis, include Boulenger's type specimens that we measured, and are distinct from other species by high bootstrap values (2) Colour and spot-pattern, which are key characters in Boulenger's species distinction, show a continuous spectrum in the natural habitat with most specimens between the extremes and not matching the species descriptions. Boulenger (1902, 1911) did not report intermediate barbs because he based his study on Degens gift of preserved samples, including only three specimens of *B. trispilopleura*, and never saw them alive in their habitat. (3) According to our observation, all 'small barb' species transferred from the lake into indoor aquariums had similar colour within one week. Such variation and change in pigment patterns was recently also reported for other 'small barbs' (Farm, 2001). Apparently, a dark body colour is not species specific but induced by environmental cues. The same holds for the number of spots. For example, in a revision of small barbs, Banister (1987) mentions that 32 out of 145 *B. perince* specimens have 1 to 3 more or less visible spots. In Southern Africa similar problems exist concerning the taxonomic status of *B. trimaculatus*, also living among vegetation, and *B. poechii* (Skelton, 1993).

So neither morphometry, nor body colour, nor spot pattern can be used to unambiguously identify *B. humilis* and *B. trispilopleura*. Moreover, the diets of *B. humilis* and *B. trispilopleura* look very similar with few zooplankton and more benthos. Body colour and spot patterns seem to be more *B. trispilopleura*-like in shallow clear rocky areas with vegetation (CRV), and more *B. humilis*-like in turbid and muddy areas without vegetation (TNV). This suggests that Boulenger's *B. trispilopleura* and *B. humilis* represent at the best two ecotypes of a single species, distributed from clear water with vegetation over rocks to turbid areas without vegetation. *B. humilis* has by far the widest distribution, *B. trispilopleura* has only been found in a few square kilometres shore area along the city of Bahar Dar. We have not found it yet at some distant CRV-areas along the long shoreline of Lake Tana.

Table 2.5: Preliminary data on reproduction and parasite load in the two habitat groups of small barbs in lake Tana.

Habitat	TNV-barbs	CRV-barbs
Spawning period	March-August	March-August
L_{50} females	58.8 mm	51.4 mm
Mean absolute fecundity	1269 eggs per ind.	656 eggs per ind.
Mean egg diameter	0.870 mm	0.863 mm
Cestode infection rate	3 %	10 %

Some more differences than colour and spots vary between the two presumed ecotypes: spatial distribution, length-weight relationships, fecundity, length at first maturity and infection rate by tapeworms. Together they may point to the ecological pressure causing this variation. The dark back and silver belly of *B. trispilopleura*-likes in the clear rocky area effects a countershading protection of fish against bird predation from above and fish predation from below. High predation pressure by piscivorous large barbs, in the shallow rocky area especially *Barbus dainellii*, *B. gorguari* and *B. acutirostris*, is evident from their gut contents (de Graaf unpublished results). Bird predation is apparent from the prevalence of cestode parasites in the CRV-group (Table 2.5). Indeed, many fish-eating birds (pelicans, cormorants, kingfishers) concentrate near the fish landing sites along the shore of Bahar Dar. The birds, attracted by fish offal, also forage on the clearly visible CRV-small barbs, thus completing the cestode lifecycle: birds (primary host releasing cestode eggs) - free swimming larvae - procercoid larvae in copepods - plerocercoid larvae in small barbs - birds. The parasite load has high impact on the intermediate host condition and will decrease growth rate, length at first maturity (L_{50}) and fecundity of the small barbs (*cf.* Aeschlimann *et al.* (2000)), all according to our observations. The co-occurring lateral pigment spots in preyfish may well reduce their conspicuousness for predators and decrease their apparent size. The caudal spot is most frequently kept and may confuse predators by suggesting the position of the eye. The highest number of spots per fish is observed in clear waters.

It is concluded that *B. trispilopleura* is a synonym of *B. humilis*, and less appropriate since three spots are not often found. Therefore we conclude for future research to use *B. humilis* as the valid species that occurs in Lake Tana.

Just like the 'large barbs' have radiated into unoccupied niches of Lake Tana after its formation in early Pleistocene times (Nagelkerke, 1997; Sibbing *et al.*, 1998), also small cyprinid species will have utilised new opportunities offered by the lake. For the genus *Garra* new species have already been proposed (Getahun, 2000), for the small barbs a new species has recently been discovered (*B. tanapelagius*, de Graaf *et al.* (2000a)). The ecology and evolution of the small and large barbs in Lake Tana are intimately linked. The large piscivorous barb species highly depend on preyfish like *B. humilis*, which transfer the energy and nutrients from benthos up to predators, and on *B. tanapelagius* feeding on zooplankton. To understand the peculiar evolution of Lake Tana's ecosystem as a whole, studies on its composition need first priority, also in view of its conservation.

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Chapter 3

Barbus tanapelagius, a new species from Lake Tana (Ethiopia): its morphology and ecology [1]

The endemic cyprinid species flock in Lake Tana comprises of 15 species of large hexaploid barbs, eight of which are piscivorous. Previously, it was assumed that all piscivores preyed on the same small barb species, *Barbus trispilopleura*. In this paper we present a description of morphology and ecology of a new abundant small barb species, *Barbus tanapelagius* sp. nova (holotype RMNH 33731) from Lake Tana, Ethiopia, which appears to be the major prey species for the large pelagic piscivorous barbs. *Barbus tanapelagius* differs clearly in morphology from the other 3 small, diploid *Barbus* species known from Lake Tana, *B. trispilopleura* Boulenger 1902, *B. humilis* Boulenger 1902 and *B. pleurogramma* Boulenger 1902. Conspicuous differences are its, elongated body, large eye diameter, prominent and hooked lower jaw contour and colouration. Preliminairy data suggest that *B. tanapelagius* also differs ecologically from the other small *Barbus* spp. by its pelagic, strictly zooplanktivorous feeding and its occurrence mainly in the deeper, offshore waters. The other small *Barbus* species are most probably largely benthic feeders and dominant in the shallow inshore waters. Previous views about the evolution of the present 8 endemic piscivorous large barb species therefore require reconsideration, as the present paper shows a more complex scenario including several prey species.

3.1 Introduction

Lake Tana is situated in the north-west of Ethiopia at an altitude of 1830 m. It is a turbid, oligo-trophic shallow lake (average depth 8 m, maximum 14 m) covering an area of 3200 km^2 and is the source of the Blue Nile. The lake is isolated from the lower Blue Nile basin by 40 m high waterfalls, 30 km downstream from the Blue Nile

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[1] **de Graaf, M., Dejen, E., Sibbing, F.A., Osse, J.W.M. (2000).** ***Env. Biol. Fish.*** **59, 1-9.**

outflow (Fig. 3.1).

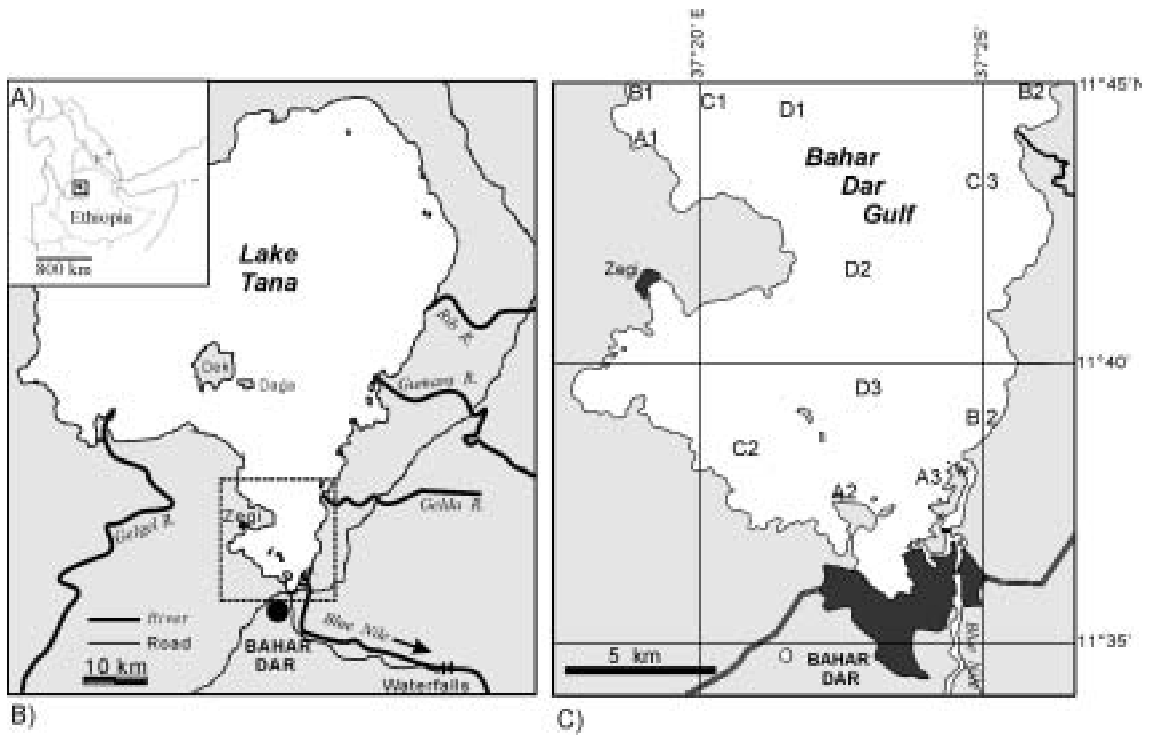

Figure 3.1: (a) Location of Ethiopia in the Horn of Africa, (b) Lake Tana and its main in- and outflowing rivers, and (c) the positions of the sampling stations in the Bahar Dar Gulf. Habitat A: A1, A2, A3, Habitat B: B1, B2, B3, Habitat C: C1, C2, C3 and Habitat D: D1, D2, D3 (*cf.* Fig. 3.3).

The largest fish family in the lake are the cyprinids, represented by 3 genera, *Varicorhinus*, *Garra* and *Barbus*. *Varicorhinus* Rüppell 1836, is represented by a single species *V. beso* Rüppell 1836. The genus *Garra* Hamilton 1822 (formerly *Discognathus*, Heckel 1846), according to Boulenger (1911) has 2 species in Lake Tana, *G. quadrimaculata* (Rüppell 1836) and *G. dembeensis* (Rüppell 1836) and maybe even more (Abebe Getahun, pers. comm.). The genus *Barbus* Cuvier & Cloquet 1816, has been revised several times. The latest revision of the large hexaploid barbs of Lake Tana was completed by Nagelkerke (1997); Nagelkerke and Sibbing (2000), which resulted in the distinction of 15 different species, of which 8 were new.

Boulenger (1911) mentioned 3 small diploid barb species (< 10 cm SL), which are not only distinct from the large barbs (up to 100 cm SL) by their size, but also by their morphology. The small *Barbus* species can without difficulty be separated from juvenile large *Barbus* species by a weakly developed first dorsal spine and radiating striae on the scales. Bini (1940) considered these small barbs as belonging to the subgenus *Enteromius* Cope 1869, and mentioned the same 3 species.

Most recent studies in Lake Tana have focused on the large, hexaploid *Barbus* species (Golubtsov and Krysanov, 1993; Mina *et al.*, 1996a,b; Nagelkerke and Sibbing, 2000). One intriguing and interesting aspect of this endemic species flock of large barbs, is the high number of piscivorous species (8). Cyprinids are not well equipped for piscivory because they lack oral teeth, have a slit-shaped narrow pharyngeal cavity and lack a distinct stomach with low pH for digesting large prey. Why is this feeding mode, quite rare among cyprinids in general, so common in Lake Tana barbs? How have they evolved and what factors were driving this process? Piscivorous specialists from other genera appear to be absent in Lake Tana, leaving this niche open for cyprinids (Sibbing *et al.*, 1998). The morphological differences between both the piscivorous and non-piscivorous species and among the piscivorous species themselves are mainly found in the head and feeding apparatus. Specialisation for different prey fish might be an option to investigate. After the introduction of motorized fisheries in 1986, the large piscivorous barbs became the target species of the commercial fisheries in Lake Tana. The large barbs form roughly a third of the total commercial catch (Wudneh, 1998). Also, for rational management of the piscivorous barbs data are required on their, function in the ecosystem, recruitment, annual production and population dynamics. Such data would enhance the predictions of possible top-down cascading effects of exploitation of particular piscivores for the fish community.

To answer these biological and fisheries related questions on prey-predator interactions in the Lake Tana food web, we decided to study also the identity and ecology of the small barb species, being the main prey fish. Preliminary surveys were conducted to gain insight in the distribution and abundance of the small barbs in the Bahar Dar Gulf of Lake Tana in the beginning of 1999. Next to the three small *Barbus* species mentioned by Boulenger (1911) and Bini (1940), *B. trispilopleura*, *B. humilis* and *B. pleurogramma*, we found a fourth previously unknown small barb in large numbers (up to 500 individuals in a single 15 min trawl) predominantly in the unexplored offshore, deep waters of the lake. We have compared its characters with the species described by Bini (1940) and Boulenger (1911) and concluded that one more species of small *Barbus* is abundant in the lake.

This paper provides a description of the morphology and ecology of *Barbus tanapelagius* and will briefly discuss some possible consequences of its discovery for existing hypotheses as to the food web of Lake Tana and the evolution of piscivory within the species flock of large *Barbus*.

3.2 Materials and methods

3.2.1 Collection of type material and morphometrics

B. tanapelagius were caught in July 1999 by trawl (cod-end 5 mm and 10 mm bar mesh) in the middle of the Bahar Dar Gulf of Lake Tana between sampling stations d1, as defined below, (North Mid Gulf, $11°45'$ latitude (N), $37°22'$ longitude (E)) and d2 (Mehal Zegi, $11°42'$ latitude (N), $37°23'$ longitude (E)) in July 1999. Fifty-five parameters were used to describe the species. For sources and descriptions of the counts, measurements and coded qualitative characters, see Nagelkerke and Sibbing (2000). Fifteen fresh specimens ranging between 43 mm and 52.4 mm standard length (SL) were used for morphometric analysis. Gut length was determined in 15 fresh additional specimens ranging in length between 39 and 51 mm SL, to prevent the deposited type material from being damaged. The specimens described in this study, have been deposited at the Naturalis Museum, Leiden, The Netherlands (RMNH 33731-33745). The specimens were preserved in 4 %, pH neutral formaldehyde solution. After at least one month, the specimens were rinsed and transferred to ethanol solutions of gradually increasing concentration (from 30-70 %).

3.2.2 Spatial distribution sampling program

In the Bahar Dar Gulf of Lake Tana four habitats (A-D) were selected, differing in substrate, depth and distance to the shore (see Fig. 3.1). Three sampling stations (a1, a2, a3 - d1, d2, d3) were chosen within each of these habitats (Fig. 3.1). The area covered by the littoral zones (habitat A and B) is approximately 10 % of the total area sampled. The fraction covered by the intermediate (habitat C) and deep (habitat D) zone is estimated to equal 45 % each. Data on fish distribution were collected using multi-mesh monofilament gillnets with 5 different mesh sizes: 5, 6.25, 8, 10, and 12.5 mm bar mesh respectively. Panel length and depth were 3 m and 1.5 m respectively for each mesh. Three multi-mesh bottom nets were set simultaneously at each site. At the deep and intermediate sites 3 additional nets were set at the surface.

Nets were set from 18:00 to 21:00 hours and from 6:00 to 9:00 hours the following morning, monthly from October to December 1999. The fish from the evening catch were stored in 4 % formaline before analysis the next day, the fish from the morning setting were transported fresh and analysed. The catches from the different nets, settings, sampling dates and stations were pooled per habitat during analysis

3.2.3 Analysis of gut content

Six stations (b1-2, c1-2, d1-2, see Fig. 3.1 and 3.3) were sampled once using a bottom trawl (5 mm bar mesh cod-end) at daytime between October and December 1999. Five fish per site were selected to determine diet composition and stored in 4 %, *pH* neutral formaldehyde. The relative biovolumes of food items in the gut were estimated according to the points method (Hynes, 1950) using a microscope. The following food categories were distinguished: calanoid copepods, cyclopoid copepods, *Daphnia*, *Bosminia*, *Daphniosoma*, *Ceriodaphnia*, insects, chironomid larvae, detritus and unidentified zooplankton. The gut contents of all fish ($n = 30$) were pooled during analysis.

3.3 Results

3.3.1 Morphology

The results of the morphometric analysis are listed in Table 3.1.

B. tanapelagius spec. nov. (Fig. 3.2)

Material. - Holotype, 49,4 mm *SL*, RMNH 33731 Mehal Zegi, Lake Tana, Ethiopia, 5.vii.1999, M. de Graaf; paratypes (14), 43-52.4 mm *SL*, RMNH 33732 - 33745, Mehal Zegi and North Mid Gulf, Lake Tana, Ethiopia, 5.vii.1999 - 29.vii.1999, M. de Graaf.

Etymology. - The name is derived from the Latin ‘pelagius’ and the name of Lake Tana. The name refers to the habitat of the fish in the lake, the offshore deep waters.

Habitus and diagnosis. - A small sized (maximally 68 mm *SL*), shallow and narrow-bodied barb. Head depth (18 % *SL*) and body depth (20.5 % *SL*) are about equal. The smaller depth of the caudal peduncle renders the fish slender, gradually tapering towards the tail. The dorsal head inclination is small (21°) and the dorsal profile is nearly straight. The eyes are large (eye diameter 34 % $HL >$ snout length 27 % HL), with a small interorbital width (interorbital width 28.3 % $HL <$ eye diameter 34 % HL). The lower jaw is rather long (43.3 % HL), has a high inclination ($> 40°$) and makes a pronounced angle with the ventral head profile. The lower jaw extends beyond the upper jaw with the mouth closed. The barbels are short (anterior barbel length 4.7 % $HL<$eye diameter 34 % HL). The oral gape (31-35.5 % HL) is large and (sub)terminal (protrusion angle 14°). The pharyngeal tooth formula is 5-3-2:2-3-5. Specimens from 15 to 68 mm SL have been observed.

Colouration. - Living specimens are in general silvery white and the dorsal side of the head is blackish. The dorsal body scales bear many dispersed pigment cells rendering its dorsal side greyish. The ventral parts are silvery white, as are the fins. The silvery colour disappears in 4 %, pH neutral formaldehyde solution and the whole fish turns white except for the darker spots on the head and dorsal scales. Size range: Specimens from 15 to 68 mm SL have been observed.

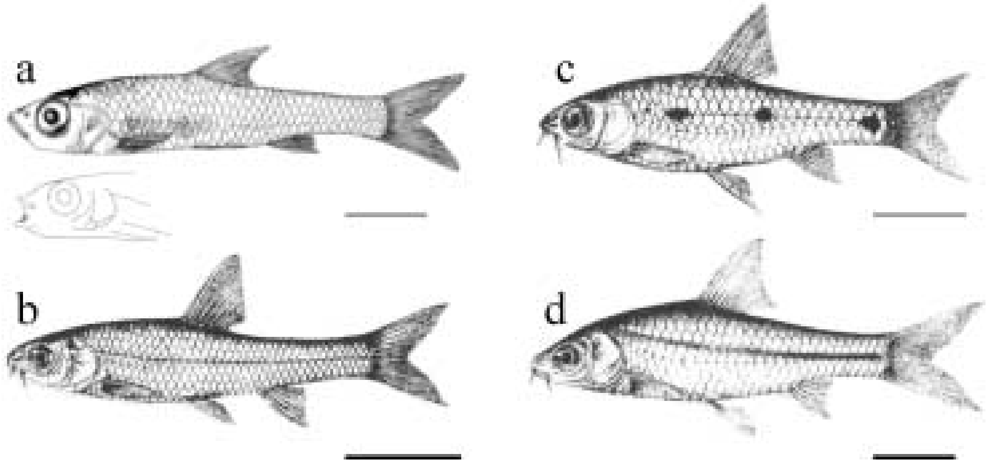

Figure 3.2: The small *Barbus* species of Lake Tana. (a) *Barbus tanapelagius* spec. nov. Holotype, RMNH 33731, SL of 49,4 mm, lateral view with expanded head contours beneath, (b) *B. pleurogramma* (after Boulenger (1911)), (c) *B. trispilopleura* (after Boulenger (1911)) and (d) *B. humilis* (after Boulenger (1911)). Scales equal 10 mm. (Size scales in b, c and d were derived from Boulenger's drawings supposing his scale lines indicate real total length in mm)

3.3.2 Spatial distribution

The four most important fish species in the gill net catches were *B. tanapelagius*, *B. humilis*, *Garra* spp. and juvenile large *Barbus* spp. Together these species composed 99.8 % of the numerical proportion. *Clarias gariepinus*, *Oreochromis niloticus*,

Table 3.1: Morphometry of *Barbus tanapelagius*. Measurements according to Nagelkerke and Sibbing (2000).

	Mean	Median	Min	Max	*Sd*	*n*
Meristic measures						
Dorsal fin rays (simple)	3.1	3.0	3	4	0.26	15
Dorsal fin rays (branched)	8.9	8.0	8	9	0.35	15
Anal fin rays (simple)	3.0	3.0	3	3	0	15
Anal fin rays (branched)	6.1	6.0	5	8	0.59	15
Pectoral fin rays (total)	13.7	14.0	11	15	1.05	15
Ventral fin rays (total)	8.0	8.0	8	8	0	15
Scales on lateral line (total)	30.3	30.0	28	33	1.53	15
Predorsal scales	11.0	11.0	10	12	0.76	15
Scales from dorsal fin to lateral line	4.5	4.5	4.5	4.5	0	15
Scales from anal fin to lateral line	2.9	3.0	2	3	0.26	15
Scales from ventral fin to lateral line	3.0	3.0	3	3	0	15
Circumpeduncular scales	11.1	11.0	11	13	0.52	15
Circumference scales	17.8	18.0	16	18	0.56	15
Morphometric measures in % of standard length						
Head length	26.6	26.7	25.1	28.2	1.06	15
Body depth	20.5	20.1	17.6	23.4	1.62	15
Body width	12.1	12.3	9.8	13.6	1.02	15
Caudal peduncle length	31.3	31.1	29.6	34.1	1.33	15
Caudal peduncle depth	10.3	10.5	8.8	11.1	0.56	15
Predorsal length	48.9	48.8	46.5	52.5	1.60	15
Preanal length	68.9	69.3	67.4	70.5	0.95	15
Preventral length	48.4	48.7	45.2	51.0	1.43	15
Pectoral-ventral length	22.2	22.5	17.9	25.3	1.76	15
Ventral anal length	22.2	22.0	20.7	23.8	0.97	15
Dorsal spine length	21.5	21.6	18.9	23.1	1.17	15
Dorsal fin base length	10.7	10.9	9.8	11.7	0.64	15
Anal fin length	13.2	13.4	12.1	13.9	0.67	15
Anal fin base length	6.7	6.6	6.1	7.6	0.41	15
Pectoral fin length	16.4	16.7	13.4	17.7	1.13	15
Ventral fin length	15.8	15.9	13.6	16.9	1.05	15
Upper lobe length of caudal fin	29.2	29.0	27.5	31.4	1.38	15
Lower lobe length of caudal fin	29.0	29.0	27.2	30.8	1.15	15
Gut length	82.4	85.1	60.5	100.0	11.62	15
Morphometric measures in % of head length length						
Head depth at occiput	66.9	66.7	62.8	73.3	2.53	15
Head width	50.3	49.5	47.7	54.7	1.85	15
Snout length	27.2	26.9	24.4	31.5	2.32	15
Snout width	35.1	34.5	30.2	41.1	2.78	15
Eye diameter	34.0	34.1	31.2	38.2	1.87	15
Orbit diameter	36.3	36.6	34.1	39.7	1.47	15

Continued from previous page.

	Mean	Median	Min	Max	*Sd*	*n*
Postorbital length	37.6	37.8	35.3	39.8	1.55	15
Interorbital width	28.3	28.2	23.8	31.2	1.61	15
Operculum depth	35.3	34.6	30.2	40.5	3.24	15
Anterior barbel length	4.7	4.5	3.1	6.4	1.04	15
Upper jaw length	30.1	29.2	25.0	36.3	2.85	15
Lower jaw length	43.3	43.2	40.3	49.4	2.49	15
Angular measures						
Dorsal head inclination (°)	20.8	22.0	16	27	3.53	15
Gape inclination (°)	42.0	41.0	38	46	2.75	15
Coded qualitative measures						
Head profile	2.73	3	2	3	0.46	15
Nuchal hump development	1.33	1	1	2	0.49	15
Upper lip development	1	1	1	1	0	15
Lower lip development	1	1	1	1	0	15
Anterior extension of lower jaw	3.87	4	3	4	0.35	15
Protrusion measures in % of head length						
Protrusion length	32.1	32.7	26.9	35.1	2.30	15
Horizontal oral gape	31.0	30.5	24.9	35.6	2.98	15
Vertical oral gape	35.5	35.3	31.5	40.0	2.13	15
Protrusion angle (°)	14.1	14.0	9	20	3.86	15

B. trispilopleura, *B. pleurogramma* and *Varicorhinus beso* were only caught occasionally and were not included in further study. The species composition of the gillnet catches (Fig. 3.3) shows the numerical dominance of *B. humilis* in the shallow inshore habitats A and B. The intermediate and especially the offshore habitat are dominated by *B. tanapelagius*. *Garra* and juvenile large *Barbus* spp. contribute minor fractions in all the four habitats. The overall fish densities are 4 times higher in the littoral habitats A and B compared to the intermediate and offshore habitats C and D.

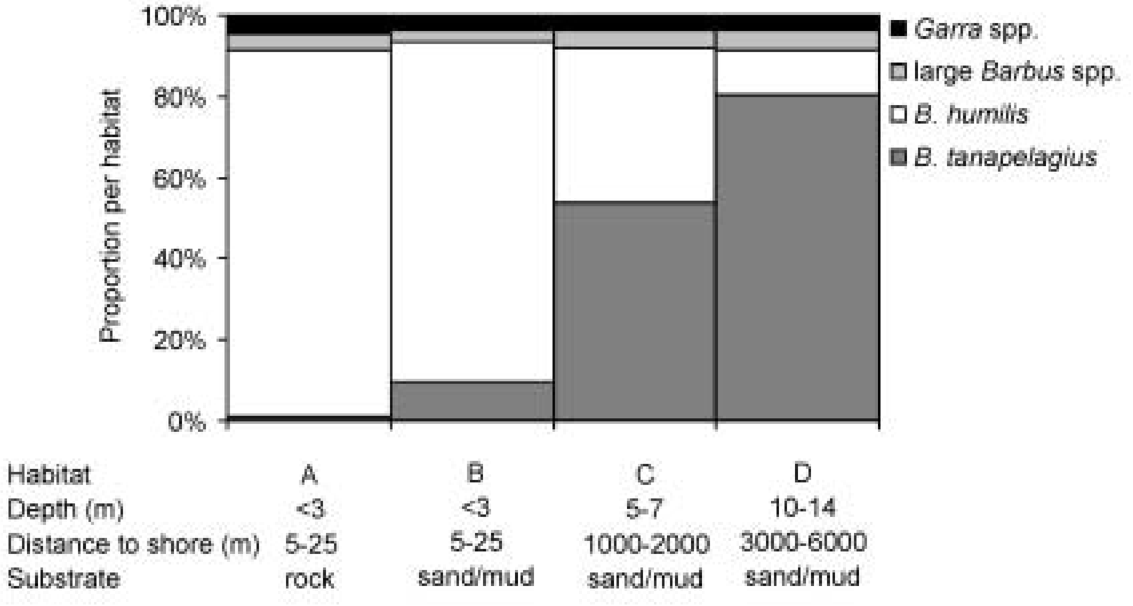

Figure 3.3: Species composition (%) per habitat. Total number of specimens per habitat: A = 5597, B = 6909, C = 3000, D = 3144.

3.3.3 Diet composition

B. tanapelagius is a strict zooplanktivore (Fig. 3.4). Its diet consists mainly of cyclopoid and calanoid copepods and *Daphnia*.

3.4 Discussion

It is no surprise that this small but abundant *Barbus* species from Lake Tana was not found by ichtyologists to date. Firstly, most work has concentrated on the highly intriguing species flock of large barbs and its complicated taxonomy (Rüppell, 1836;

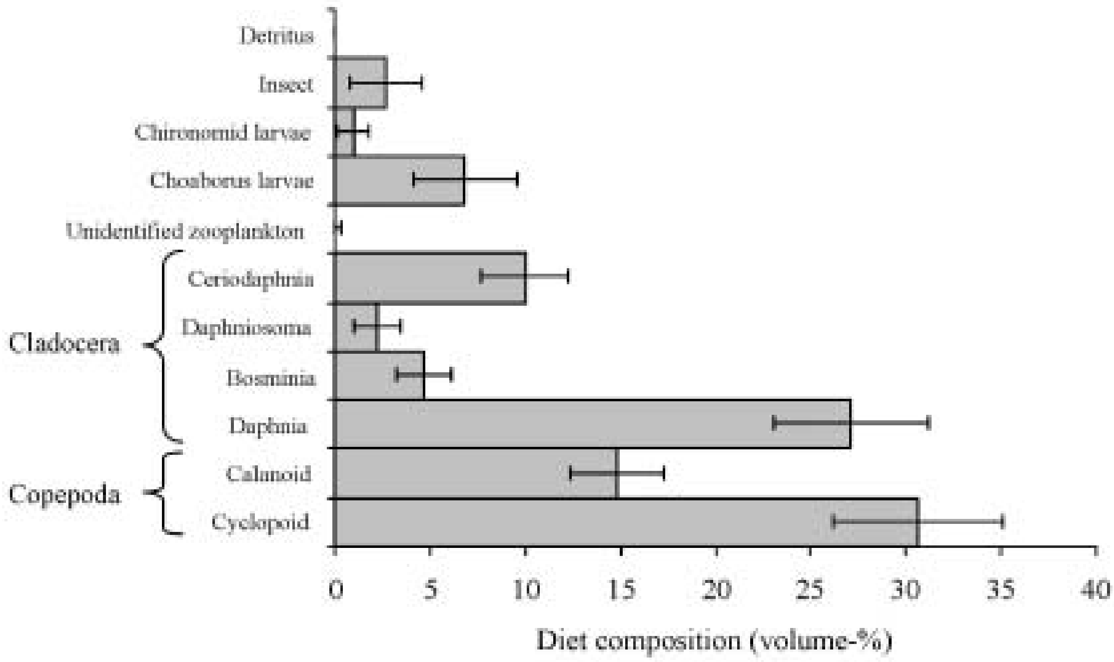

Figure 3.4: Diet composition (volume-%) of *B. tanapelagius* ($n = 30$) with standard error, pooled from habitats B, C and D over the period October-December 1999.

Boulenger, 1911; Bini, 1940; Banister, 1973; Golubtsov and Krysanov, 1993; Mina *et al.*, 1996a,b; Nagelkerke, 1997; Nagelkerke and Sibbing, 2000). Secondly, the habitat of *B. tanapelagius*, the offshore deep waters was not accessible by scientists in the 19^{th} and early 20^{th} century. The typical diploid small barbs of Lake Tana can easily be distinguished from the large hexaploid barbs by a small size (< 120 mm SL), a weakly developed first dorsal spine and radiating striae on the scales. *B. tanapelagius* differs clearly in morphology from the other three small barbs *B. trispilopleura*, *B. pleurogramma* and *B. humilis*, occurring in Lake Tana, by its distinctive elongated body, its large eye diameter, its small anterior barbel length, its pronounced and hooked lower jaw and its light body colouration. Species descriptions of *B. trispilopleura* and *B. humilis* by Boulenger (1911) are, however, insufficient for their distinction. Preliminary evidence suggests that *B. trispilopleura* and *B. humilis* are conspecifics (Dejen, unpublished data). A thorough morphometric analysis of these species and a revision of the small barbs of Lake Tana is urgently needed and currently being executed.

The discovery of *B. tanapelagius* may have important implications for the food web of Lake Tana, as reconstructed by Nagelkerke (1997) and affects the current scenario's about the evolution of piscivory among the large barbs. Nagelkerke (1997) suggested that *B. trispilopleura* is a key species in the Lake Tana food web, supposing that the most important flow of energy and mass to the large *Barbus* biomass production, leads from phytoplankton, via zooplankton, especially via *B. trispilopleura*. Benthos was considered to be far less important. These authors suggested further that *B. trispilopleura* occurs in all habitats and is the major prey fish for the 8 species of piscivorous large *Barbus* (*B. acutirostris*, *B. dainellii*, *B. gorguari*, *B. longissimus*, *B. macrophtalmus*, *B. megastoma*, *B. platydorsus* and *B. truttiformis*). This scenario probably is, however, oversimplified.

The dominant prey species in the four selected habitats in Lake Tana are *B. humilis* and *B. tanapelagius*. *B. humilis* occurs mainly in the shallow shore areas (0-4 m depth) over both rocky and sandy/muddy substrate and decreases sharply in abundance with increasing depth and distance from the shore. *B. tanapelagius*, however, is the abundant prey species in deep (8-14m), offshore waters and decreases sharply in abundance with decreasing depth and distance to the shore. *B. pleurogramma* seems to occur only in the affluent rivers of the lake between the shore vegetation and floodplains at depths shallower than 1 meter (M. de Graaf, personal observation).

Benthic organisms and detritus were not found in *B. tanapelagius* and their diet consisted mainly of copepods and cladocerans in the period October-December 1999. The copepods (mean density 32 l^{-1}), containing two cyclopoid species *Mesocyclops* sp. and *Thermocyclops* sp. and one calanoid species *Thermodiaptomus galebi*, constituted the major zooplankton fauna followed by the Cladocera (mean density 20 l^{-1}) in the Bahar Dar Gulf (Wudneh, 1998). In general, the spatial fluctuations in zooplankton densities is larger than their seasonal fluctuations. Densities of copepods and cladocerans were highest in the littoral zone of the lake during March-May prior to the start of the rainy season. *B. tanapelagius* is most likely a strict zooplanktivore as these prey organisms are available year round in the intermediate and deeper waters in similar or higher densities compared with the period October-December covered in this study (Wudneh, 1998).

Therefore the energy flow to the large piscivorous *Barbus* species and the main source of their biomass production is more likely to run from phytoplankton, via zooplankton, via the pelagic feeding zooplanktivore *B. tanapelagius* in the intermediate and deeper waters. Preliminary evidence suggests that in the littoral zone an important energy flow to large piscivorous *Barbus* biomass runs from benthos, via *B. humilis*. The diet of 30 *B. humilis* and 30 *B. trispilopleura* collected between October and December 1999 consisted mainly of insects, chironomid larvae and detritus, suggesting a benthic feeding mode for these species (Dejen unpublished data).

The process of adaptive radiation of 8 endemic, piscivorous barb species within Lake Tana is still unknown. It seems unlikely that they all specialised on feeding on the same prey item, *B. trispilopleura/humilis*, because of differences in trophic morphology (Nagelkerke, 1997). Present knowledge on the differences in morphology, distribution and ecology between the potential prey species leaves options open for specialisation, segregation and speciation of varied piscivores within Lake Tana. The first aim of current research on the evolution of piscivory within the large *Barbus* species flock is to find evidence (morphological, ecological, and behavioural) linking the diversity of the piscivores with the diversity of their prey.

Acknowledgements

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Chapter 4

Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (L. Tana, Ethiopia)[1]

The spatial and seasonal distribution of microcrustacean zooplankton of Lake Tana (Ethiopia) was monthly studied for two years. Concurrently, various environmental parameters were measured and related to zooplankton distribution. Canonical Correspondence Analysis (CCA) was used to estimate the influence of abiotic factors and chlorophyll a content in structuring the zooplankton assemblage. Among the environmental factors, zooplankton abundance correlated most strongly with turbidity. Turbidity was negatively correlated with species abundance, especially for *Daphnia* spp. and to the least extent for *Diaphanosoma* spp. Analysis of variance (ANOVA) was used to determine spatial (littoral, sublittoral and pelagic zone) and temporal (four seasons) variation in zooplankton abundance. We observed significant temporal differences in zooplankton abundance, with highest densities during dry season (November-April). Only cladocerans showed significant differences in habitat use (highest densities in the sublittoral zone).

4.1 Introduction

In Lake Tana, microcrustacean zooplankton constitutes a major component of the food chain. It is an important link between primary production and planktivorous fish, mainly two ‘small barbs’, *Barbus tanapelagius* and *B. humilis* (de Graaf *et al.*,

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[1] **Dejen, E., Vijverberg, J., Nagelkerke, L.A.J., Sibbing, F.A. (In press: *Hydrobiologia*)**

2000b; Dejen *et al.*, 2002). As preyfish for top-predators, like many of the 'large barbs' (Nagelkerke *et al.*, 1994; de Graaf *et al.*, 2000b), these 'small barbs' are the basis for the commercial fish production. In addition, most larval and small juvenile fish more or less exclusively utilize zooplankton for growth (Post and Kitchell, 1997).

There have been few previous studies on zooplankton in L. Tana, so our knowledge is scanty. The first general account of the aquatic fauna and flora of the lake was documented by Brunelli and Cannicci (1940) and Rzóska (1976). Recently Wudneh (1998) conducted a preliminary study about the zooplankton species composition and distribution in L. Tana. The taxonomical resolution of this study was low and some of the species identifications are debatable. Effects of environmental factors and food (chlorophyll a) on the distribution have not been analyzed.

In tropical systems, probably due to an extended growing season, seasonality is often not so pronounced as in temperate lakes (Hart, 1985). Seasonal succession in zooplankton assemblages in lakes and reservoirs has been attributed to both biotic and abiotic mechanisms. Abiotic factors such as wind, precipitation, turbidity and hydrology have been identified as critical factors in the seasonality of zooplankton in the tropics (*e.g.* Serruya and Pollingher (1983); Hart (1990); Mengistu and Fernando (1991b)).

Inflowing rivers often carry loads of suspended solids into lakes and reservoirs. Horizontal gradients in turbidity may affect the occurrence and distribution of zooplankton organisms (Hart, 1990). In Lake Tana, inflowing rivers carry a heavy silt load into the lake during the rainy season. Annual soil loss in the L. Tana catchment area ranges from 31 to 50 tons per hectare and showed a substantial increase during recent years (Teshale *et al.*, 2001). A high silt load may have both adverse and beneficial consequences for zooplankton growth and survival. Food availability for zooplankton tends to decline with turbidity due to light limitation of the primary production (*e.g.* Lind *et al.* (1992)). In addition to reduced production of algal food resources one can expect interference of silt particles with the filter feeding processes in zooplankters (McCabe and O'Brien, 1983; Hart, 1988). Also, suspended sediments reduce the under water light intensity and reactive distance of visual planktivores, which may lead to declining foraging rates (Vinyard and O'Brien, 1976; Bruton, 1985).

We studied the environmental factors associated with temporal and spatial distribution of microcrustacean zooplankton in a shallow turbid tropical lake, addressing the hypothesis that turbidity is the most important factor regulating zooplankton community structure over seasons and space. This study will provide a baseline for future studies since the L. Tana catchment is under alarming threat from increased human activities (*e.g.* deforestation), soil erosion and changes in climate (*e.g.* erratic rainfall).

4.2 Materials and methods

4.2.1 Study site

Lake Tana is an oligo-mesotrophic shallow lake (average depth 8 m, maximum 14 m) covering a surface area of 3200 km^2 and it is the source of the Blue Nile River. The lake is well mixed and a thermocline is lacking (E. Dejen, unpublished). The lake is located at an altitude of 1830 m and has been isolated from the lower Blue Nile basin by 40 m high falls, 30 km downstream from the Blue Nile outflow. The catchment area of the Lake (16,500 km^2) has a dendritic type of drainage network. Four major permanent rivers, the largest of which is the Gelgel Abbay (Little Blue Nile) feed the lake. Montmorillonite rich clay soil dominates the eastern shore of L. Tana where most inflowing rivers originate and flood the lake during the rainy season (Tekalign *et al.*, 1993).

The climate of L. Tana is characterized by a major rainy season with heavy rains, during June-October, and sometimes a minor rainy season during February-March. Average annual rainfall in the lake area over 1997-2000 was 1418 mm (Dejen *et al.*, 2003a). The water level of the lake fluctuates with rainfall up to 1 m.

The study was carried out from January 2000 to October 2001 in southern part of L. Tana. Three habitats were sampled: a) shallow littoral zone (*ca.* 2 m deep) with sandy/muddy bottom without vegetation, b) sublittoral zone (*ca.* 6 m deep) and c) pelagic deep water (*ca.* 10 m deep) (Fig. 4.1).

4.2.2 Environmental conditions

Measurements of temperature, conductivity, *pH* and dissolved oxygen were taken with a portable probe. Total dissolved solids were measured with a TDS meter, and turbidity with a portable turbidometer measuring NTUs. These variables were measured in the field immediately after the water sample was taken. Chlorophyll a content was estimated by filtering 750 ml of lake water through Whatman GF/C

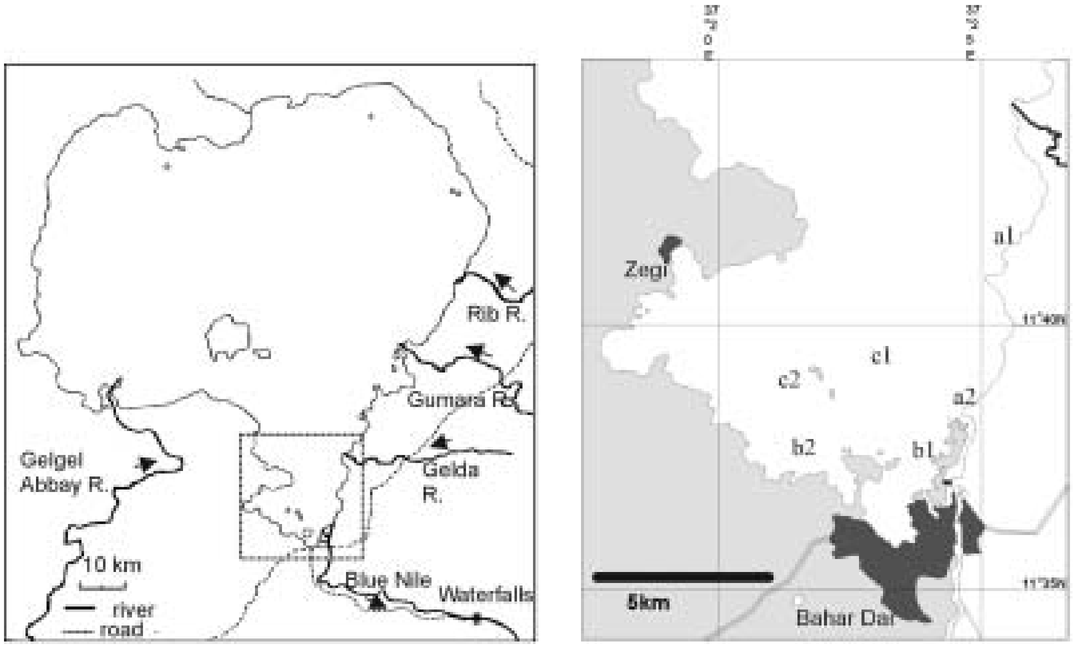


Figure 4.1: Lake Tana. Left hand panel showing the whole lake with the southern bay study area and four inflowing and one outflowing river (Blue Nile). Right hand panel showing study area with sampling stations. Three habitats were sampled: a=shallow littoral zone without vegetation; b=sublittoral zone and c=pelagic zone. Zooplankton was sampled at two stations per habitat (a1, a2, b1, b2, c1, c2). Water samples for environmental variables at one station per habitat (a1, b1, c1).

glass-fiber filters. Chlorophyll a was determined spectrophotometrically after extracting the filters overnight at dark using cold 90 % methanol and concentrations were calculated without correcting for phaeopigments (Talling and Driver, 1963). For practical reasons, in each sampling month environmental variables were measured only once in each habitat. Since Lake Tana is shallow and well mixed we considered these measurements to be representative for the whole water column during day and night.

4.2.3 Zooplankton sampling and analysis

Zooplankton samples were collected every 1-2 month with a 3.5 l Friedinger type volume sampler at two stations per habitat (Fig. 4.1). In the sublittoral and pelagic zones two samples per station were taken, one just below the surface and one just above the bottom. These two samples were pooled into one sample. In the shallow littoral zone only one sample per station was taken at intermediate depth. Per sampling date samples were taken both during day-time (between 7.00 - 9.00 am) and during night-time (between 19.00 - 21.00 pm). Since at the same sampling date zooplankton densities in day-time samples did not differ from densities in night-time samples (paired t-test with densities per station and per sampling date from day- and night-time sampling as pairs, $N = 124$, $P > 0.05$), these densities were averaged, resulting in one density estimate per station per sampling date. After collection, zooplankton was concentrated by filtering through 80 mm-mesh sieve. Samples were preserved in 4 % formaldehyde. Sub-samples of 15 ml were taken with an automatic pipette from a well-mixed whole sample (100 ml) and counted under a microscope. Per sample a minimum number of 100 individuals were counted, or if the sample contained less than 100 individuals the whole sample was counted. Four copepod species could be distinguished, one calanoid and three cyclopoid copepods. The density estimates of the calanoid copepod species are based on all copepodite stages (C1-C6), but the densities of the cyclopoid copepod species were estimated on basis of the total number of cyclopoid copepodites and the proportion of advanced copepodite instars (C4-C6) of each species in the sample. Nauplii were counted as a group and not classified at lower taxonomic levels. Water samples for environmental variables were taken monthly using the same sampler as for zooplankton, but only at one station per habitat.

4.2.4 Zooplankton taxonomy

One sample per station in each of the three habitats and four seasons ($N = 12$) was identified to the species level. For most Korinek (1999)'s identification guide to limnetic Cladocerans of African inland waters was used. *Daphnia hyalina* was identified following Flössner (2000) and confirmed by using mitochondrial DNA sequences from the small sub-unit ribosomal RNA (Schwenk *et al.* (2000); Table 4.1). *Chydorus sphaericus* was identified using Smirnov (1996). For copepods the identification keys of Defaye (1988) and Van de Velde (1984) were used. In all other samples ($N = 259$) zooplankton was identified to the genus level only.

4.2.5 Data analysis

Seasons were identified through a multivariate analysis of environmental variables. A correlation matrix was calculated from the monthly means of nine environmental parameters (water level, rainfall, water temperature, turbidity, conductivity, total dissolved solids, oxygen content, pH, and chlorophyll a concentration). This matrix was clustered with the unweighted pair-group method, using arithmetic averages (UPGMA-clustering; Rohlf (1993)), and bootstrap values were calculated (1000 repeats). Distinct clusters of months were regarded as distinct seasons. Clustering was performed with NTSYS-pc 2.01c (Exeter Software, Applied Biostatistics Inc., Setauket, New York, USA).

Spatial and temporal distribution patterns of the zooplankton were studied through analysis of variance (ANOVA), using SAS software (SAS Institute Inc., Cary, NC, USA). Since the counts were not normally distributed, they had to be log-transformed before ANOVA could be applied. This implied that we had to deal with 0-counts that could not be log-transformed. Often a constant (usually 1) is added to all counts to tackle this problem, but may pose statistical problems, because the choice of the constant might affect the outcome of the ANOVA (Berry, 1987). Therefore we chose to assign the zooplankton taxa to larger categories (cladocerans, copepodites, and nauplii) which contained no 0-counts. The zooplankton counts were analyzed for differences among seasons, habitats (littoral, sublittoral, pelagic), and the interaction between season and habitat. Group means could be compared by the confidence limits around the geometric means.

Multivariate analysis was used for relating the structure of the zooplankton community as a whole with environmental variables. Since we had several zooplankton samples ($N = 259$) and only one set of environmental variables per habitat per sampling month, we took the arithmetic mean of the zooplankton counts for each habitat and sampling month, resulting in 39 samples. The zooplankton community dataset consisted of counts of copepods and cladocerans that were identified either to the species or the genus level. Water temperature, turbidity, conductivity, total dissolved solids, oxygen content, pH, and chlorophyll a concentration were not transformed prior to analysis.

Multivariate ordinations were performed with the computer program CANOCO 4 (ter Braak and Šmilauer, 1998). We first performed an indirect gradient analysis by means of detrended correspondence analysis (DCA), in order to reveal prevailing patterns of response curves in relation to environmental gradients (Jongman *et al.*, 1995). Ordination axes smaller than two standard deviations indicate approximately linear responses, suggesting that redundancy analysis (RDA) is the proper method for direct gradient analysis. If the axis is larger, then canonical correspondence analysis (CCA) is a more appropriate method. RDA was run with the zooplankton variables centered and standardized by subtracting the mean and dividing by the standard deviation. CCA was run without standardization and centering. Biplots were focused on inter-sample correlations.

4.3 Results

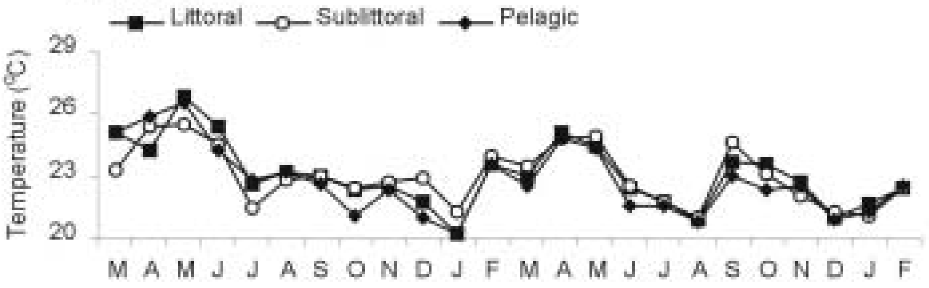
4.3.1 Environmental factors and seasonality

Only turbidity and temperature showed conspicuous seasonal differences (Fig. 4.2). Turbidity is highest during the wet season (June-November) and lowest during the dry season (December-May). Turbidity varied among habitats with the highest values generally in the littoral. Water temperature was relatively low for a tropical lake with a maximum of *ca.* 27 °C in May and a minimum of *ca.* 20 °C in January. Temperatures were similar in the three habitats. Chlorophyll a content varied in time between ca. 3-12 μg l^{-1}, but did not show a seasonal pattern. Variation among habitats was high with the highest chlorophyll a concentrations in the littoral zone. Like chlorophyll a concentration, also conductivity, total dissolved solids, and pH showed only small stochastic differences over time (Table 4.1).

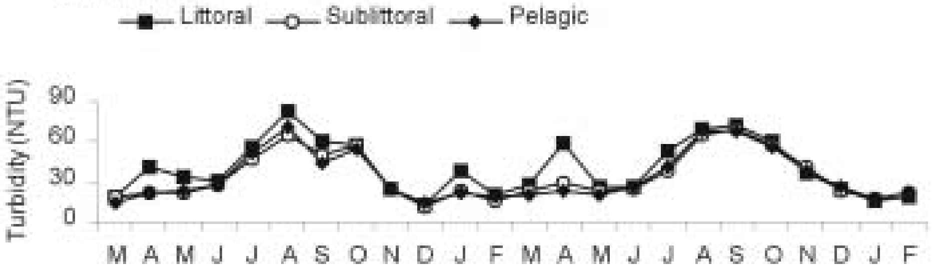
Table 4.1: Environmental parameters at Southern Gulf of L. Tana from March 2000 to February 2002, annual means $\pm SD$, range and the month of minimum and maximum values.

Variable	Mean $\pm SD$	Range	Month Minimum	Month Maximum
Temperature (°C)	23.2±1.5	20.2-26.9	January	May
Turbidity (NTU)	23.2±1.5	20.2-26.9	January	May
Conductivity (μS cm^{-1})	132.8±11.2	115-147.9	October	February
Total dissolved solids (mg l^{-1})	163.6±10.1	148.4-178.1	August	February
Chlorophyll a (μg l^{-1})	6.4±1.1	3.4-12.9	March	January
Oxygen (mg l^{-1})	6.7±0.5	5.9-7.3	December	April
pH	7.7±0.6	6.8-8.3	August	January

a) Temperature



b) Turbidity



c) Chlorophyll *a*

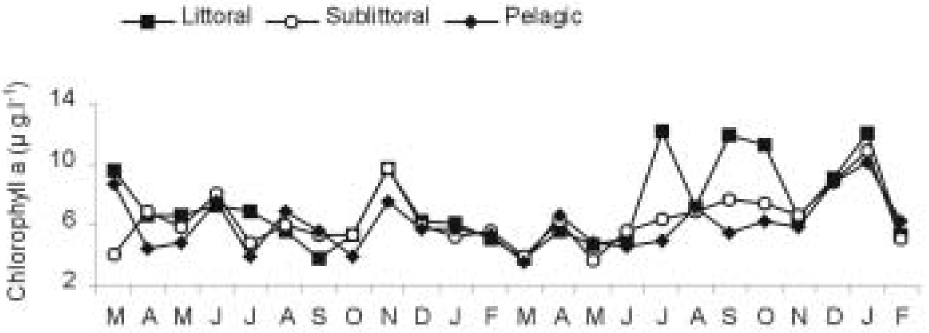


Figure 4.2: Seasonal variation per habitat of temperature, turbidity and chlorophyll a content from March 2000-February 2002 in the southern Gulf of Lake Tana.

Dissolved oxygen (mg l^{-1}) was relatively high with lowest values in December and highest in April. The measured oxygen contents corresponded to oxygen saturation values of 70-90 %. The environmental variables showed a clear seasonality in L. Tana (Fig. 4.3). There was a clear distinction between the dry period (November-April), and the wet period (May-October). Within the wet period July and August stand out, as the period of the heaviest rains. Although May-June is not distinct from

September-October, we regard them as different seasons as they were situated before and after the period of heavy rains, and therefore can be expected to have different zooplankton communities. In conclusion we distinguished four seasons: dry season (November-April), pre-rainy season (May-June), main-rainy season (July-August), and post-rainy season (September-October).

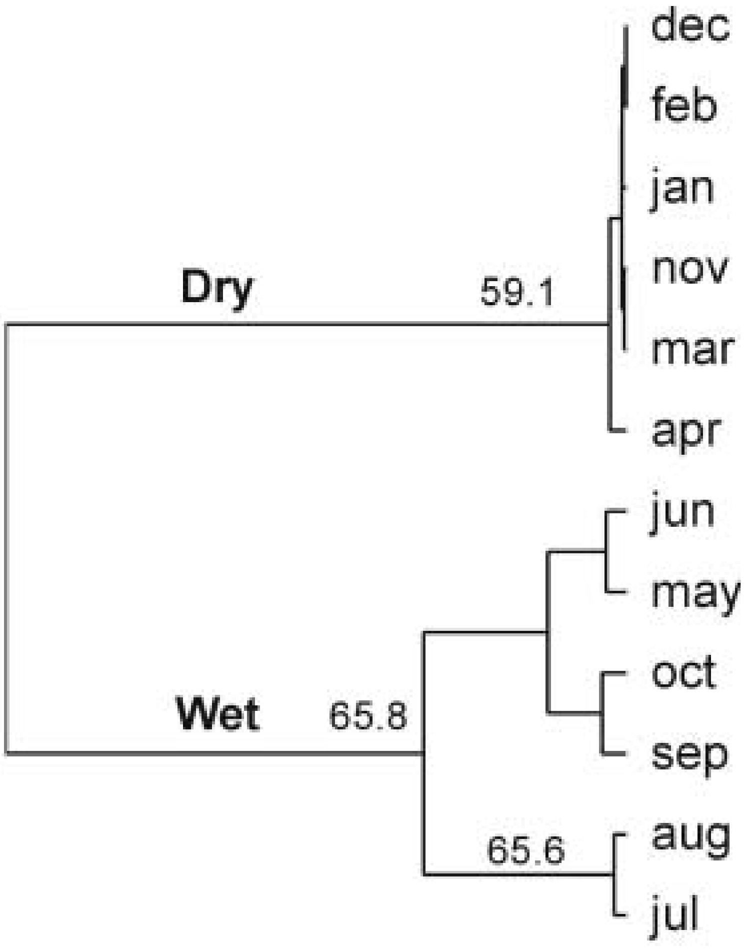


Figure 4.3: Similarity dendrogram of months based on the correlation matrix of monthly mean values for environmental parameters in southern Lake Tana over 2000 and 2001. Clustering was performed according to the unweighted pair-group method, using the arithmetic average (UPGMA-clustering; Rohlf (1993)). Numbers indicate the most important bootstrap values. Seasons: Dry period (Nov.-April), Pre-rainy period (May-June), Main-rainy period (July-Aug.) and Post-rainy period (Sept.-Oct.).

4.3.2 Spatial and temporal patterns in the zooplankton community

Table 4.2: Zooplankton species found in Lake Tana with their mean relative abundance (n, %) ($N = 124$; three habitats, four seasons).

Species	Relative Abundance (%)
Copepoda	
Mesocyclops aequatorialis similis Van de Velde, 1984	4.2
Microcyclops varicans (G.O. Sars, 1863)	< 0.1
Thermocyclops ethiopiensis Defaye, 1988	15.2
Thermodiaptomus galebi lacustris Defaye, 1988	31.2
Cladocera	
Bosmina longirostris (O. F. Müller, 1776)	13.9
Ceriodaphnia cornuta Sars, 1885	0.3
Ceriodaphnia dubia Richard, 1894	1.4
Chydorus sphaericus (G.O. Müller, 1785)	< 0.1
Daphnia hyalina Leydig, 1860	9.1
Daphnia lumholtzi Sars, 1885	8.1
Diaphanosoma excisum Sars, 1885	3.3
Diaphanosoma sarsi Richard, 1894	10.8
Moina micrura Kurz, 1874	2.5

A total of 13 species, four copepods and nine cladocerans were identified, 11 of these together contributed more than 99 % of all individuals collected (Table 4.2). Copepod nauplii were not classified to lower taxa, and were, therefore, not included in this account. Approximately half of the numbers encountered were copepods and the other half cladocerans. The calanoid copepod *Thermodiaptomus galebi lacustris*, dominated the zooplankton community, and is endemic for L. Tana. Of the three cyclopoid copepod species, *Thermocyclops ethiopiensis* was the most abundant. *Bosmina longirostris*, *Daphnia hyalina*, *Daphnia lumholtzi* and *Diaphanosoma sarsi* were the most abundant cladoceran species. Of the two rarely encountered species, *Microcyclops varicans* and *Chydorus sphaericus*, the latter species is probably not limnetic. We observed it in the open water, but always in the neighborhood of macrophyte vegetation.

For the three main zooplankton categories, copepodites, nauplii and cladocerans a highly significant seasonality was found (Table 4.3, Fig. 4.4), with the highest

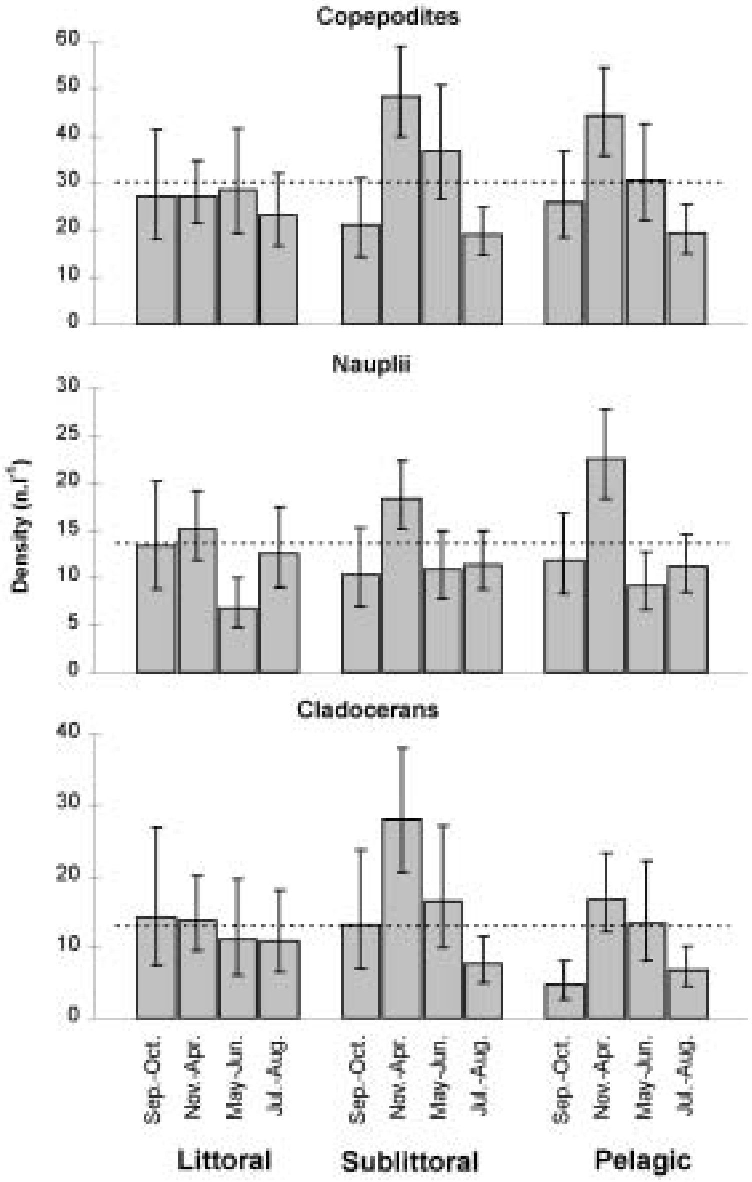


Figure 4.4: Geometric mean densities (n l^{-1}) ± 95% confidence intervals of major zooplankton categories per season and habitat in southern Lake Tana. Dotted lines indicate the overall geometric mean per category. For results of analysis of variance see Table 4.3. Seasons: Dry period (Nov.-April), Pre-rainy period (May-June), Main-rainy period (July-Aug.) and Post-rainy period (Sept.-Oct.).

densities in dry season for all three groups, and the lowest densities in main-rainy and post-rainy seasons, except for nauplii, which are least abundant during the pre-rainy season. Only cladocerans showed a significant effect of habitat with the highest densities in the sublittoral, and the lowest densities in the pelagic. The cladocerans were also the only group that showed a significant interaction between habitat and season: the temporal pattern in the shallow littoral was almost absent, in contrast to the temporal pattern in the sublittoral and pelagic habitats (Table 4.3, Fig. 4.4). This trend was also noticeable for the copepod distributions, but it was not statistically significant ($0.05 < p < 0.1$).

Table 4.3: Results of the analysis of variance in densities of copepodites, nauplii and cladocerans. The degrees of freedom (*df*), the mean squares (*ms*), and the level of significance (*p*-value) of the sources of variation are indicated. A hyphen indicates a non-significant effect.

	Copepodites			Nauplii			Cladocerans		
Source of variation	*df*	*ms*	$p <$	*df*	*ms*	$p <$	*df*	*ms*	$p <$
Season	3	1.35	0.0001	3	1.4	0.0001	3	2.37	0.0001
Habitat	-	-	-	-	-	-	-	-	-
Interaction	-	-	-	-	-	-	6	0.43	0.05
Error	251	0.09		251	0.08		243	0.20	

4.3.3 Structure of the zooplankton community in relation to environmental variables

The standard deviation of the scores on the first ordination axis in the diagnostic detrended correspondence analysis (DCA) was 1.983, which indicates that the relationship between the zooplankton and environmental variables could be either linear, or unimodal. Therefore, both a redundancy analysis (RDA) and a canonical correspondence analysis (CCA) were performed. Since the CCA explained more of the zooplankton variation than the RDA in the first three axes (CCA: 43.4 %, RDA: 30.2 %), and also more of the species-environment relationship (CCA: 92.0 %, RDA: 88.3 %) we chose for the CCA. The first axis was positively correlated with oxygen content ($r = 0.62$), total dissolved solids ($r = 0.36$), and turbidity ($r = 0.44$) (Fig. 4.5).

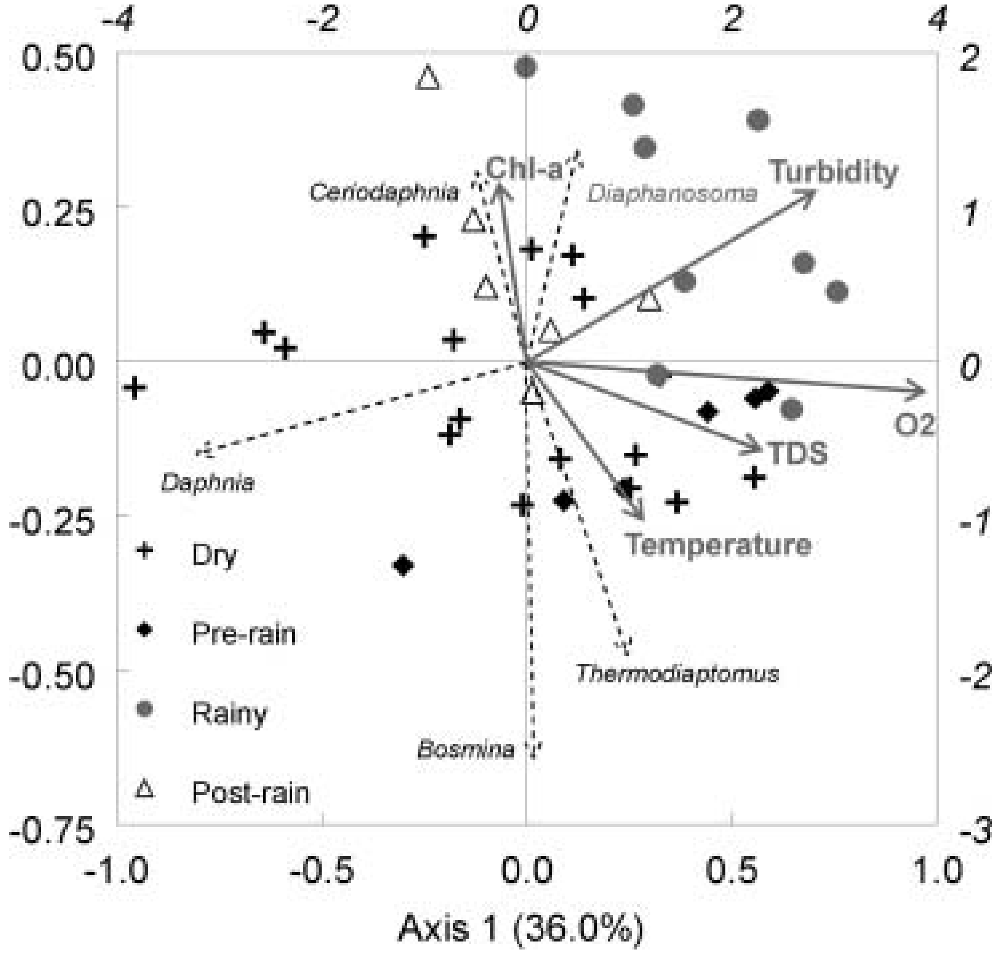


Figure 4.5: Biplot of a canonical correspondence analysis (CCA, ter Braak and Šmilauer (1998)). Data points indicate the position of 39 zooplankton communities in relation to environmental parameters (solid arrows) and species composition (stippled arrows). Different seasons are indicated by different markers. Both axes together explain 40.3 % of the variance in the samples. The left and bottom axes indicate values for the data points and species vectors; the right and top axes indicate the values for the environmental variables. The data point of the shallow station of April 2001 is outside the graph area variables. The data point of the littoral station April 2001 is outside the graph area (co-ordinates: 1.6, -0.09). Seasons: Dry period (Nov.-April), Pre-rainy period (May-June), Main-rainy period (July-Aug.) and Post-rainy period (Sept.-Oct.).

The second canonical axis was positively correlated with the chlorophyll a concentration ($r = 0.42$) and turbidity ($r = 0.40$), and negatively with temperature ($r = -0.36$). The main-rainy season (July-August) was characterized by high turbidity and high oxygen concentrations, whereas zooplankton densities were generally low. Especially *Daphnia* abundance was strongly reduced. In the pre-rainy season (May-June) water temperatures were high and both *Bosmina* and *Thermodiaptomus* showed higher densities. In contrast, the post-rainy season (September-October) was characterized by low water temperatures, and low densities of *Bosmina* and *Thermodiaptomus*. Chlorophyll a concentrations were relatively high during this season and this was positively associated with the densities of *Ceriodapnia* and *Diaphanosoma*. During the dry season (November-April) both oxygen concentrations and turbidity was low and the zooplankton densities, especially of *Daphnia* spp., were high. Generally, zooplankton densities were negatively correlated with oxygen concentrations and turbidity levels, but some species were more affected than others. Correlation of zooplankton density with algal biomass (chlorophyll a concentration) was positive in some species (*Ceriodapnia* and *Diaphanosoma*), but negative in others (*Bosmina* and *Thermodiaptomus*). Temperature was positively related to the densities of *Bosmina* and *Thermodiaptomus*.

4.4 Discussion

4.4.1 Species composition

Consistent identification of zooplankton species is essential for assessing the long-term status and trends in taxonomic structures of the assemblages. Our investigations showed four species of cladocerans (*Diaphanosoma sarsi*, *Daphnia hyalina*, *Daphnia lumholzi* and *Moina micrura*) that were not reported earlier for Lake Tana. Copepod species that have been reported previously (Van de Velde, 1984; Defaye, 1988) were confirmed. For a tropical lake, the cladoceran species composition is rather unusual, since it contains a relatively high proportion of temperate species, *i.e. Daphnia hyalina*, and *Ceriodaphnia dubia*. This is most probably due to the lake's location at an altitude of 1800 m; as a result water temperatures in L. Tana are low for a tropical lake. Diversity of the limnetic cladocerans is relatively high in L. Tana as compared with other African Lakes and reservoirs (*cf.* Dumont (1994); Marshall (1997): table 4), but diversity of copepods is relatively low (*cf.* Marshall (1997): table 4). The relatively high biodiversity of cladocerans is probably related to the relatively low water temperatures in L. Tana (range: 20.2-26.9 °C). This permits both temperate and tropical species to co-occur in the lake. The relatively low biodiversity of copepods is probably caused by the much slower dispersal of copepods relatively to cladocerans. In contrast to copepods, most cladoceran species are able to produce resting eggs (ephippia) to overcome periods with harsh conditions. Viable resting eggs of Cladocera have been recovered repeatedly from waterfowl, both in their digestive tract and in their feathers (Charalambidou and Santamaría, 2002; Green *et al.*, 2002) and are probably the reason for the fast dispersal of cladocerans (De Meester *et al.*, 2002). Aquatic birds are common and the most diverse vertebrate group in L. Tana. Among these birds are many Palearctic migrants that include osprey (*Pandion haliaetus*), great black-headed, lesser black-backed, and herring gulls (*Larus ichthyaetus*, *L. fuscus* and *L. argentatus*), and whiskered and white-winged black terns (*Chlidonias hybridus* and *C. leucopterus*) (Nagelkerke, 1997). Most likely the *Daphnia hyalina* and the *Ceriodaphnia dubia* we found in the lake were transported from the Palearctic Region by these birds.

4.4.2 Zooplankton distribution

Zooplankton densities correlated strongly negatively with oxygen concentration and turbidity, whereas correlations with all other abiotic factors were only weak. It seems unlikely that oxygen concentration itself is a steering factor for zooplankton density. Firstly, because oxygen concentration was relatively high and constant in L. Tana (range: 5.9-7.3 mg l^{-1}). Secondly, because oxygen concentrations affect zooplankton generally only at much lower concentrations (<2.5 mg l^{-1}) (Hanazato *et al.*, 1989; Bertilsson *et al.*, 1995; Aka *et al.*, 2000).

Many reports associate reduced zooplankton densities with turbid conditions (*e.g.* Hart (1986); Koenings *et al.* (1990); Aka *et al.* (2000). Furthermore, enclosure experiments showed that the clay-type (montmorillonite) found in L. Tana is more detrimental than other types of clay (*e.g.* kaolinite) (Cuker and Hudson Jr, 1992). In the present study we found that zooplankton densities were negatively correlated with suspended clay concentrations. There is a theoretical possibility that there was no direct relationship between turbidity and zooplankton abundance and that the correlations between them only resulted from seasonality in both. By performing the CCA ordination with season as a co-variable (thereby correcting for the overall seasonal influence) the probability of finding such ‘false’ correlations could be decreased. However, our dataset did not allow for the use of season as a co-variable, because of the uneven spacing of our samples in time. Moreover, this still would not prove any causal relationship between turbidity and zooplankton dynamics.

However, we feel confident that the relationship between turbidity and zooplankton dynamics is real. Since the seasonal changes in turbidity are so large (range of 12.8-84.2 NTU: Table 4.1), to our opinion it is highly unlikely that turbidity does not have profound effects on the functioning of the ecosystem in the water column, including the zooplankton.

We also found that the densities of all taxa were negatively correlated with turbidity, but not to the same degree. *Daphnia* was most affected, *Diaphanosoma* least, the others intermediate. Our findings appear to agree with what is known about the effects of silt on zooplankton densities. Strong negative affects on *Daphnia* densities were also observed by Hart (1986), whereas in most cases calanoid copepods, cyclopoid copepods and *Diaphanosoma* were least affected (Threlkeld, 1986; Koenings *et al.*, 1990; Cuker and Hudson Jr, 1992; Hart, 1992). The detrimental effect of clay is primarily the result of food limitation caused by clay particles filling the zooplankton guts and thus lowering the ingestion rates of algal cells (McCabe and O'Brien, 1983; Hart, 1988; Koenings *et al.*, 1990; Kirk and Gilbert, 1990), or with the simple light-limitation of autotrophic food sources (Hart, 1992). Direct observations on the feeding behavior showed that clay reduced the cladoceran feeding rate by mechanically interfering with both collection and ingestion of algal cells (Kirk, 1991). Food limitation will reduce the fecundity and ultimately the birth rate (McCabe and O'Brien, 1983). A direct negative effect of suspended sediments on survivorship of *Daphnia* was reported too (Zurek, 1982).

Only cladocerans showed significant differences in habitat use with the highest density in the sublittoral. This effect was most clear during the dry season (November-April) with low water turbidity. This is in contrast with Wudneh (1998), who reported that in Lake Tana the cladocerans were most abundant in the littoral zone and least abundant in the pelagic zone as compared with the sublittoral zone. The relative large difference in cladoceran densities in the littoral zone reported by Wudneh as compared with our study may have been caused by differences in the locations of sampling stations. Our littoral stations were all in open water sites whereas Wudneh's stations were often located very near to macrophyte vegetation. The higher densities in the sublittoral in our study are not easily explained since all environmental factors except turbidity are essentially the same for the three habitats. Turbidity can also not explain the observed differences since there is only a difference between littoral zone (mean 41 NTU) on one hand and sublittoral and pelagic zones on the other hand (mean 35 NTU).

4.4.3 Conclusions

The zooplankton community structure of L. Tana is unusual for tropical lakes because of its relatively high proportion of temperate species. Most probably this effect is due to its high altitude. The addition of temperate species to its zooplankton community resulted in a relatively high biodiversity of limnetic microcrustacean zooplankton in this lake. Seasonal variation of microcrustacean zooplankton was mainly correlated with turbidity, which suggests a negative effect on the zooplankton densities. In such case it also appears that not all species were affected to the same extent and *Daphnia* was most affected. Turbidity probably also plays a role in the horizontal distribution of the zooplankton taxa, but most probably other factors, *e.g.* differential predation rates by visual predators, will play a role too. More field and experimental research will be necessary to unravel the causal relationships between zooplankton densities and abiotic factors and to explain the observed spatial and temporal patterns in the zooplankton community of L. Tana.

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Chapter 5

Resource partitioning in a tropical fish assemblage of obligate and facultative zooplanktivores (Lake Tana, Ethiopia) [1]

Resource use (habitat and food) of the co-occurring ‘small barbs’ *B. tanapelagius*, *B. humilis*, *B. pleurogramma* (all < 100 mm fork length, FL), the ‘large barb’ *B. brevicephalus* (< 250 mm FL) and juvenile ‘large barbs’ (44-109 mm FL) have been examined during 2 year-round sampling periods in the Southern Gulf of Lake Tana. Habitat use differed along the littoral-pelagic gradient. *Barbus pleurogramma*, *B. humilis* and juvenile ‘large barbs’ preferred the littoral shallow habitats, whereas *B. tanapelagius* and *B. brevicephalus* predominantly occupied sublittoral and pelagic habitats. This high degree of habitat segregation between the juveniles of the commercially important ‘large barbs’ and the ‘small barb’ *B. tanapelagius* opens perspectives for a subsidiary small-meshed fishery for small barbs in the pelagic habitat. Morphometrics on feeding structures showed conspicuous specialisations for *B. tanapelagius* (cruising hunting on zooplankton), *B. pleurogramma* (suction feeder on tough, benthic food) and *B. brevicephalus* (pump-filterfeeding on zooplankton), whereas *B. humilis* was intermediate in most structures predicting a generalist feeding niche. The potential niches, set by fish size and other limitations, were tested by gut contents analysis. Zooplankton constitutes the major component of the diet for *B. tanapelagius* (75 %), *B. humilis* (40 %) and *B. brevicephalus* (39 %). The predicted and actual feeding niches of the inshore-group *B. humilis*, *B. pleurogramma* and juvenile ‘large barbs’, are broad and fit to littoral and benthic areas with diversified food types. Juvenile ‘large barbs’ consumed a considerable amount of detritus (34 %) and macrophytes (18 %). In contrast, *B. tanapelagius* and *B. brevicephalus* are specialised on few food types, and adapted to their pelagic habitat with little food diversity. Adult size and feeding mode are the most distinct characters between them. The fish community of Lake Tana differs from other African lakes in the high proportion of zooplanktivorous *Barbus*

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[1] **In preparation: Dejen, E., Sibbing, F.A., de Graaf, M., Osse, J.W.M. (2003).**

species.

5.1 Introduction

The ichthyofauna of Lake Tana is dominated by cyprinids. Recent studies have revealed an endemic species flock of 15 hexaploid 'large barbs' (*Barbus* spp.) (Nagelkerke *et al.*, 1994; Nagelkerke, 1997; Nagelkerke and Sibbing, 2000). In addition to these 'large barbs' (up to 800 mm fork length, FL), three diploid species of 'small barbs' ($<$ 100 mm FL) have been reported: *Barbus tanapelagius* (de Graaf *et al.*, 2000a), *B. humilis* and *B. pleurogramma* (Dejen *et al.*, 2002). A serious decline of the endemic stocks of 'large barbs' in Lake Tana (de Graaf, 2003) raises the question if shifting fishery efforts to the 'small barb' species ($<$ 100 mm FL) could repair this decline. Such a shift also may utilise lake production more efficiently by harvesting lower in the food chain. The feasibility of 'small barb' fishery much depends on the annual production of 'small barbs' and on the resource partitioning between 'small' and 'large' barbs.

In Lake Tana, zooplankton constitutes a major component of the food chain (Dejen *et al.*, 2003b). It is an important link between primary production and planktivorous fish, mainly small barbs. Studies on the ecology of fishes in Lake Tana was limited to the distribution and feeding habits of the commercially exploited communities of large size fish (Nagelkerke, 1997; Wudneh, 1998; Sibbing and Nagelkerke, 2001; de Graaf, 2003). These studies produced a preliminary picture of the food web of Lake Tana with large number of piscivorous barbs (8 species) and only one 'large barb' species eating a substantial amount of zooplankton when adult (*B. brevicephalus*). In addition to this, zooplankton is an interesting food source for juveniles of all 'large barbs' species up to 150 mm FL (Nagelkerke, 1997). Data on distribution and trophic patterns of the three 'small barbs' and juveniles of 'large barbs' are scant. To what extent makes resource partitioning along the trophic and spatial dimensions in Lake Tana co-existence of species in the zooplanktivorous fish guild possible? Answers are needed before recommending a subsidiary fishery on the 'small barbs'.

In tropical freshwater ecosystems, zooplanktivorous fish are usually poorly represented, and generally only play a minor role in the foodweb (Fernando, 1994). However, in some tropical lakes a few obligate zooplanktivorous species seem to have well adapted to the lacustrine environment. In Lake Tanganyika such small pelagic fish are represented by two species of freshwater sardines (*Stolothrissa tanganicae*, *Limnothrissa miodon*), in man-made Lake Kariba by *L. miodon*, in Cahora Bassa Reservoir by *L. miodon* (migrated from Lake Kariba), and in man-made Lake Volta by *Pellonula afzelius*. Lakes Victoria, Malawi and Tana are somewhat exceptional as not clupeids but small cyprinids, *Rastrineobola argentae*, *Engraulicypris sardella* and two small barbs (*Barbus tanapelagius* and *B. humilis*) respectively, dominate the fish fauna in terms of numbers and production. How has the occupation of Lake Tana by zooplanktivorous barbs arisen and developed?

Implementation of ecosystem-based approaches to lake management requires understanding the ecology of the fish community. Sibbing and Nagelkerke (2001) have generated valuable information on the potential and actual niche of 15 'large barbs' based on morphological measurements, distribution patterns and gut contents. In depth quantitative studies on diet composition and food consumption rate of the 'large barbs' and the optimum size of their prey ('small barbs') are currently undertaken (de Graaf, unpublished). The zooplanktivorous feeding guild addressed in this study is therefore part of on-going studies on the feeding ecology of the entire fish community of Lake Tana, integrating different levels of the food chain.

In the present study, we compare the habitat distribution and feeding ecology of the zooplanktivorous guild. Guided by functional morphology, we measured the feeding structures of each fish species to predict its potential food niche and we subsequently tested them from the actual diets, an ecomorphological approach using the food-fish model according to Sibbing and Nagelkerke (2001). The potential feeding niche is a prediction from the fish's capacities only, independent of the available food resources and actual competitors in the lake. This is important for predicting effects of environmental (natural and human) impact on the system, *e.g.*, shifts in composition and functioning of the food web. By comparing food and habitat resource use, we intend to gain insight into the relative importance of these two forms of resource partitioning in co-occurring cyprinids within the guild of zooplanktivores. The main aim of this study is to determine whether and how co-occuring 'small barbs', juvenile 'large barbs' and *B. brevicephalus* are partitioned by habitat and/or by food.

Specific objectives of the study were to (1) compare species use of six microhabitats (*i.e.*, littoral rocky, littoral sandy/muddy, sublittoral bottom, sublittoral surface, pelagic bottom, pelagic surface) and to estimate the habitat overlap among the species (2) compare diet composition of obligate and facultative zooplanktivorous species and to estimate diet overlap among them and (3) to estimate niche breadth from two dimensions (trophic and spatial), (4) to explain these findings from the properties of the species and their interactions, and (5) to judge on a potential fishery on 'small barbs' without disturbing the system.

5.2 Materials and Methods

5.2.1 Study area and sampling

Lake Tana is an oligo-mesotrophic shallow lake (average depth 8 m, maximum 14 m) covering a surface area of 3200 km^2 and it is the source of the Blue Nile River. The lake is turbid, well mixed and a thermocline is lacking (Dejen *et al.*, 2003b). It is located at an altitude of 1830 m and became isolated from the lower Blue Nile basin by 40 m high falls, 30 km downstream from the Blue Nile outflow. Four major permanent rivers, the largest of which is the Gelgel Abbay (Little Blue Nile) feed the lake.

The study was done in the Southern Gulf of Lake Tana (*ca.* 10 % of the surface area of the lake) from October 1999 to November 2001. The shallow littoral zone (depth *ca.* 0-4 m) has macrophytes and open areas and is relatively small, *ca.* 10 % of the total lake area. The sublittoral zone contains no macrophytes and occupies *ca.* 20 % of the lake area (depth *ca.* 4-8 m), whereas the pelagic zone is 70 % of the lake area and relatively deep (depth 8-14 m). In these three macrohabitats 16 sampling stations (Fig. 5.1) were selected covering six microhabitats: (a) littoral zone (0-1.5 m deep) with rocky bottom (A1-A3 Fig. 5.1); (b) littoral zone (0-1.5 m) with muddy/sandy bottom (B1-B5); (c) sub-littoral zone, surface layer (C1-C4, 0-1.5 m), (d) sub-littoral zone, bottom layer (C1-C4, 5.5-7.0 m) (e) pelagic zone, surface layer (D1-D4, 0-1.5 m) and (f) pelagic zone, bottom layer (D1-D4, 8.5-10 m). Monthly samples (day and night) were obtained using benthic and pelagic multimesh monofilament survey gillnets type 'NORDEN' (Lundgrens Company, Sweden) composed of 5 different randomly distributed meshsize-panels (5.0, 6.25, 8.0, 10.0 and 12.5 mm bar mesh). Panel length and depth were 3 m and 1.5 m respectively for each mesh size. Per sampling date, at all microhabitats three nets were set for 3 hours around dusk (18:00- 21:00 h) and around dawn (6:00-9:00 h).

The vertical distribution and diurnal migration of the two most abundant 'small barbs', *B. tanapelagius* and *B. humilis* were compared from three 24 hour sessions

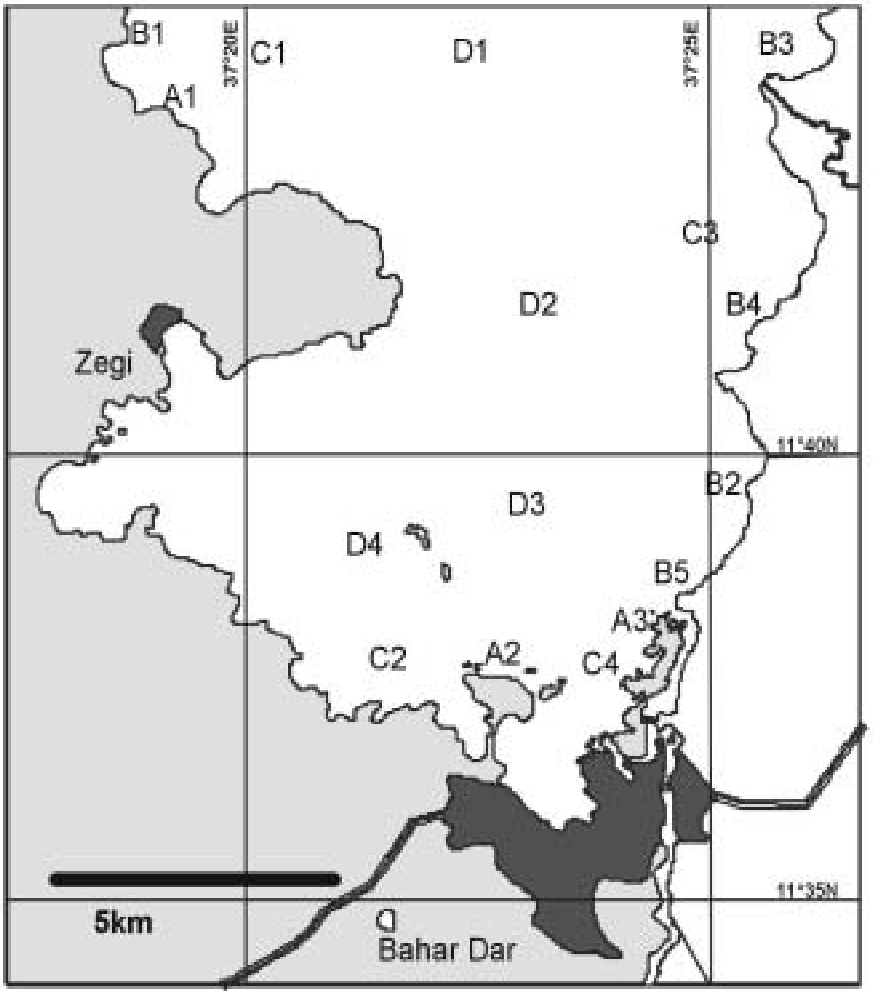

Figure 5.1: Sampling stations. Three macrohabitats: littoral (A1-A3 and B1-B5), sublittoral (C1-C4) and pelagic (D1-D4) were selected for sampling. With in the macrohabitats, six different microhabitats were sampled at: (a) littoral zone (0-1.5 m deep) with rocky bottom (A1-A3); (b) littoral zone (0-1.5 m) with muddy/sandy bottom (B1-B5); (c) sub-littoral zone, surface layer (0-1.5 m) (C1-C4), (d) sub-littoral zone, bottom layer (5.5-7.0 m) (e) pelagic zone, surface layer (0-1.5 m) and (f) pelagic zone, bottom layer (8.5-10 m) (D1-D4).

of vertical gill netting at a sublittoral station (C4, mean depth 5 m, Fig. 5.1). The vertical gillnet is composed of four different randomly distributed mesh sizes (5.0, 6.25, 8.0 and 10.0 mm bar mesh). The total panel length and depth of the vertical gillnet was 12 m and 5 m respectively. Markers were attached at every 0.5 m, in order to estimate the depth at which fish were caught. The vertical gill net was set for three hours and then lifted. The 24-h sessions were divided into six setting periods, and later the data grouped into four major groups, dawn (6:00-9:00 h), day (10:00-13:00 h and 14:00-17:00 h), dusk (18:00-21:00 h) and night (22:00-1:00 h and 2:00-5:00 h). Gut fullness and total catch were recorded to determine the peak feeding time.

Sampling of zooplankton preceded each experimental fishing survey (for methods, see Dejen *et al.* (2003b)). Samples were taken just above the bottom (littoral zone) and just below the surface and just above the bottom (sublittoral and pelagic) during day and night time.

5.2.2 Diet analysis

A total of 491 guts were examined, of which 155 from *B. tanapelagius* (29-88 mm FL), 130 *B. humilis* (45-83 mm FL), 63 *B. brevicephalus* (70-245 mm FL), 78 juvenile 'large barbs' (44-109 mm FL) and 65 *B. pleurogramma* (30-62 mm FL). Food items were identified to the lowest possible taxa most often at the genus level according to Dejen *et al.* (2003b). Volumetric data best represent the relative importance of any particular dietary category, especially when the individuals of a prey species have undergone considerable digestion (Hyslop, 1980). The contribution made by the volume of each dietary category was expressed as percentage using the points-method (Hyslop, 1980).

5.2.3 Measures of diet and habitat overlap and niche breadth

Measures of niche overlap and niche breadth should be independent of the number of resource states considered (Petraitis, 1979). We sampled every microhabitat with the same effort, which ensured that the resource states along the spatial dimension were equally available, only the availability along the trophic dimension could not be controlled. The degree of similarity between the dietary composition of each species was assessed using Schoener's overlap index α (Schoener, 1970), a robust measure of diet similarity (Wallace, 1981):

$$\alpha \quad = \quad 1 \quad - \quad 0.5 \quad \Sigma|Px_i - Py_i|$$

Px_i and Py_i are the frequencies of prey category i in predator species x and y. The index yields a value between 0 (no overlap) and 1.00 (complete overlap). In this study, a value of 0.33 or less was considered to indicate low overlap, while a value of 0.67 or higher was considered to indicate high overlap (Moyle and Senanayake, 1984).

The degree of habitat similarity between species was assessed similarly using Px_i and Py_i for the percentage composition of species x and y in habitat category i.

Niche breadth per species B was calculated using the formula of Levins (1968):

$$B = - \Sigma \quad P_i \log P_i$$

where P_i is the proportion associated with resource state i. The sampling effort was adequate for calculating resource overlap and niche breadth (six microhabitats, seven food categories, and five group of fish, sampled for two years).

5.2.4 Morphometry of feeding structures

For each part of the feeding process (search and pursuit, capture, taste-selection, size-selection, transport, mechanical breakdown, chemical breakdown), structures critically affecting the performance were measured (Fig. 5.2, Table 5.1), following the 'food-fish' model (FFM) of Sibbing and Nagelkerke (2001). Most values were expressed as a percentage of fork length (FL). For each character the average per species, its standard deviation (SD) and the 95 % confidence limit was calculated (Table 5.2). For each parameter, the value range as measured in the diversified large barbs ($>$ 150 mm FL, Sibbing and Nagelkerke (2001)) is given as a reference to the wide spectrum of feeding guilds.

For the small barb species specimens (mostly 15-20) were taken in the same size range (40-80 mm FL). Specimens of *B. brevicephalus* are larger (65-130 mm FL), since this species can only be distinguished from other 'large barbs' at $FL > 65$ mm. Therefore, some allometric growth effects may distort its comparison with 'small barbs', *e.g.* large fish use to have smaller eyes compared to fork length. Most characters, however, grow isometrically (proportional to FL) after the larval stage. Juveniles from other large barb species are hard to distinguish below 60 mm FL, and little abundant in the habitats we compared. Therefore these were excluded from analysis.

5.3 Results

5.3.1 Morphometry of feeding structures

Four barb species were compared per character (rows in Table 5.2), with the value range among the trophically diversified large adult barbs as an outgroup reference.

Table 5.1: Parameters measured, their abbreviations, their descriptions and illustrations (Fig. 5.2), according to Sibbing and Nagelkerke (2001). Metric measures are standardised by fork length (divided by FL) unless otherwise stated; mass in grams wet weight.

Abbreviation	Parameter	Description	Fig. 5.2
$ABaL$	Anterior barbel length		1
$BArF$	Body area, frontal	$(BD * BW) / FL^2$	
BD	Body depth		4
BW	Body width		5
$CbrL$	Ceratobranchial length	Between half-way joint in gill arch and oral floor	
ChW	Channel width	Width halfway gill raker, between two adjacent gill raker cushions	
CPD	Caudal peduncle depth		6
ED	Eye diameter		7
FL	Fork length	Between frontal tip of head to divergence (fork) of caudal fin lobes	
$GiAR$	Gill arch resistance	$GiRL/GiIRD$	
$GiIRD$	Gill inter-raker distance	Average of 10 inter-raker distances, lateral on ceratobranchial of gill arch 2	8
$GiRL$	Gill raker length	Average length of 10 rakers, lateral on arch 2	9
$GiRP$	Gill raker profile	Raker outgrowths, scaled from absent (1) to very elaborate (5)	10
GuL	Gut length	Between pharyngeal jaws and anus, in line after dissection	
HL	Head length	From tip snout to most posterior bony edge operculum	11
LJL	Lower jaw length	From the anterior tip to its posterior joint	13
$OGAx$	Oral gape axis	Ranging from terminal to sub- or supra-terminal; measured as $90° - OGAx$	16
$OGAr$	Oral gape area	$(OGH * OGW) / FL^2$	
$OGAr/BArF$	Oral gape / body area	$(OGH * OGW)/(BD * BW)$	
OGD	Oral gape diameter	Average of oral gape heigth and width $(OGH + OGW) / 2$	
OGH	Oral gape height	Internal height oral gape	17
OGW	Oral gape width	Internal width oral gape	18
OpD	Operculum depth	From skull to point where suboperculum and inter-operculum meet	19
$PalOAr / FL^2$	Palatal organ area	Trapezium between the first and fourth gill-arches, left and right	20
$PalTBD$	Palatal taste bud density	Number of taste buds per mm^2 palatal organ at the second gill arch	21

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PJL	Pharyngeal jaw length	Maximal length of pharyngeal jaw	23
$PJM\ /\ FL^3$	Pharyngeal jaw mass	Wet mass of cleaned pharyngeal jaw (average of left and right)	
PJM/PJL^3	Pharyngeal jaw robustness	Mass distribution over pharyngeal jaw length	
$PJSymL/PJL$	Symphysis length phar. jaws	Length of the symphysis between left and right pharyngeal jaw	29
$PLOW$	Postlingual organ width	Width of the oral floor between the left and right second gill-arch	24
$POrL$	Postorbital length	From posterior edge orbita to posterior bony redge operculum	25
$POrL/OpD$	Operculum, volume capacity	Ratio for volume displacement per unit operculum area	
$ProtL$	Protrusion length	Protrusion upper lip at opening oral gape	26
$PTA2out/PJL$	Pharyngeal tooth A2 output lever	Distance between symphysis of pharyngeal jaws and basis of tooth A2	27

Table 5.2: Critical parameters in feeding, compared among the small barbs of Lake Tana and the ‘large barb’ *B. brevicephalus*. Means, standard deviations and 95%-confidence limits are indicated. *N* is the number of specimens measured. Highest values bold, lowest values underlined. The value-range in the diversified large barb (Sibbing and Nagelkerke, 2001) is given as a reference. For parameters see Table 5.1 and Fig. 5.2.

			B. pleurogramma				*B. humilis*			
			Mean	*Sd*	95 %c.	*N*	Mean	*Sd*	95 %c.	*N*
	Fork length	*FL*	53,66	9,24	4,68	15	51,82	10,03	5,08	15
Search										
detection	Eye diameter/FL*100	*ED*	6,26	0,99	0,50	15	7,53	0,50	0,26	14
	Ant. barbel length/FL*100	*ABaL*	**4,36**	0,84	0,43	15	3,02	0,43	0,23	14
pursuit	Body depth/FL*100	*BD*	17,30	1,56	0,79	15	**22,31**	0,85	0,43	15
	Caudal peduncle depth/FL*100	*CPD*	**10,28**	0,45	0,23	15	**10,71**	0,49	0,25	15
	Oral gape area/Cross body area	*OGAr/BarF*	0,24	0,10	0,05	15	0,15	0,02	0,01	15
Capture										
size	Oral gape diameter/FL*100	*OGD*	**8,55**	1,61	0,84	14	6,80	0,50	0,25	15
location	Protrusion length/FL*100	*ProtL*	7,41	0,67	0,38	12	7,27	1,24	0,77	10
	Oral gape axis	*OGAx*	14,87	2,72	1,38	15	**18,53**	3,50	1,77	15
biting	Lower jaw length/FL*100	*LJ*	7,46	0,58	0,29	15	7,66	0,70	0,35	15
suction	Head length/FL*100	*HL*	22,98	0,74	0,37	15	22,22	1,14	0,58	15
	Post-orbital length	*POrL*	**12,00**	0,50	0,26	15	9,83	0,53	0,27	15
	Post-orbital length/Operc. depth	*POrL/OpD*	**1,28**	0,12	0,06	15	1,20	0,06	0,03	15
Taste selection										
	Palatal taste bud density	*PalTBD*	399,60	60,47	53,00	5	544,50	90,03	78,91	5
	Palatal organ area/FL^2	$PalOAr/FL^2$	**0,30**	0,08	0,03	20	0,24	0,07	0,03	14
Size selection		*FL*	48,83	8,89	3,63	23	57,96	9,85	3,65	28
	Gillraker length	*GiRL*	0,34	0,10	0,05	13	0,43	0,06	0,04	10
	Interraker distance	*GiIRD*	0,64	0,07	0,03	16	0,65	0,12	0,07	11
	Channel width	*ChW*	0,39	0,08	0,04	16	0,46	0,06	0,03	11
	Ceratobranchial length	*CbrL*	7,01	0,55	0,27	16	7,41	0,47	0,26	12
Transport										
	Postlingual organ width	*PLOW*	**2,97**	0,53	0,23	21	2,36	0,26	0,19	7
Mech. Break		*FL*	52,07	7,54	3,69	16	53,47	9,13	4,47	16
	Ph.jaw mass/FL^3*10^8	PJM/FL^3*10^8	**1,16**	0,18	0,09	15	0,88	0,17	0,10	11
	Ph.jaw mass/ Ph.jaw length^3*10^5	PJM/PJL^3*10^5	**2,41**	0,37	0,19	15	1,98	0,34	0,20	11
	Pjaw symphysis length/ Pjaw length	*PJSymL/PJL*	**0,24**	0,01	0,01	16	0,22	0,02	0,01	16
	Output lever A2 tooth/ Pjaw length	*PTA2out/PJL*	0,36	0,02	0,01	16	0,34	0,05	0,02	16
Digestion										
	Gut length	*GuL*	0,99	0,07	0,03	21	0,99	0,08	0,03	27

	B. tanapelagius				*B. brevicephalus*				Large ad. barbs	
	Mean	*Sd*	95 %c.	*N*	Mean	*Sd*	95 %c.	*N*	$FL >$	150 mm
Fork length	52,87	2,48	1,25	15	**106,52**	18,67	7,80	22	Range	
									min	max
Eye diameter/FL*100	**8,12**	0,31	0,16	15	6,41	0,60	0,25	22	3,50	5,90
Ant. barbel length/FL*100	1,13	0,25	0,13	15	2,83	0,58	0,25	21	2,30	5,80
Body depth/FL*100	18,41	1,42	0,72	15	21,37	1,02	0,44	21	21,50	27,00
Caudal peduncle depth/FL*100	9,22	0,49	0,25	15	9,27	0,58	0,25	21	8,50	10,60
Oral gape area/Cross body area	**0,32**	0,06	0,03	15	0,12	0,03	0,01	22	0,08	0,36
Oral gape diameter/FL*100	**7,95**	0,40	0,20	15	5,63	0,52	0,22	22	5,70	9,00
Protrusion length/FL*100	7,68	0,59	0,30	15	2,63	1,04	0,53	15	3,10	6,60
Oral gape axis	14,07	3,86	1,96	15	**20,82**	3,10	1,29	22	10,40	43,80
Lower jaw length/FL*100	**10,35**	0,47	0,24	15	7,82	0,63	0,26	22	7,50	11,00
Head length/FL*100	**23,93**	0,94	0,48	15	21,74	1,03	0,43	22	20,50	27,40
Post-orbital length	9,01	0,47	0,24	15	9,78	0,34	0,14	22		
Post-orbital length/Operc. depth	1,08	0,10	0,05	15	**1,38**	0,14	0,06	22	1,11	1,66
Palatal taste bud density	487,20	37,86	33,18	5	485,60	115,33	101,09	5	323,00	740,00
Palatal organ area/FL^2	0,23	0,08	0,03	20	0,24	0,04	0,02	19	0,27	0,34
Fork length	50,98	9,18	2,84	40	105,83	18,84	8,06	21		
Gillraker length	**0,48**	0,13	0,07	13	**0,51**	0,06	0,03	18	0,53	0,75
Interraker distance	0,62	0,10	0,05	13	0,45	0,06	0,03	21	0,39	0,61
Channel width	0,41	0,07	0,04	13	0,26	0,06	0,03	20		
Ceratobranchial length	7,22	0,42	0,24	12	**8,17**	0,56	0,24	21		
Postlingual organ width	1,94	0,24	0,13	12	2,20	0,57	0,24	21	0,77	1,51
Fork length	48,19	14,23	6,40	19	96,30	32,34	13,51	22		
Ph.jaw mass/FL^3*10^8	0,59	0,12	0,07	12	0,74	0,12	0,07	10	1,00	5,49
Ph.jaw mass/ Ph.jaw length^3*10^5	1,57	0,30	0,17	12	1,65	0,25	0,15	10	2,17	6,64
Pjaw symphysis length/ Pjaw length	0,19	0,03	0,01	19	0,22	0,02	0,01	18	0,18	0,27
Output lever A2 tooth/ Pjaw length	**0,41**	0,04	0,02	19	0,34	0,09	0,04	18	0,39	0,53
Gut length	0,82	0,12	0,06	15	**2,02**	0,37	0,18	18	1,52	3,40

Whereas *B. tanapelagius*, *B. pleurogramma* and *B. brevicephalus* each have a large set of extreme characters (minimal or maximal values) among the present species, *B. humilis* has very few and is intermediate in most values. *Barbus brevicephalus* has the largest branchial sieve area (combining the longest gill arches and longest rakers), with the smallest meshwidth ($GiIRD$ and ChW). *Barbus pleurogramma* combines the largest oral gape with the longest opercula ($POrL$) and the largest barbels. It has the smallest branchial sieve area, however, the largest palatal organ area and postlingual organ width and the heaviest, most robust pharyngeal jaws. *Barbus tanapelagius* has minimal barbels but the largest eye, the longest head and the most streamlined body, however, it has the most slender and lightest pharyngeal jaws.

5.3.2 Spatial distribution

From their distribution over the six habitats it is clear that *B. pleurogramma*, *B. humilis*, and juvenile 'large barbs' preferred shallow littoral habitats whereas *B. tanapelagius* and *B. brevicephalus* preferred sublittoral and pelagic habitats (Fig. 5.3). Since *B. brevicephalus* was not caught in our gillnet program, we compared data from De Graaf (unpublished data from his large-meshsize gillnet program) to identify its habitat preference.

A total of 73,398 fish was caught by benthic and pelagic multi-mesh monofilament survey gillnets. *Barbus humilis* accounts for 75.8 %, *B. tanapelagius* 22.5 %, juvenile 'large barbs' 1.6 % and *B. pleurogramma* for 0.1 % of the total number. The shallow inshore habitats (rocky, sandy and muddy bottom) were occupied mainly by *B. humilis*, due to both its preference and density, and by few juvenile 'large barbs' and *B. pleurogramma* (Fig. 5.4). The sublittoral and pelagic habitats were mainly occupied by *B. tanapelagius.* Although also *B. brevicephalus* were mainly caught in the sublittoral and pelagic habitats, we can not compare its density because of different fishing efforts.

The vertical depth distribution of the two most abundant 'small barbs', *B. tanapelagius* and *B. humilis* was compared over three 24 h sessions of vertical gill netting in the sublittoral zone (Figs. 5.5 5.6). Based on gut fullness, both *B. humilis* and *B. tanapelagius* were more actively feeding at dawn and dusk (80 % gut fullness) than at day and night (30 %). For *B. tanapelagius* the total catch during dawn and dusk ($n = 248$) was two fold higher than for day and night ($n = 142$). For *B. humilis*

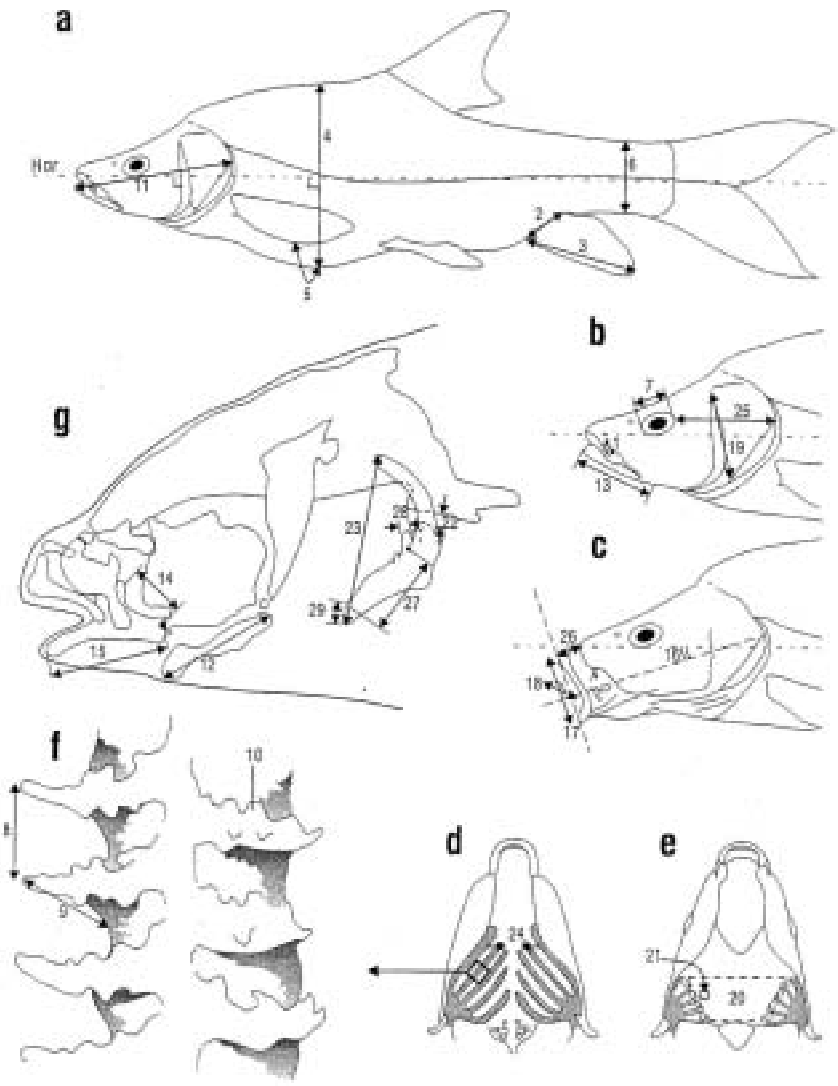

Figure 5.2: Parameters of the food-fish model (FFM), as measured on the 'small barbs' of Lake Tana: (a) external fish characters (Hor: Horizontal line as reference for angular measurements); (b) head with the mouth closed; (c) head with open, protruded mouth; (d) oro-pharyngeal roof; (e) oro-pharyngeal floor; (f) detail of gill arch showing a raker profile (10), coded as value 3 (on a scale from 1 to 5); (g) elements of the head skeleton. Numbers refer to description of parameters in Table 5.1.

the catch during dawn and dusk (n = 911) was even higher compared to day and night (n = 374). High catches during dawn and dusk provided additional evidence for high activity compared to day and night.

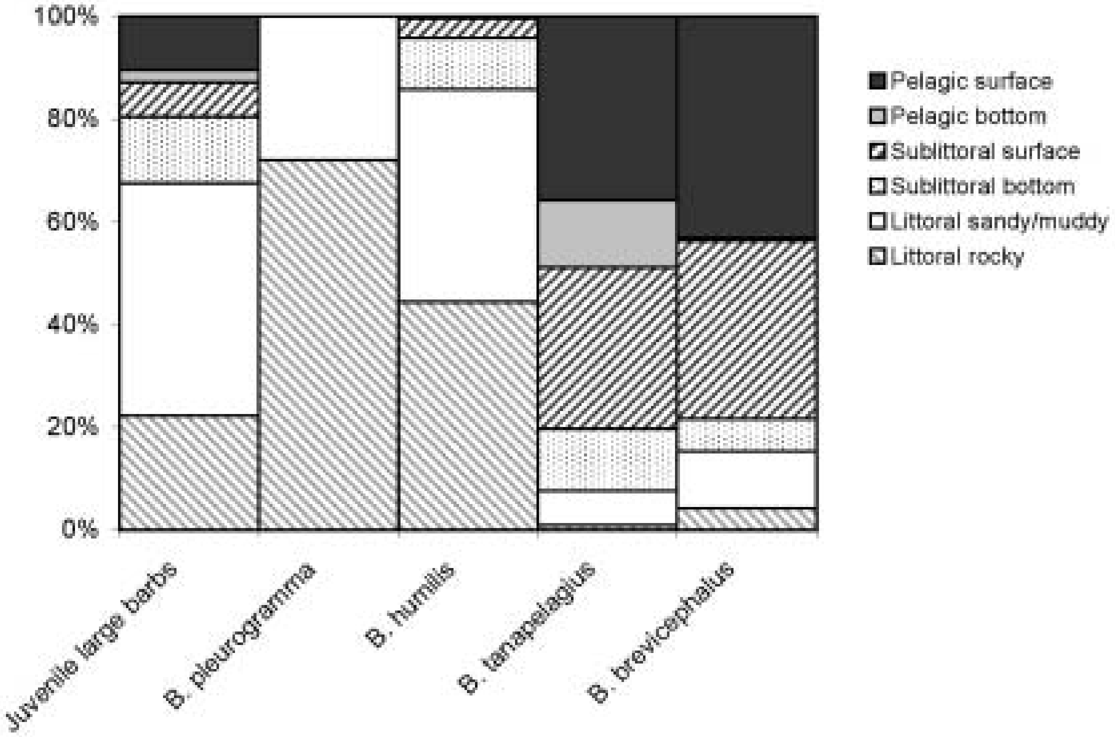

Figure 5.3: Habitat preference per species (%) across six habitats (littoral rocky, littoral sand/mud, sublittoral surface, sublittoral bottom, pelagic surface and pelagic bottom). Total number of fish caught per species: *B. humilis* (55,608), *B. tanapelagius* (16,506), juvenile 'large barbs' (1,173) and *B. pleurogramma* (111). The effort for all species, except *B. brevicephalus* (13,245) is the same.

During intensive feeding and a high horizontal activity (dusk, dawn) *B. tanapelagius* was present higher in the water column than during periods of low-feeding intensity (day, night) (Fig. 5.5). *Barbus humilis* did not show a difference in vertical position during a 24 h period (Fig. 5.6).

5.3.3 Diet composition

The volume percentages of all major food categories per species were calculated and summarised in Fig. 5.7. The overall contribution of zooplankton (35 %) to the diet of the five fish species was highest. Detritus, adult insects and algae were the second most important food items.

Zooplankton was the main food of *B. tanapelagius*, constituting *ca.* 75 % of its

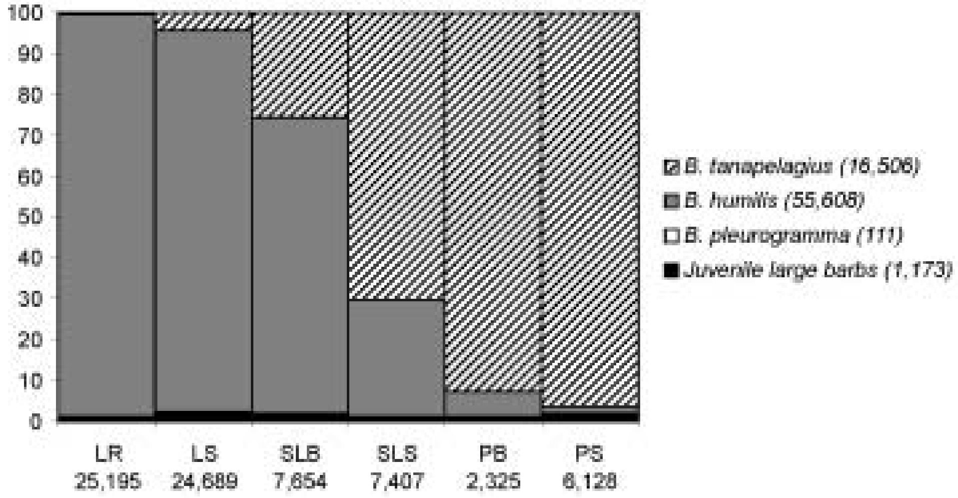

Figure 5.4: Habitat utilization by four small fish taxa (%) over six habitats (littoral rocky (LR), littoral sand/mud (LS), sublittoral bottom (SLB), sublittoral surface (SLS), pelagic bottom (PB) and pelagic surface (PS)). Percentages are taken from the total number of fish which is indicated in the bottom of the bar. Note that fish density decreases towards pelagic areas.

diet. Algae were its second most important food item (Fig. 5.7). *Barbus brevicephalus* mainly consumed zooplankton (*ca.* 39 %) and adult insects (*ca.* 35 %). *Barbus brevicephalus* also consumed a significant amount of algae. The diversity of the diet in pelagic species was low compared to the littoral species. Gut contents of *B. humilis* consisted mainly of zooplankton (*ca.* 40 %), detritus (*ca.* 21 %) and algae (*ca.* 12 %). Additional foods were macrophytes, adult insects and insect larvae (Fig. 5.7). In comparison to *B. tanapelagius*, less zooplankton was eaten and much more detritus and even macrophytes. All *B. pleurogramma* caught in the floodplains consumed a substantial proportion of insect larvae (predominantly mosquito larvae) and adult insects. Also the variety of insects was bigger than in the other fish species. Detritus and macrophytes were the second most important food items. Detritus was the most important component in the guts of juvenile 'large barbs'. Macrophytes followed by algae, insect larvae and adult insects contributed too (Fig. 5.7).

Densities of zooplankters in the environment (Table 5.3) and in the fish guts (Table 5.4) were largely different. Calanoida were the most abundant (*ca.* 35 %) in all habitats (Table 5.3), however, only little consumed (*ca.* 10 %) by mere *B. humilis*

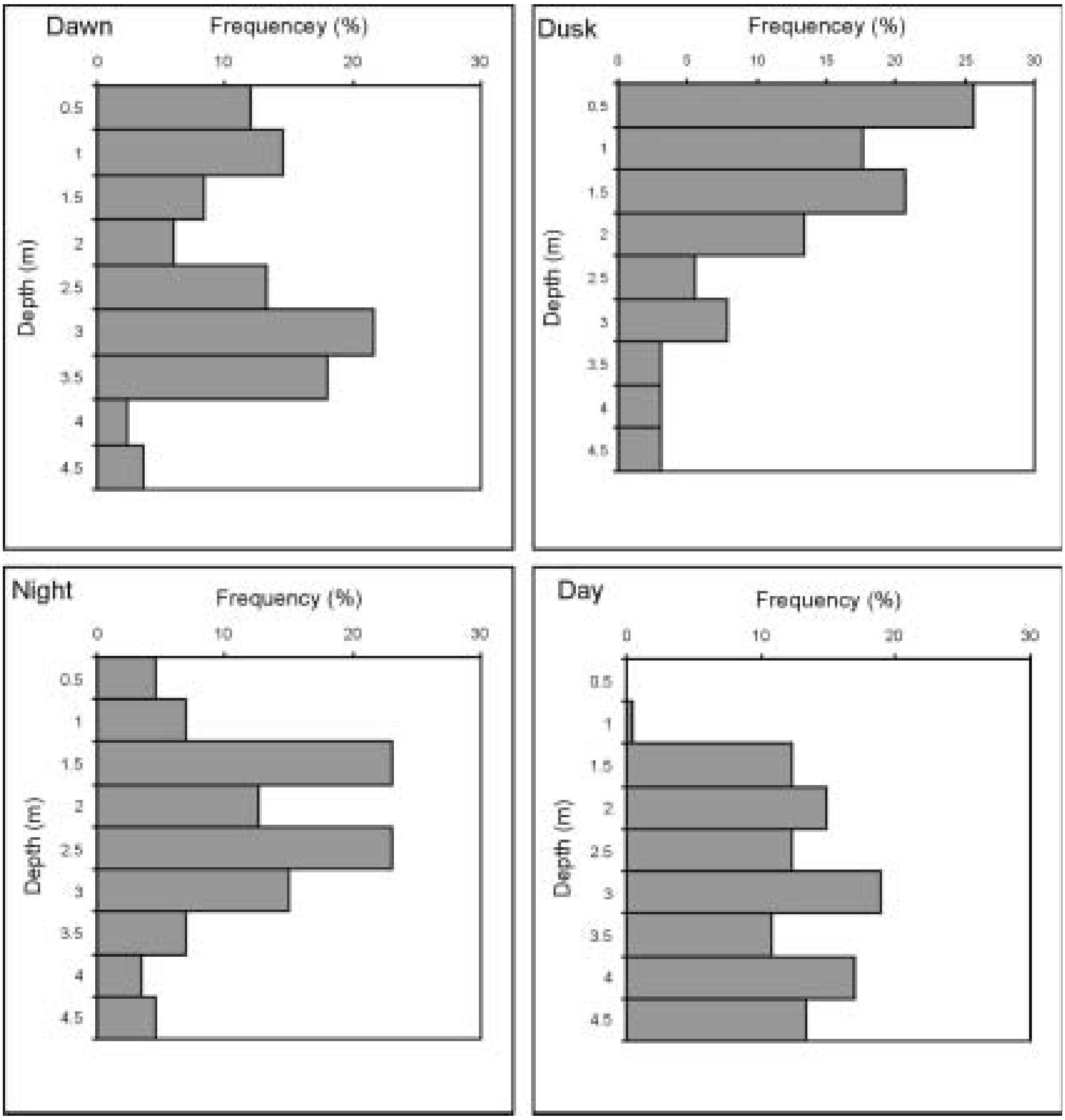

Figure 5.5: Average depth distribution of *B. tanapelagius* at 5 m deep station (Debre Mariam) at dawn (6:00-9:00), day (10:00-13:00 and 14:00-17:00), dusk (18:00-21:00) and night (22:00-1:00 and 2:00-5:00). The graph is based on three 24-h sessions of vertical gill netting between January-April, 2002. Please note that the total catch during dawn and dusk ($n = 248$) is higher than day and night ($n = 142$).

and *B. pleurogramma* (Table 5.4). *Daphnia* was the dominant food for the pelagic zooplanktivores *B. brevicephalus* (81 %) and *B. tanapelagius* (35 %,) and for *B. pleurogramma* in the floodplain (30 %, Table 5.3) even though *Daphnia* density was low in

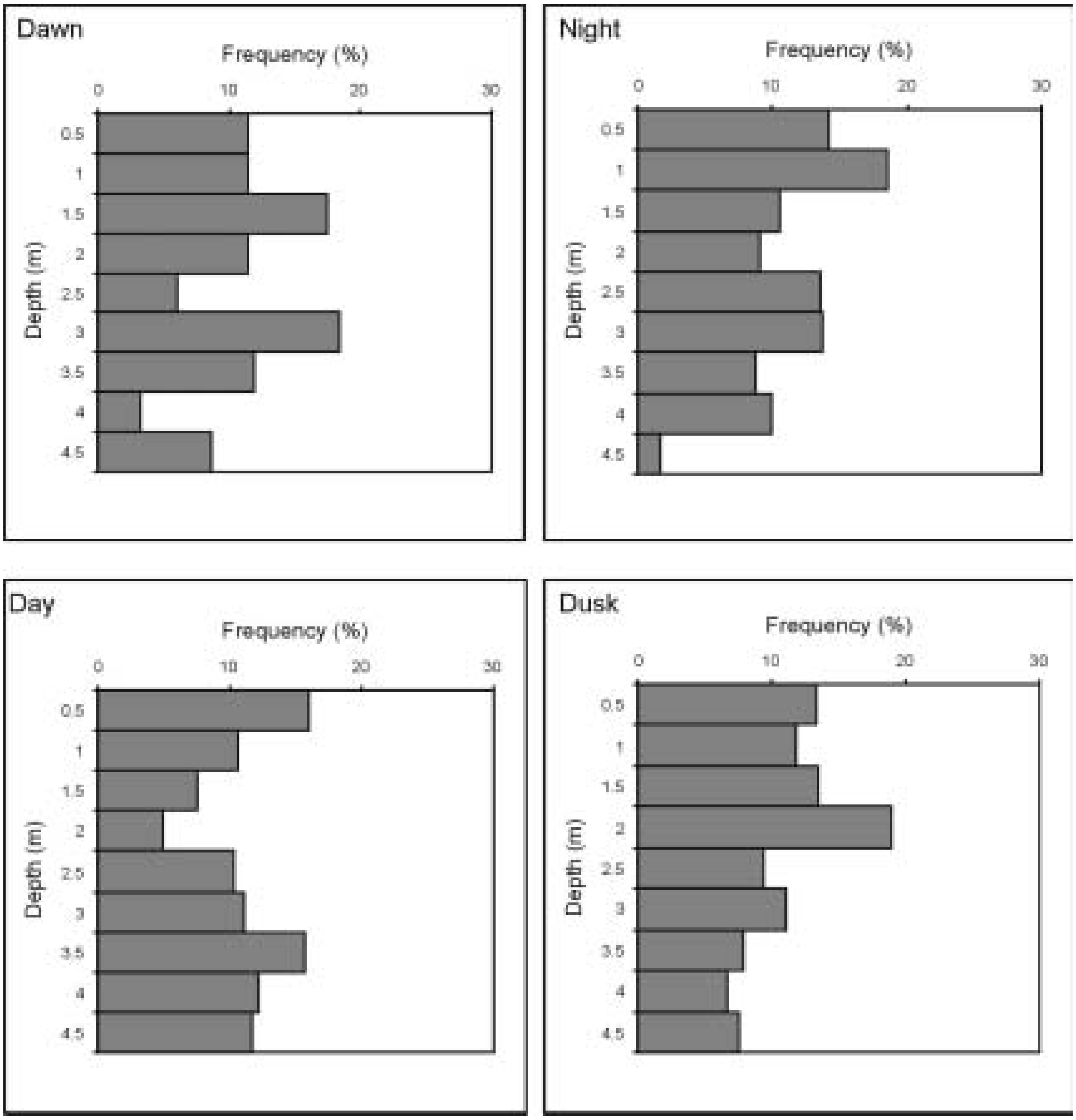

Figure 5.6: Average depth distribution of *B. humilis* at 5 m deep station (Debre Mariam) at dawn (6:00-9:00), day (10:00-13:00 and 14:00-17:00), dusk (18:00-21:00) and night (22:00-1:00 and 2:00-5:00). The graph is based on three 24-h sessions of vertical gill netting between January-April, 2002. The catch during dawn and dusk ($n = 911$) was higher than during day and night ($n = 374$).

the littoral zone (Table 5.3). *Diaphanosoma* was more abundant in the littoral areas, and mainly consumed by the littoral dwelling *B. humilis*. The cladoceran zooplankter

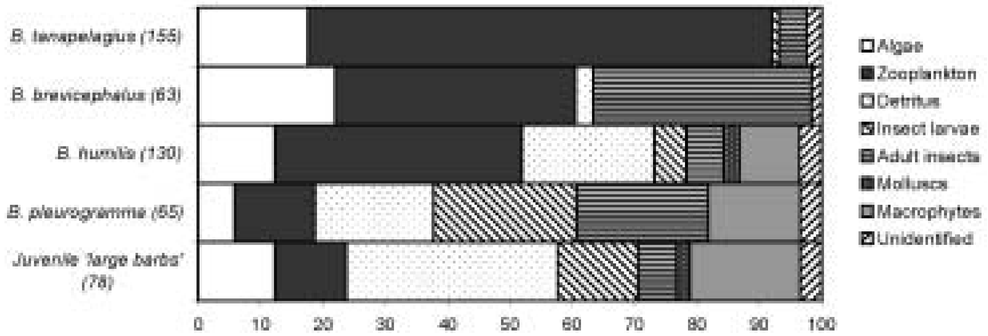

Figure 5.7: Major diet components by percentage of volume for *B. tanapelagius* (29-88 mm *FL*), *B. brevicephalus* (70-245 mm *FL*), *B. humilis* (45-83 mm *FL*), *B. pleurogramma* (mainly from the flood plain 30-62 mm *FL*) and juvenile 'large barbs' (44-109 mm *FL*).

Table 5.3: Availability of zooplankton taxa in the littoral, sublittoral and pelagic of Lake Tana by percentage of number recorded for two years (259 samples). Length ranges measured for 100 individuals per group.

Zooplankton taxa	Composition (%)			Length
	Littoral	Sublittoral	Pelagic	range (mm)
Bosmina longirostris	17.7	18.1	11.9	0.30-0.50
Calanoida	33.5	31.0	41.3	0.50-1.33
Ceriodaphnia spp.	3.0	1.8	1.6	0.37-0.70
Chydorus sphaericus	0.3	0.0	0.1	0.17-0.35
Cyclopoida	19.4	16.4	15.2	0.40-1.13
Daphnia spp.	6.9	23.9	17.7	0.53-1.46
Diaphanosoma spp.	19.1	8.9	12.3	0.57-0.97

Chydorus sphaericus, by far the smallest and scarcest zooplankter, was found significantly in the guts of littoral fish species (*B. humilis*, *B. pleurogramma*, and juvenile 'large barbs'). This zooplankter was mainly restricted to the littoral habitat with macrophytes. *Bosmina longirostris* was similarly contributing to environment and gut contents, however, conspicuously absent in *B. brevicephalus* and juvenile 'large barbs'. Cyclopoids were positively selected by juvenile 'large barbs' and *B. humilis*, *Ceriodaphnia* by *B. pleurogramma* and *B. tanapelagius*.

Size selective predation was investigated for *B. humilis*, *B. tanapelagius* and *B. brevicephalus* (Fig. 5.8). All three species showed a positive size selective predation. In

Table 5.4: Zooplankton taxa composition by % of volume in the diet of *B. humilis* (n = 130, 45-83 mm FL), *B. pleurogramma* (n = 65, 30-62 mm FL), *B. tanapelagius* (n = 155, 29-88 mm FL), *B. brevicephalus* (n = 63, 70-245 mm FL) and juvenile 'large barbs' (n = 78, 44-109 mm FL) pooled samples over two years.

Zooplankton taxa	*Barbus humilis*	*Barbus pleurogramma*	*Barbus tanapelagius*	*Barbus brevicephalus*	Juvenile 'large barbs'
Bosmina longirostris	16.6	13.5	12.0	1.5	0.8
Calanoida	9.6	11.2	2.7	0.2	-
Ceriodaphnia spp.	3.1	18.2	23.8	10.9	-
Chydorus sphaericus	15.4	10.4	-	1.4	31.4
Cyclopoida	29.0	16.7	23.1	3.1	64.0
Daphnia spp.	5.9	30.1	34.5	81.4	3.8
Diaphanosoma spp.	20.4	-	3.8	1.6	-

view of average body size, *B. brevicephalus* selected the largest zooplankton, closely followed by *B. tanapelagius*.

5.3.4 Habitat and diet overlap

According to Schoener's overlap index (α), habitat similarity was highest (0.82) for *B. brevicephalus* and *B. tanapelagius* (Table 5.5), segregating only offshore along the vertical water column. There was little habitat overlap between the two abundant 'small barbs', *B. tanapelagius* and *B. humilis* (0.25) (*cf.* Fig. 5.3).

The diet similarity was relatively high in the inshore fish group *B. humilis*, juvenile 'large barbs' and *B. pleurogrammma* (Table 5.5). There was little diet overlap between the inshore fish group and the pelagic fish group (*B. tanapelagius* and *B. brevicephalus*).

Table 5.5: Conventional niche overlap values along the spatial dimensions (S) (six habitats: littoral rocky, littoral sand/mud, sublittoral surface, sublittoral bottom, pelagic surface and pelagic bottom); and seven trophic dimensions (T) (adult insects, algae, detritus, insect larvae, macrophytes, mollusc and zooplankton).

Species	*Barbus humilis*	*Barbus pleurogramma*		*Barbus tanapelagius*		*Barbus brevicephalus*		Juvenile 'large barbs'	
		S	T	S	T	S	T	S	T
B. humilis	-	0.61	0.59	0.25	0.47	0.23	0.30	0.47	0.71
B. pleurogramma		-		0.08	0.25	0.15	0.41	0.50	0.66
B. tanapelagius				-		0.82	0.56	0.39	0.28
B. brevicephalus						-		0.40	0.26

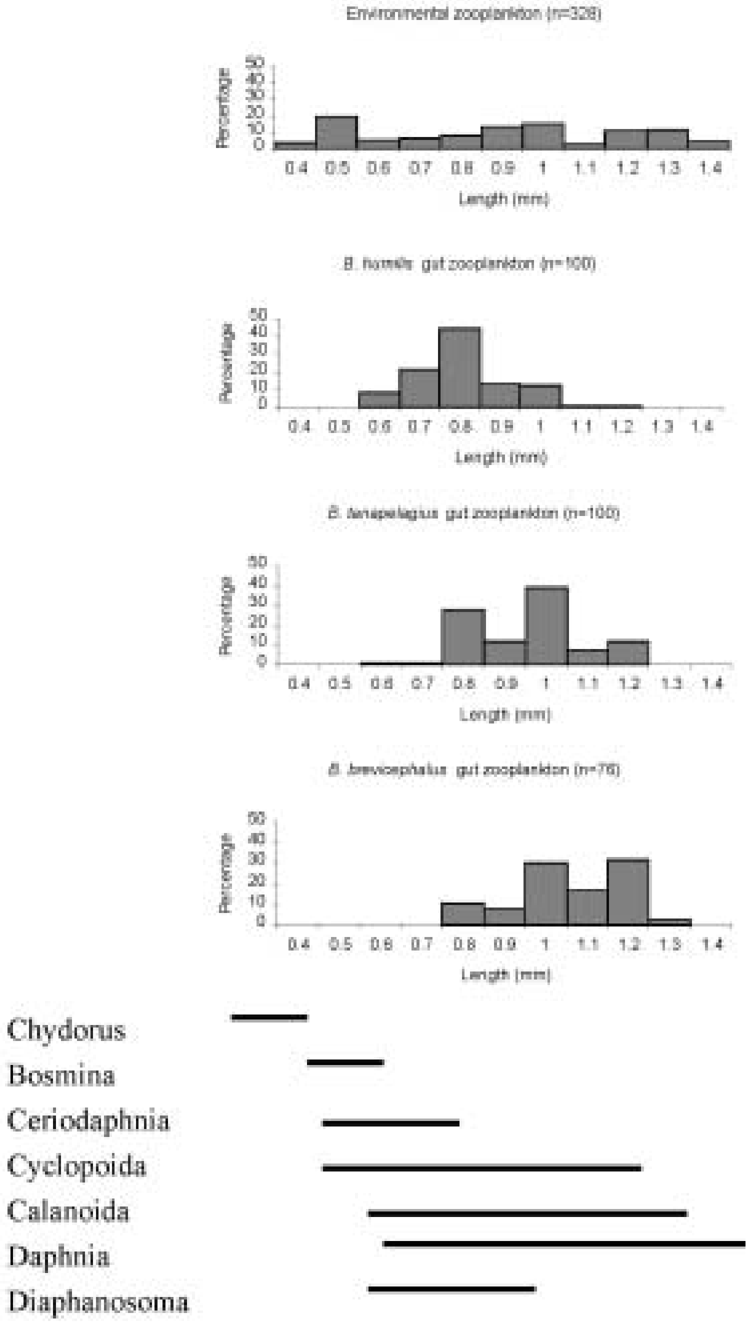

Figure 5.8: Zooplankton length-frequency distribution in the environment, and in the guts of *B. humilis*, *B. tanapelagius* and *B. brevicephalus* sampled at the same time on six stations from December 1-5, 2000. *N* refers the number of zooplankton samples measured. From each fish species 10 guts were investigated for zooplankton length measurement. Lines indicate the length range (mm) of the taxa.

5.3.5 Niche breadth

Niche breadth along the trophic dimension differed considerably between species (Table 5.6). The most specialised species along the trophic axis was the zooplanktivore, *B. tanapelagius*. In contrast the benthivorous, *B. pleurogramma* showed the most diverse diets.

Along the spatial dimension, *B. pleurogramma* with the lowest niche width (0.14) showed a clear preference for littoral rocky habitat compared with the other fish species (Table 5.6, Fig. 5.3). *Barbus tanapelagius* has the widest spatial niche (0.56), and may in fact be found in all six habitats. It is clear that a very specialised diet necessitates a wider habitat, where as more generalised feeding habit allows staying in a specific habitat and eating what ever available.

Table 5.6: Conventional values of niche breadth for two resource dimensions: six habitats (littoral rocky, littoral sand/mud, sublittoral surface, sublittoral bottom, pelagic surface and pelagic bottom), and seven food categories (adult insects, algae, detritus, insect larvae, macrophytes, mollusc and zooplankton).

Species	Trophic	Spatial
B. humilis	0.55	0.33
B. pleurogramma	**0.78**	**0.14**
B. tanapelagius	**0.12**	**0.56**
B. brevicephalus	0.35	0.42
Juvenile ‘large barbs’	0.69	0.50

5.4 Discussion

The common use of resources by organisms determines their ecological interactions and the dynamics of resources. Understanding the resource requirement of a species is essential to evaluate factors governing distribution and abundance patterns. Competition within a fish community will be reduced by partitioning of resources within and among species along spatial, temporal and trophic axes (Ross, 1986).

We found that both the trophic and the spatial dimension were important in segregating the ‘small barbs’. The observed strong spatial differences in diets (interaction between trophic and spatial dimensions) can at least partly be explained by the differences in food availability among the habitats. In ecosystems where habitats differ less in food spectrum, this need not to be the case (*e.g.* Piet *et al.* (1999)).

Questions have focused on how and to what extent competition should be reduced between species that co-occur in ecological communities. Several mechanisms could enable the long-term co-existence, *e.g.*, specialisation in morphology, physiology and behaviour on specific resources (Sibbing *et al.*, 1994; Motta *et al.*, 1995). The divergence over evolutionary time in morphology and/or behaviour of co-existing species will facilitate and improve the use of different resources. In other words, changes in both morphology and behaviour enable fish to diversify patterns of prey use (*cf.* Sibbing and Nagelkerke (2001)).

5.4.1 Potential and actual food niches

'Small barbs' are size-limited in feeding, the upper food-size limit being set by the diameter of their oral gape, the lower limit by the mesh-size of their branchial sieve. Food items wider than the oral gape can not be utilised by cyprinids, since they lack teeth on the oral jaws. The most abundant size class of 'small barbs' (*ca.* 60 mm FL), has an oral gape diameter of ca. 4.8 mm (8 % FL) and a mesh size of *ca.* 0.24 mm (channel width 0.4 % FL), setting the size range of their potential food items. Body size will also limit other performances, *e.g.* absolute swimming speed. In view of size, fish, large insects, large crustaceans, and macrophytes will not be accessible by 'small barbs'. In view of size only, and pending the availability of food resources in Lake Tana, zooplankton, smaller algae and benthic larvae are the major resources to prey upon, but diversified in itself. Small seeds and molluscs are a potential food source for small barbs if they are able to break down these strong and tough materials, however, these food categories are scarce in Lake Tana (Nagelkerke, 1997).

Availability of zooplankton was higher in the sublittoral habitat (81 individuals l^{-1}) than in the pelagic (53 individuals l^{-1}) and littoral (38 individuals l^{-1}) (Dejen *et al.*, 2003b). The availability of other food resources was not quantified due to logistic and practical problems. From personal observation, detritus was abundant, whereas macrophytes occurred only in part of the littoral areas. Aquatic insects and molluscs were scarce in all habitats, even in the littoral. Few insect larvae, mainly from chironomids and mosquito's were found by bottom grabbing (Sibbing and Nagelkerke, 2001), but in the weed beds they may live in patches of high density.

Based on the morphometrics of 25 feeding structures and functional morphology, *B. tanapelagius* is characterised as a cruising hunter, possibly pursuing its prey over short distance. Its largest eyes and its minimal barbels (all compared among the present species investigated) render it a visual forager. The smallest depth of body and caudal peduncle render its body streamlined. These characters, combined to a frontally protruding large oral gape area (OGAr/BArF) make *B. tanapelagius* an effective cruising, sometimes may be pursuit hunter. This is, however, at the cost of benthivory capacities (due to a low opercular suction capacity, by the narrowest postlingual organ and by the smallest palatal organ area for selecting between food and non-food). Also, the shortest gut of *B. tanapelagius* is not effective for processing detritus. Its small and most slender pharyngeal jaws (lowest in weight), can neither resist the high stresses involved in breaking down tough materials (*e.g.*, seeds and molluscs) nor stabilise the high loads (smallest symphysis) required for such food items. The shortest symphysis allows, however, a wide array of masticatory movements while the frontal teeth make large deformations (largest outputlever). The long gill rakers tapering into peculiarly forked tips enable *B. tanapelagius* to retain small particles. Cruising hunting is especially effective for prey capture in the pelagic, where hiding places for ambush-hunting are lacking.

The actual diet of *B. tanapelagius* (75 % zooplankton) and its preference for the pelagic habitat closely matches its potential niche. If we take the zooplankton length (measured) roughly as twice its width, then the actual smallest size in their guts (> 0.5 mm, Fig. 5.8) closely corresponds to the predicted lower food-size limit for small barbs (around 0.48 mm). Smaller sizes of zooplankton are available in the environment, but not in the guts. They will hardly be retained. The upper size limit for zooplankton is not only set by size, but also by its escape capacity. Although calanoid copepods are the most abundant zooplankters in all six habitats (Table 5.3), they are hardly found in the guts probably because of their high evasive capacities (Drenner and McComas, 1984), not due to size. Larger but slower *Daphnia* (up to 1.5 mm) and cyclopoids contribute 35 % and 23 %, respectively, to the *B. tanapelagius* diet. Benthos is completely absent, both in its potential and in its actual diet.

Most of *Barbus brevicephalus* extreme feeding characters are related to filtering small particles: it has the largest filter area (combining the longest gill arches and the longest rakers), with the smallest mesh-width (high raker density and a secondary profile on each raker). The palatal and postlingual organ area give way to the branchial sieve and are among the smallest among the presently analysed species. Pharyngeal jaws are slender, built rather for piercing and lacerating than for merely crushing. This species may forage by filtering large volumes of water, combining continuous slow swimming (streamlined by narrow peduncle) for searching and repetitive suction, like in pump-filterfeeding (Sibbing, 1991a). Particulate feeding (*i.e.* visually, on single prey) will hardly be profitable for this size of fish. Eyes and barbels are of intermediate size, and may aid in finding patches of high food density.

Their actual diet is dominated by the larger zooplankton (0.8-1.3 mm, 81 % *Daphnia*) occurring in the offshore surface layers, and by small dipteran insects (probably from the surface). Small zooplankters have not been retained, even though relative mesh size was smallest in *Barbus brevicephalus.* Note, however, that its absolute mesh size is twice as large due to double fish size. Some algae in the gut contents of all small barbs investigated may well be a concurrent catch by filterfeeding, since these species have poor capacity for mechanical breakdown and no cellulases for chemical breakdown of cell walls.

The potential diet of *Barbus pleurogramma* contrasts with the previous species and is typically benthivorous. It has the largest barbels and the smallest eyes. This species can utilise large, tough food items, by combining a large oral gape, a high opercular suction capacity, the widest postlingual organ, and the heaviest pharyngeal jaws. Together these characters render *Barbus pleurogramma* a benthic suction feeder, searching the environment with long ‘antennae’ for medium-sized food (diameter up to 5 mm). Pharyngeal jaws are designed for processing tough materials (like seeds, molluscs, insects and fibrous plants) requiring both high stresses and large deformation (Sibbing, 1991b). The widest postlingual organ will facilitate internal handling and transport. The largest palatal organ area, covered with taste buds, suggests a sufficient capacity for internal sorting between food and non-food. In carp densities go up to 800 mm^{-2} (Sibbing and Uribe, 1985). The smallest branchial sieve area, with large interraker distance on the shortest rakers, prevents the effective retention of small food particles. It may enhance the rejection of waste particles through the gill slits.

The actual diet was quite diverse, containing significant volumes of many food types, including detritus and insects. Although *Barbus pleurogramma* has a specialist outfit to process highly demanding food items (mechanically tough, large items mixed with non-food), benthic seeds, bivalves, gastropods were not abundant, both in their habitat and in their guts. Its potential niche may give it a strong competitive position in inshore floodplains rather than in the lake.

Barbus humilis is intermediate in almost all characters, rendering it the least specialised, and therefore the most opportunistic feeder (for definitions, see Sibbing and Nagelkerke (2001)). This species can direct its oral gape 19° down, by protrusion of its upper jaws, thus not giving up a horizontal escape position while foraging (Osse, 1985), and has a fair density of palatal taste buds. This points to taste rather than size-selection, and to benthic rather than pelagic feeding. The higher body shape stabilises manoeuvring at foraging. The actual diet spectrum of *Barbus humilis* has much in common with *Barbus pleurogramma*, although zooplankton contributes more (40 % and 10 % respectively) and both larval and adult insects less. This will also be due to the lacustrine rather than inshore habitat of *Barbus humilis*. The juveniles of 'large barbs' are a cluster of unidentified species, as a group most similar in diet to *Barbus pleurogramma*, more benthivorous and less zooplanktivorous than *Barbus humilis* (Fig. 5.7). These large barbs pass through several ontogenetic diet shifts before growing into their adult food niche (de Graaf, 2003). Only *Barbus brevicephalus* maintains the zooplankton food niche as adult, by specialising during growth. Since fish-size has a high impact on food partitioning, the small size of juvenile 'large barbs' will make their potential niche more equal to adult 'small barbs'. Still, the juveniles as a group of species will cover a wide diet spectrum in view of the trophic diversity among the adult large barbs.

5.4.2 Diet and habitat overlap

The feeding potentials of *B. humilis*, *B. pleurogramma* and juvenile 'large barbs' are wide and fit to littoral and benthic areas with diversified food types. The diet composition of these littoral fish differs from the pelagic fish by relatively large proportions of detritus, pieces of macrophytes and insect larvae. Furthermore, the zooplankton composition in the guts of the littoral fish differs also from the pelagic fish by its relatively high proportion of *Chydorus sphaericus*. The proportions of *C. sphaericus* in the guts of the littoral barbs were *ca.* 10-30 times higher than in the guts of the pelagic barbs (Table 5.3). At first glance this is difficult to explain on basis of their observed densities in the field since we found only ca. twice as many *C. sphaericus* in the littoral as compared with the pelagic (Table 5.4). In oligo-mesotrophic lakes *C. sphaericus* is mainly confined to the littoral zone (Peljer, 1975) where it is creeping along submerged surfaces, either macrophytes or bottom substrates (Fryer, 1968). Because of its association with macrophytes and/or bottom substrates we certainly underestimated the densities of this species since we sampled only patches of open water within the littoral zone. Detritus, insect larvae, macrophytes and *C. sphaericus* are basically only available in the littoral and sublittoral zones. Therefore, their importance in the diets of these three fish taxa is not only the results of their morphological adaptations but also the result of their availability in these habitats. The actual diets of the littoral barb species showed a large overlap, whereas their spatial distribution differed. The two pelagic barbs, *Barbus tanapelagius* and *B. brevicephalus* show a high degree of spatial overlap, however, their feeding modes differ and they utilise the zooplankton taxa often to a different degree. Only *B. brevicephalus* utilises adult insects floating on the surface.

From the gut fullness and total catch, *B. tanapelagius* and *B. humilis* showed peak feeding time at dawn and dusk. Temporal variation in the vertical distribution of fish can be expected due to abiotic and biotic factors, or by their combination. However, neither dissolved oxygen nor temperature in Lake Tana shows variations over 24 hours (Eshete Dejen, unpublished). The vertical migration of *B. tanapelagius* towards the surface, observed at dawn/dusk, may well follow the migration of their prey zooplankton, like demonstrated for other fish species (Begg, 1976; Gliwicz, 1986). In Lake Tana, diel vertical migration of the zooplankton has not been observed (Dejen *et al.*, 2003b). Other biological interactions such as avoidance of predators and competitors may play a role and need further investigation.

5.4.3 Predation by large piscivores

Cyprinid fish are poor competitors for preyfish (Sibbing and Nagelkerke, 2001). Yet, in absence of specialised non-cyprinid piscivores in Lake Tana, eight species of 'large barb' became piscivorous (Sibbing and Nagelkerke, 2001; de Graaf, 2003). They prey on *B. humilis* (40 % of the gut contents), *B. tanapelagius* (32 %) and on small benthic *Garra* species (21 %) (de Graaf, 2003). In the littoral area four species of piscivorous 'large barbs' mainly prey upon the littoral dwelling *B. humilis*. In the pelagic area three piscivorous 'large barbs' prey predominantly on the related *B. tanapelagius*. In the sublittoral habitat, where the two 'small barbs' co-occur, they are the potential prey of 5 to 6 species of 'large barbs'. The optimal prey size for all piscivorous 'large barbs' in Lake Tana is in the range of 40-50 mm FL (de Graaf, 2003). This length class is the most abundant size group from the small barb length frequency data (chapter 8). Such predation pressure will affect distribution patterns, and possibly prevent zooplanktivores from foraging in surface areas at light periods.

5.4.4 Role of zooplanktivory in tropical food webs

In many tropical freshwater ecosystems, herbivorous/detritivorous fish play a dominant role and zooplanktivorous fish are poorly represented (Fernando, 1994; Piet and Vijverberg, 1998). This is especially true for S.E. Asia where natural lakes are almost lacking. It is assumed that reservoirs in S.E. Asia carry only a small number of pelagic zooplanktivores, since most reservoir fish have a riverine origin, and inhabit the littoral zone leaving the pelagic largely unoccupied (Fernando and Holcik, 1982; Sarnita, 1987; Fernando, 1994). In Lake Victoria, the small cyprinid *Rastrineobola argentae* manages to utilise the zooplankton and is a major prey species for the introduced Nile perch (Wanink, 1998). In other African lakes and reservoirs (L. Tanganyika, Kariba Resevoir and L. Kivu) endemic sardines *Limnothrissa miodion* and *Stolothrissa tanganicae* utilise zooplankton and are exploited by commercial pelagic fisheries (Duncan, 1999). Kainji and Volta reservoirs are colonised by riverine clupeids (*Pellonula afzeliusi*, *Sierrathrissa leonensis* and *Cyanothrissa mento*) (Fernando and Holcik, 1991). However, in Lake Tana there are three zooplanktivorous cyprinids: two 'small barbs' (*B. tanapelagius* and *B. humilis*) and one 'large barb', *B. brevicephalus*. Barbs in general (*Barbus*, Cyprinidae) have a riverine origin and need rivers for spawning. The occurrence of a large filterfeeding zooplanktivore like *B. brevicephalus* is rare in tropical ecosystems (Vijverberg *et al.*, 2001) and probably a recent 'face' in Lake Tana. This may be explained by the open niche for zooplanktivores which developed after Lake Tana owes its present form to damming by a 50 km long Quaternary basalt flow, which filled the exit channel of the Blue Nile river *ca.* 10,000 years ago (Chorowicz *et al.*, 1998). Small barbs were among the few riverine species present and could probably start utilising this resource, expanding their habitat from the littoral to the pelagic.

The two zooplanktivorous 'small barb' species are major preyfish for large predators (Nagelkerke, 1997; de Graaf, 2003). In such away they are crucial in linking the primary production of the lake to the production of the larger piscivorous barbs, the target for commercial/artisanal fisheries. As these 'small barbs' occupy a central position in Lake Tana's ecosystem it is important to assess possible scenarios on the food web dynamics if a pelagic fishery would be feasible. Targeting 'small barbs' will definitely decrease the density of zooplanktivorous fish. According to the cascading trophic interaction theory (Carpenter *et al.*, 1985) this will result in a lower predation pressure on the zooplankton, which in turn will probably lead to higher zooplankton densities, a higher grazing rate on the phytoplankton and consequently lower phytoplankton densities. Following the same argument the current decline of piscivorous barbs gives an alternative lake food web state. In this scenario the density of zooplanktivorous fish will increase which will result in a lower zooplankton biomass and a higher phytoplankton biomass (Hart, 2002).

5.4.5 Fisheries management aspects

One of the major problems of the existing fisheries at Lake Tana is over-exploitation of the 'large barbs'. This problem could be overcome by selective exploitation of the presently untapped resources of small pelagic cyprinids. In order to avoid adverse effects on the large barb stocks, the habitat of 'small barbs' and the habitat of the juvenile 'large barbs' must be different. We showed above a high degree of habitat segregation between the latter juveniles and *B. tanapelagius*. Therefore targeting *B. tanapelagius* for subsidiary small-meshed fishery in the pelagic habitat will, from our present knowledge, probably not have important adverse consequences on the stocks of the commercially important 'large barbs'. However, there is no prospect for a fishery on the inshore dwelling 'small barb', *B. humilis* because of the habitat overlap with the juveniles of 'large barbs' (unless the nurseries of large barbs appear to concentrate among weed beds).

Acknowledgements

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Chapter 6

Reproductive strategies of two sympatric ‘small barbus’ (*Barbus humilis* and *B. tanapelagius*) in Lake Tana, Ethiopia [1]

The reproductive strategies of two species of ‘small barbs’ (< 100 mm forklength, FL), the benthic-littoral *Barbus humilis* and the pelagic *B. tanapelagius* from Lake Tana (Ethiopia) were investigated. Monthly samples were collected from five different habitats over a 1-year period ($> 12,000$ fish). Both species have a long breeding period (from March to September), and the distinct bimodal size-frequency distributions of eggs suggest multiple spawning for both species. Absolute fecundity increased exponentially with fish size, and was significantly higher for *B. humilis* than for *B. tanapelagius*. Egg size was similar. Relative fecundity was significantly higher in *B. humilis*. In most habitats *B. tanapelagius* reached size at first maturity at smaller size (58.5 mm) than *B. humilis* (64.5 mm). However, in shallow habitats with clear water *B. humilis* females have a much smaller size at first maturity (48.3 mm), possibly due to high infection rates with tapeworm. The range of fecundity in small barbs from Lake Tana (172-339 eggs per gram) was low compared with small lacustrine cyprinids and clupeids from other African lakes. The reproductive strategies of the two barbs were discussed in relation to their feeding potentials, food availability, parasite infection rate and risk for predation.

6.1 Introduction

Lake Tana, the largest (3150 km^2) and most elevated (1830 m) lake in Ethiopia, is a circular basin 70 km in diameter, with a maximum depth of 14 m (average 8.9 m). The lake is considered to have originated by volcanic blocking of the Blue Nile River 2 million years ago (Mohr, 1962). It owes its present form to damming by a 50 km long

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[1] **Dejen, E., Sibbing, F.A., Vijverberg, J. (2003).** ***Neth. J. Zool.*** **52, 281-299.**

Quaternary basalt flow, which filled the exit channel of the Abbay (Blue Nile) river (Chorowicz *et al.*, 1998). The age of this lava flow is estimated to be some 10,000 years. Lake Tana is characterised as oligotrophic with chlorophyll content of *ca.* 3.7 μg l^{-1} (Rzóska, 1976; Wood and Talling, 1988).

Previous research (Nagelkerke, 1997; Nagelkerke and Sibbing, 2000) has revealed an endemic species flock of 15 so called 'large barbs' (hexaploid, *Barbus* spp.: Cyprinidae). The other fish species found in Lake Tana are common in rivers and lakes of the Ethiopian highlands: *Oreochromis niloticus* (Cichlidae), *Clarias gariepinus* (Clariidae), *Varicorhinus beso* and the genus *Garra* (Cyprinidae). In addition to the endemic large barbs (up to 80 cm fork length, FL), four species of small barbs ($<$ 10 cm FL) have been reported from Lake Tana: the recently discovered *Barbus tanapelagius* (de Graaf *et al.*, 2000a), *B. humilis*, *B. pleurogramma* and *B. trispilopleura* (all Boulenger (1902)). Up till now the scarce biological information about these species focused on taxonomy. Small barbs are diploid and characterised by radiating striae on their scales. *Barbus trispilopleura* is an ecotype bound to shallow transparant rocky areas with vegetation and has recently been synonymised with *B. humilis* (Dejen *et al.*, 2002). *Barbus humilis* has a brown-blue back, and a lateral band or up to three pigment spots on its side. *Barbus tanapelagius* is fully silvery, and also distinct by its hooked lower jaw and large eyes.

To provide a rational basis for whole lake management, knowledge of the food web dynamics of Lake Tana's ecosystem is required. *Barbus pleurogramma*, found only in the flood plain during the rainy season, is of less importance for the lake management. The role of the small barbs *B. humilis* and *B. tanapelagius* in the food web is currently investigated. Preliminary investigations suggest that they constitute the main link in the food chain between primary consumers (zooplankton) and top predators, the piscivorous large barbs (Nagelkerke, 1997; de Graaf *et al.*, 2000a,b; Nagelkerke and Sibbing, 2000; Sibbing and Nagelkerke, 2001). Small pelagic fish species have generally a short life cycle and are characterised by a high individual growth rate, a high reproductive rate, and an early age at first reproduction (Miller, 1996).

Barbus tanapelagius is endemic to Lake Tana (de Graaf *et al.*, 2000a) and probably evolved following the rise of large pelagic zooplankton resources in the incipient Lake Tana. *Barbus humilis* is a riverine species and more widely distributed in the inflowing rivers of Lake Tana and other parts of Ethiopia (Froese and Pauly, 2001). The two species are sympatric in Lake Tana, but spatially and trophically, they have different positions in the riverine-lacustrine gradient. This different history of the species provides an opportunity for comparing their reproductive strategies.

This paper has three main objectives. First, to describe the reproductive biology of two important species of small barbs in Lake Tana. Second, we aim at increasing our understanding of the adaptive value of their reproductive strategies in view of the habitat they occupy. Finally, in a wider perspective, we compared their reproductive characters with other tropical small barbs and small zooplanktivorous freshwater clupeids.

6.2 Materials and Methods

6.2.1 Sampling of fish

Sampling of fish was monthly over 2000, limnological parameters were monitored every two months over 2000 and 2001. Fish were collected from five different habitats (*cf.* Dejen *et al.* (2002)). Four of these habitats are turbid and have no vegetation: a) littoral zone with rocky bottom (*ca.* 2 m deep); b) littoral zone with muddy/sandy bottom, bordered by papyrus, grass or agricultural land (*ca.* 2 m deep); c) sublittoral zone (*ca.* 6 m deep) with sandy/muddy bottom; d) open water with sandy/muddy substrate (*ca.* 10 m deep). Four replicate samples were taken from each habitat (total of 16 sampling stations). A fifth habitat e) is clear and shallow (*ca.* 2 m deep), with rocks and floating vegetation (*Ceratophyllum*). This station is near the town of Bahir Dar where dumping of fish wastes induces high density of fish-eating birds, which are known to be the primary host for the cestode *Ligula intestinalis* (Bush *et al.*, 2001).

Multi-mesh monofilament gillnets (type Norden from Lundgrens, Stockholm; 5, 6.25, 8, 10 and 12.5 mm bar mesh) were used. The size of a single mesh panel was 3 x 1.5 m. Three multimesh nets were combined as one set. The sampling programme with gillnets was carried out two times per month (day and night in the same week). At the shallow stations a-b only a bottom-net was set. At deep stations in habitat c-d both bottom and surface-nets were used. Nets were set between 06.00 and 09.00 h for daytime sampling and between 18.00 and 21.00 h for nighttime sampling. A bottom trawl was used at the non-rocky stations in habitat b-c-d during dusk and dawn. Trawling speed was 1.0 m s^{-1} and trawl hauls lasted for 15 minutes each. The mouth opening of the trawl (3 m wide and 1 m high) was kept open with a 3 m beam.

The barmesh in the cod-end is 5 mm. Scoop and lift nets were used in station ‘e’.

To monitor environmental conditions once every two months from January 2000 - January 2002, in addition to transparency, dissolved oxygen and water temperature, zooplankton samples were taken using a 3.5 l universal water sampler (Hydrobios, Kiel, Germany). After sieving with 80 μm mesh, microcrustacean zooplankton densities per litre were assessed. Copepod nauplii were not included in the zooplankton density estimates. Three replicate hauls during day and night, surface and bottom over six stations (shallow, intermediate and deep sites) were taken.

6.2.2 Measurements and data analysis

Spotted fish collected at the clear station ‘e’, previously described as *B. trispilopleura* but recently as an ecotype synonymised with *B. humilis* (Dejen *et al.*, 2002), were yet treated separately from *B. humilis* collected at turbid stations, since they possibly represent different groups. All together, 6981 specimens of *B. humilis* from turbid habitats ‘a-d’, 2860 *B. humilis* from the clear habitat ‘e’ and 4319 specimens of *B. tanapelagius* were collected. In the data analysis for *B. humilis* ecotypes, the data from turbid stations (a-d) are used as the base. Only in cases where a difference may be expected, station ‘e’ data have been analysed for comparison.

From each sampling station monthly 30-40 fish (if available) were randomly picked for analysis. Lengths, weights, sex and maturity stages were recorded from the fresh sample immediately after catch. Fork length (FL) was measured to the nearest mm, total weight to the nearest 0.1 gram. Fish were carefully inspected for the presence of cestode larvae, *Ligula intestinalis*, in the body cavities. Comparing length-weight relationships between species or groups an analysis of covariance was used to test for a difference in adjusted mean weight.

Ovaries were assigned to I-V maturity scales according to Nikolsky (1963). Stage I, ovaries small, thin and translucent; stage II, ovaries small to moderate size and translucent, with small but distinct ova; stage III, ovaries mature, enlarged, filling most of the body cavity, yellowish and the nucleus obscured by yolk deposition; stage IV, ovaries fill the entire body cavity and distinctly yellow colour; and stage V, ovaries small, retaining only few mature ova and pale yellow. It was difficult to use a five-stage maturity scale for males. Therefore male gonad maturity was based on only two stages: stage I, immature males (opaque white testes) and stage II, mature (white creamy milt comes out with pressing on the abdomen).

Five ovaries in stage IV of each species were taken monthly in the spawning period for determination of egg diameter frequency distributions. Each ovary was preserved in 4 % formalin. After removal of the ovarian membrane, the eggs were shaken vigorously and poured in to a petridish engraved every 5 mm for random measurement of ova. Only the eggs that touched the grid lines were taken. Up to 100 eggs from each female were measured to the nearest 0.1 mm using a micrometer eyepiece. Oocytes below 0.3 mm were not measured. A sub-sample (20) of the largest eggs were measured to calculate the mean diameter of fully matured ova.

For studies on fecundity about 20 stage IV ovaries over a wide size range of fish (49-80 mm FL) were preserved in formalin. The vial was shaken until the eggs separated, and the contents transferred to a grooved petridish counting tray of 50 squares. Ten squares were counted as a sub-sample.

Size at first maturity, the FL at which 50 % of the individuals are mature (L_{50}) (Willoughby and Tweddle, 1978), was determined for females and males. Eggs in stage III and above were considered as mature. The proportion of mature fish per length class was calculated and L_{50} was estimated according to Ni and Sandeman (1984). The relationship between the percentage of mature fish (P) per length class and fish length (X in mm) was described with a logistic curve: a, intercept and b, slope of the logistic regression.

$$P = \frac{e^{a+bX}}{1+e^{a+bX}}$$

The L_{50} was then derived from the equation $L_{50} = -a/b$. The data were not distributed normally after transformation, so non-parametric statistics (Mann-Whitney U test) were used to test group differences in fecundity and egg diameter, using a significance level $\alpha = 0.05$. For the statistical analysis SPSS for Windows software (version 9.05) was used.

6.3 Results

6.3.1 Environmental conditions

Annual rainfall at Lake Tana over 1997 - 2000 was 1418 mm at average (Bahir Dar Meteorological Station). During 2000 monthly rainfall data ranged between 0 - 517 mm (Fig. 6.1). The main rainy season was from June to October, peaking in August. Small rains in March are an exception rather than a rule.

Maximum water temperature, as a monthly average, ranged between 21 and 26 °C (Fig. 6.1), with lowest values in January, a sharp increase in February, peak values in May and sharp decline with the big rains in June-July.

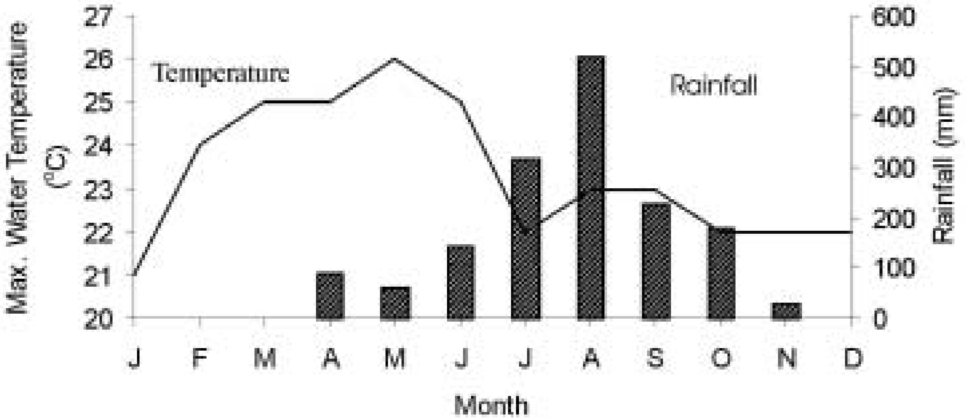

Figure 6.1: Average monthly maximum water temperature (°C, line) and monthly total rainfall (mm, bar) over January - December 2000.

6.3.2 Zooplankton densities

Average microcrustacean zooplankton densities (without nauplii) over all stations showed a distinct seasonal variation. The highest densities (47-125 ind. l^{-1}) were observed in the dry season (December-April) and the lowest densities (32-37 ind. l^{-1}) in the wet season (June-October). There was also a clear spatial pattern in the average zooplankton distribution. Lumping all daily and seasonal data resulted in average densities of 38 ind. l^{-1} in the littoral areas, 81 ind. l^{-1} in the sublittoral, and 53 ind. l^{-1} in the pelagic zone.

6.3.3 Abundance and distribution of small barbs

Trawling data from all (except the two rocky) habitats show that about half of the total catch by mass (kg) are ‘small barbs’. The other half is composed of ‘large barbs’ (26 %), tilapia (18 %) and others (6 %). Comparing the mass of *B. humilis* and *B. tanapelagius* in gillnet catches over all habitats shows that *B. humilis* dominates in shallow inshore areas (*ca.* 98 %) whereas *B. tanapelagius* dominates (99 %) the offshore areas of Lake Tana (*cf.* Table 6.1). In sublittoral areas of intermediate depth both species co-occur, *B. humilis* (54 %) near the bottom and *B. tanapelagius* (46 %) near the surface.

Table 6.1: Tapeworm-infection rate (P, %) in *B. humilis* and *B. tanapelagius* across different habitats (depth between brackets), from surface and bottom. Sampling from January - December 2000. Number of fish investigated (N) is indicated for each station.

		B. humilis		*B. tanapelagius*	
Habitat	Station	N	P (%)	N	P (%)
Clear Water					
Littoral (0-3 m)	e	2860	10		
Turbid Water					
Littoral (0-3 m)	a, b	4996	3	120	3
Sublittoral (4-8 m)	c	1985	1	1676	13
Pelagic (8-14 m)	d			2523	7

6.3.4 Length-weight relationship

Both species are small (< 100 mm FL), and the females are relatively larger than the males. Length-frequency distribution data from gillnet and trawl catches at turbid stations (a-d) show that *B. humilis* specimens are relatively larger (mode, 57-67 mm FL) than *B. tanapelagius* (52-62 mm FL) (Fig. 6.2). Mean length (FL) and standard deviations ($\pm SD$) were 63.2 ± 8.5 mm (females) and 55.6 ± 6.6 mm (males) for *B. humilis* and 58.6 ± 7.9 mm (females) and 53.3 ± 5.5 mm (males) for *B. tanapelagius*. Based on fish collected in four of the five habitats (habitats a-d) length-weight relationships (FL in mm; fresh weight (W) in gram) were calculated for *B. humilis* ($W = 1.97 * 10^{-5} FL^{2.898}$; $N = 4886$; $r^2 = 0.92$) and for *B. tanapelagius* ($W = 1.54 * 10^{-5} FL^{2.919}$; $N = 2926$; $r^2 = 0.91$). *B. humilis* from the clear habitat (e) had significantly higher weight ($W = 1.70 * 10^{-5} FL^{2.945}$; $N = 2351$; $r^2 = 0.91$) than its conspecifics from the more turbid habitats a-d (ANCOVA, $P < 0.0001$).

6.3.5 Tapeworm infection

The tapeworm (*Ligula intestinalis*) infection rate differed between species and habitats. At turbid stations (habitat a-d) *B. humilis* had a low infection rate (1-3 %) compared with *B. tanapelagius* (3-13 %) (Table 6.1). A higher prevalence (10 %) in *B. humilis* was found at the clear shallow station with rocks and vegetation (habitat e). The highest (13 %) prevalence in *B. tanapelagius* was found in the sublittoral.

6.3.6 Sex ratio

The total number of *B. tanapelagius* ($N = 3966$) comprised 26.2 % males and 73.8 % females, while *B. humilis* from turbid stations ($N = 6253$) consisted of 22.4 % males and 77.6 % females. For both species, females dominate throughout the year. When the adults are relatively small, the sex ratio remains close to 50 % (Fig. 6.2), but from FL 52 mm onwards the proportion of females increases steeply until > 90 % at $FL > 62$ mm.

6.3.7 Breeding season and area

The high abundance of mature females and males between March and September suggests high breeding activity during this period (Fig. 6.3). The overall turbidity of Lake Tana did not allow direct observations of spawning behaviour. However, the distribution patterns of mature (stage IV) females across habitats may indicate the preferred spawning location. For *B. humilis*, the proportion of mature females in shallow rocky habitats was higher (80 %, $N = 191$) than in shallow sandy/muddy (60 %, $N = 400$) and sublittoral habitats (57 %, $N = 475$). In the case of *B. tanapelagius*, the proportion of mature females was higher at the surface of deep offshore habitats (66 %, $N = 388$) compared to sublittoral habitats (47 %, $N = 231$). *Barbus tanapelagius* is rare in shallow littoral habitats (Table 6.1).

6.3.8 Ova diameter frequency

In both species the ovaries contained two kinds of oocytes, each with its own distinct peak in egg size-frequency distributions (Fig. 6.4): previtellogenic oocytes with a diameter less than 0.6 mm and vitellogenic oocytes (mature eggs) that are golden and yolky ranging from 0.7-1.1 mm in diameter. Only the vitellogenic eggs were counted to determine fecundity because only these oocytes would be spawned during the subsequent peak. The mean diameter of fully matured eggs was 0.77 ± 0.07 (mean standard deviations) for *B. humilis* from turbid stations, 0.76 ± 0.07 for *B. humilis* specimens at the clear rocky habitat and 0.80 ± 0.07 mm for *B. tanapelagius*.

6.3.9 Fecundity

Absolute fecundity, the number of eggs per female, increased with a power function of fish size (Fig. 6.5). This exponential increase was significantly higher for *B. humilis*

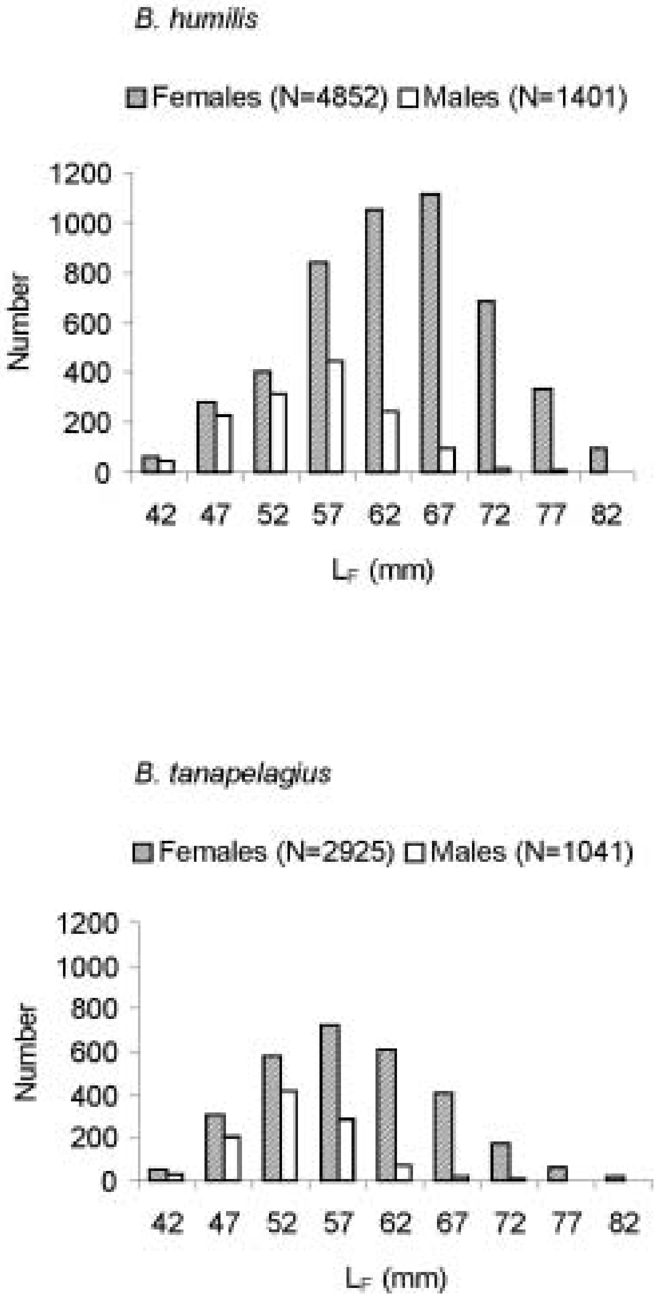

Figure 6.2: Length-frequency distributions of females and males, from gillnet and trawl catches from habitats a-d. a) *B. humilis*, and b) *B. tanapelagius.* Cumulative data from monthly catches January - December 2000.

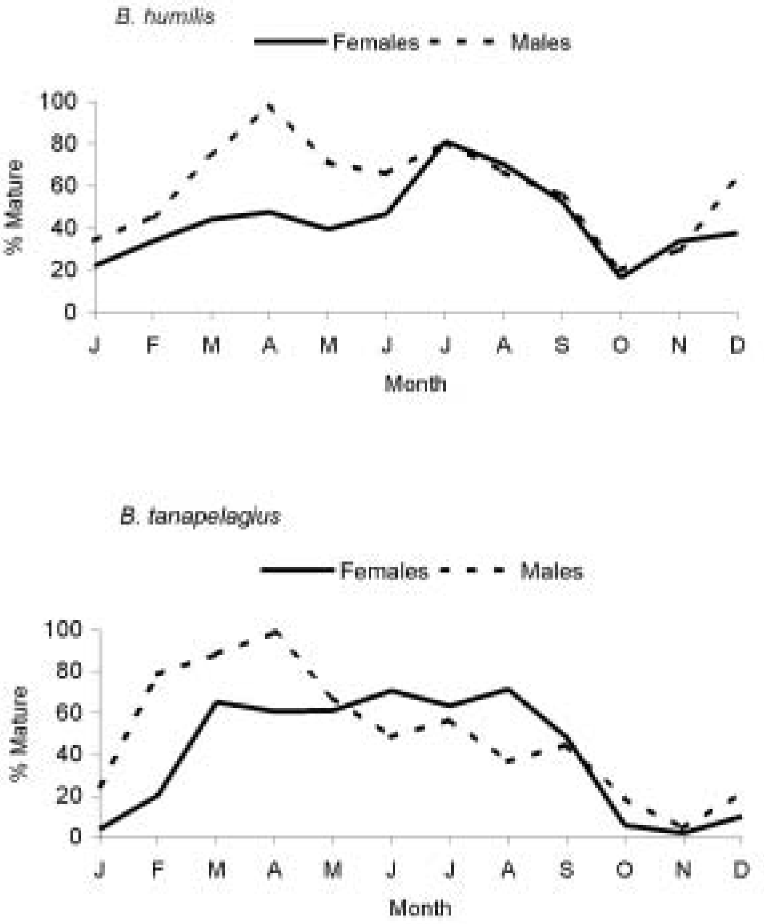

Figure 6.3: Monthly percentage of mature females (solid line) and mature males (dashed line) caught at habitats a-d during January-December 2000. a) *B. humilis* ($N = 6188$) and b) *B. tanapelagius* ($N = 3970$). Note that males have one clear peak during February-May.

than for *B. tanapelagius*. To rule out the size effect, relative fecundity (number of eggs per gram fresh body mass) was calculated (Table 6.2). For *B. humilis* (from turbid stations a-d) relative fecundity increased in a size series 55-65-75 mm FL from 279-275-339 eggs per gram. For the same size series of *B. tanapelagius* relative fecundity decreased 232-226-184 eggs per gram. Relative fecundity of the two species is statistically different (Mann-Whitney U test $p < 0.017$). The relative fecundity

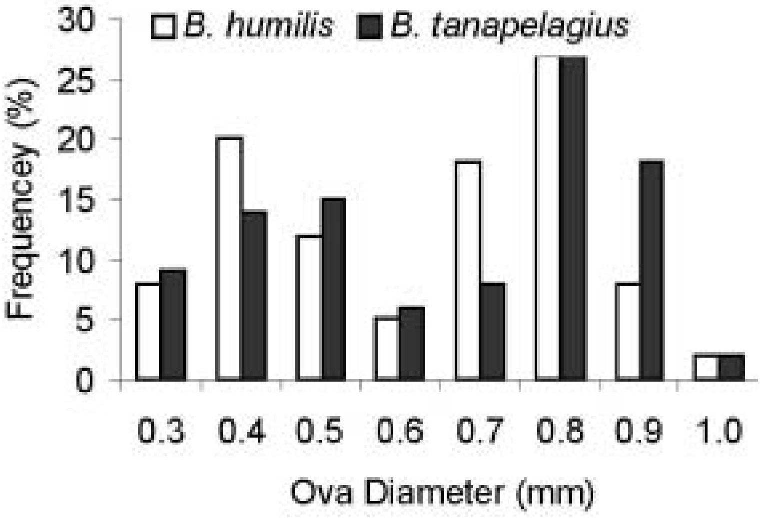

Figure 6.4: Egg-diameter distribution for *B. humilis* from turbid stations (open bar, $N = 30$, 3255 eggs) and for *B. tanapelagius* (black bar, $N = 30$, 3172 eggs) over their 6 months spawning season. Note the two modes for each species.

of *B. humilis* from the clear shallow rocky vegetated habitat (station e), which had a high prevalence of tapeworms, was 189-172-200, significantly lower than the value observed for that species in the more turbid habitats (a-d) (Mann-Whitney U test $p < 0.001$) and more comparable to *B. tanapelagius*.

Table 6.2: Relative fecundity (number of eggs per gram fresh body mass) in relation to fork length (FL) of small lacustrine cyprinids and clupeids in other African lakes.

Species	FL(mm)			Locality	Reference
	50-59	60-69	70-79		
B. pleurogramma	221	200		L. Tana	Dejen, unpublished
B. tanapelagius	232	226	184	L. Tana	This study
B. humilis (habitats: a-d)	279	275	339	L. Tana	This study
B. humilis (clear habitat: e)	189	172	200	L. Tana	This study
B. anoplus		975		L. le Roux	Cambray and Bruton (1984)
Limnothrissa miodon	1532	1481	1322	L. Kariba	Marshall (1993)
Rastrineobola argentea	583	550		L. Victoria	Wanink (1991)

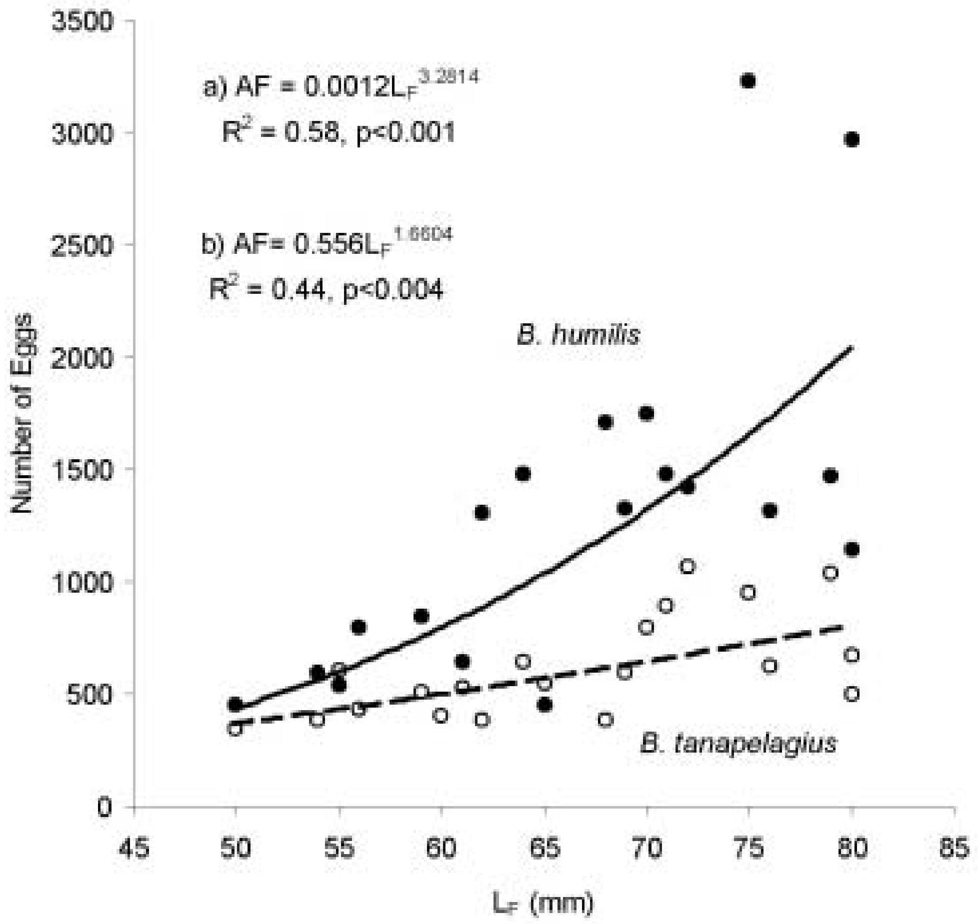

Figure 6.5: Absolute fecundity (*AF*) of a) *B. humilis* from turbid stations (black circles and lines) and b) *B. tanapelagius* (open circles and dashed line) as a function of fork length (*FL*).

6.3.10 Mean size at maturity

Mean size at first maturity (L_{50}) of *B. humilis* (habitats a-d) was 64.5 mm (females) and 48.5 mm (males), and for *B. tanapelagius* 58.5 mm (females) and 50.1 mm (males) (Fig. 6.6, Table 6.3). Mean size at maturity was significantly different between the species only for females, since the confidence interval of males overlapped at L_{50} (Fig. 6.6). Mean size at maturity of female *B. humilis* from the clear habitat with rocks and vegetation (high tapeworm prevalence) was significantly lower (48.3 mm) than the value (64.5 mm) found for the turbid habitats (low tapeworm prevalence) (Table 6.3).

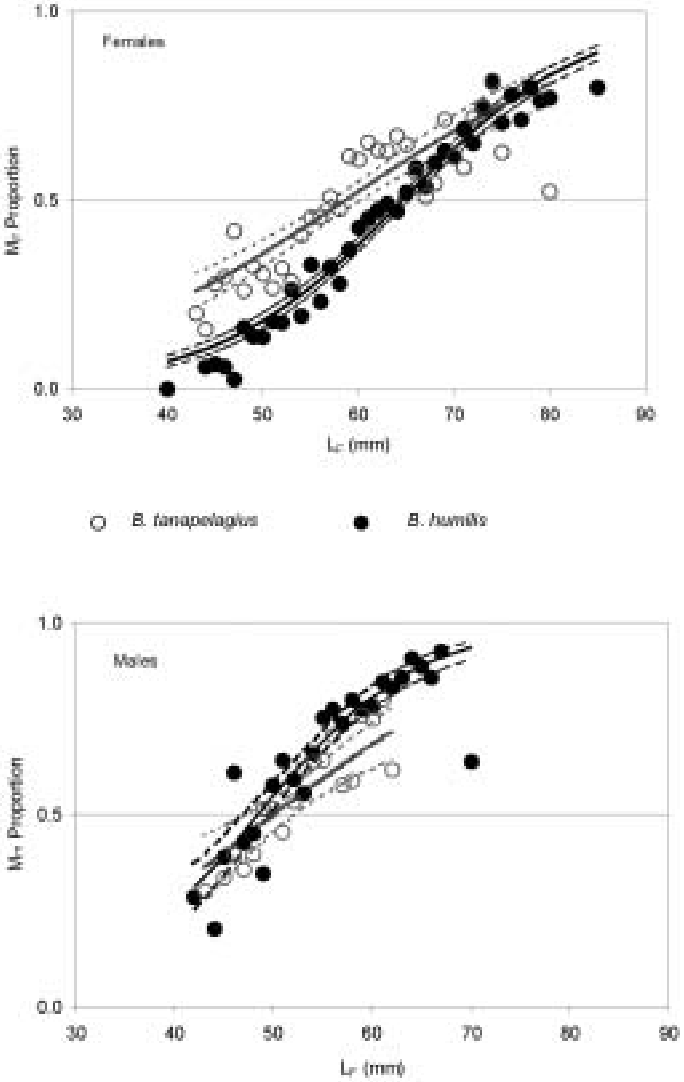

Figure 6.6: Percentage of mature individuals per size class of *B. humilis* (black circles) and *B. tanapelagius* (open circles) from gillnet and trawl catches from a-d habitats: a) females (M_F proportions) and b) males (M_M proportions). Note that solid lines indicate predicted mature proportions and broken lines the upper and lower limit confidence intervals.

6.4 Discussion

6.4.1 Timing of spawning

Reproduction of tropical freshwater fish species seems to be triggered mainly by rainfall patterns and water level variations (Lowe-McConnell, 1975; Payne, 1986; Wootton, 1990). In Lake Tana the breeding periods of *Clarias gariepinus* (1.5 months,

Table 6.3: Mean length at first maturity (L_{50}, estimated according to Ni and Sandeman (1984)) for *B. humilis* and *B. tanapelagius*. Number of specimens (N), parameters values for a and b from logistic regression, mean length at maturity (L_{50} in mm, $-a/b$) and 95 % confidence limits of L_{50}.

Species/ecotype	Sex	N	a	b	L_{50}	95% limits	
						Lower	Upper
B. humilis - turbid habitat	Female	4830	-6.707	0.104	64.53	63.83	65.26
	Male	1360	-6.026	0.124	48.51	47.10	49.66
B. humilis - clear habitat	Female	2329	-3.460	0.072	48.29	40.13	52.23
B. tanapelagius	Female	2877	-3.950	0.067	58.52	56.85	60.26
	Male	983	-3.920	0.078	50.14	46.29	52.51

June-July), *Oreochromis niloticus* (3 months, June-September), and ‘large *Barbus*’ species (4 months, half June-half October) follow this general pattern. They coincide with heavy rainfall and increase of water level (Nagelkerke and Sibbing, 1996; Wudneh, 1998).

Seasonality in breeding of *B. humilis* and *B. tanapelagius* was conspicuous, from March to September. Gonad development and increase in maturity seem to be triggered by the sharp increase in water temperature in February (dry season). The end of the spawning season appeared after the big rains and maximal lake level in September (compare Figs. 6.1, 6.3). Therefore, the sharp increase of water temperature may start the reproductive cycle, and sharply declining rainfall (or its effects on inflow and turbidity) may trigger its end. Vlaming (1972) suggested that the length of photoperiod would regulate the reproductive cycle of cyprinids. At Lake Tana, however, light period in summer is only one hour longer than in winter, rendering such trigger less probable.

The reproductive strategy of a species should aim at a high survival of offspring. Apart from developing anatomical and physiological adaptations, this can be achieved by utilising periods and areas of high food density and by minimising predation pressure on the larvae. The protracted duration of the reproductive period (6 months) in both *B. humilis* and *B. tanapelagius* is typical of many small barbs in Africa (Cambray and Bruton, 1984). Both species start breeding in March, utilising the abundance of zooplankton, which is peaking in the dry season. Their larvae and juveniles are expected to grow in the shallow inshore nurseries, often sheltered by vegetation. From July to November, the ‘large’ piscivorous barbs migrate to affluent rivers for spawning (Nagelkerke and Sibbing, 1996), which will minimise predation risk for the juvenile 'small barbs'. Therefore, the timing of the breeding cycle between March and September by the two small barb species in Lake Tana may well be an adaptation to first optimise growth and then minimise predation pressure, giving a high initial survival of their offspring.

6.4.2 Frequency of spawning

Small *Barbus* species of Africa can be grouped into one-time spawners and multiple spawners. The one-time spawners, *e.g. B. ablabes* (Ivory Coast, Daget & Iltis, 1965 cited by Cambray and Bruton (1984)) and *B. liberiensis* (streams of Sierra Leone and Liberia, Payne (1975)), usually reproduce early in the rainy season. Examples of multiple spawners are *B. apleurogramma* (Lake Victoria, Payne (1969)), *B. macrops* (Lake Volta, Reynolds (1973)), *B. paludinosus* (Lake Chilwa, Furse (1979)) and *B. anoplus* (Lake le Roux, Cambray and Bruton (1984)).

B. humilis and *B. tanapelagius* in Lake Tana spawn at least twice a year. Their two distinct modes in ova size-frequency distribution (Fig. 6.4) and their long period of maturity even suggest multiple spawning. Many species with extended spawning season are multiple spawners with individual females producing several clutches of eggs (King *et al.*, 1998). In small, fast growing fish this is a strategy for utilising favourable conditions at the maximum, for reducing intraspecific food competition among fish larvae and for spreading the mortality risk in year class formation. Multiple spawning will provide more adaptability to cope with high environmental variability.

6.4.3 Fecundity, egg size and maturity

Little is known about the fecundity of pelagic species in African lakes (Marshall, 1995). Absolute fecundity is positively correlated with fish size, which appears true for both Lake Tana small barb species (Fig. 6.5). However, both absolute and relative fecundity of *B. humilis* was much higher than of *B. tanapelagius* (Fig. 6.5, Table 6.2), whereas egg size was very similar (Fig. 6.4). The higher fecundity of *B. humilis* might be attributed to the better food conditions in the littoral zone as compared with the pelagic zone in combination which the wide food spectrum of *B. humilis* (adult insects, insect larvae, zooplankton). In contrast, the pelagic *Barbus tanapelagius* is an obligate zooplanktivore with a much narrower food spectrum (de Graaf *et al.* (2000a); Dejen, unpublished results), competing for the relatively low densities of zooplankton with *Barbus brevicephalus*, *Clarias gariepinus* and *Chaoborus* (Wudneh, 1998).

As to relative fecundity, *Barbus tanapelagius*, like *Limnothrissa miodon*, *B. pleurogramma* and *Rastrineobola argentea*, show higher relative fecundity in smaller adults, the reverse of *B. humilis* (Table 6.2). This might be a strategy for maintaining reproduction in spite of intense predation on the large adults. In Lake Turkana, Kolding (1993) reported a decrease in maturation size of *Oreochromis niloticus* caused by increased predation pressure. Similarly, in Lake Victoria the mean adult size of the pelagic fish *Rastrineobola argentea* decreased by 20-30 % following predation pressure by the Nile perch (*Lates niloticus*) (Wanink, 1991). In Lake Tana, especially the large pelagic piscivorous barbs impose a high predation on *B. tanapelagius* (de Graaf, unpublished results). Also birds are predators, as is suggested by *B. tanapelagius*' high infection rate with cestode larvae (*Ligula intestinalis*), to be caught again by piscivorous birds for completing the tapeworm's lifecycle. *Barbus tanapelagius* is the only small prey species at the offshore surface with high chance for encountering predators, either fish or bird. The different strategy of *B. humilis* is possibly related to its more sheltered littoral habitat where it is less vulnerable for predation by piscivores.

Size at maturity appears also decreased by tapeworm infection. *Barbus tanapelagius* is highly infected with tapeworm larvae, ingested with the zooplankton: > 10 % of all observed specimens, compared to 3 % of *B. humilis* from turbid habitats. The tapeworm plerocercoid larvae were mainly found in the large size group of fish and infected specimens never have mature gonads. The effect of tapeworm infection on maturity is best demonstrated by the two habitat groups of *B. humilis.* Specimens from the clear station with rocks and vegetation have a high infection rate (10 %), lower relative fecundity, and mature much earlier (Table 6.3) than their conspecifics at shallow turbid stations with low infection rate (3 %).

Relative fecundity in small barb species from Lake Tana, including *Barbus pleurogramma*, are low (172-339 eggs per gram) in comparison with the cyprinids *Rastrineobola argentea* from Lake Victoria ($>$ 550 eggs per gram), *Barbus anoplus* from Lake le Roux (South Africa; 975 eggs per gram) and the clupeid *Limnothrissa miodon* from Lake Kariba ($>$ 1322 eggs per gram; Table 6.2). These differences will not just be caused by low primary productivity in Lake Tana (3.7 μg l^{-1} chlorophyll a, Rzóska (1976); Wood and Talling (1988)) as compared to Lake Victoria (8.4-24.5 μg l^{-1}, Mugidde (1992)), Lake Kariba (2-11 μg l^{-1}; Cronberg (1997)) and lake le Roux (1-4 μg l^{-1}; Hart (1999)).

Therefore, it might be concluded that the main cause for differences in reproductive characters among the small barb species in Lake Tana is the level of infection with tapeworm, whereas predation pressure and food density are possible co-factors.

6.4.4 Biased sex ratio

Sex ratio (proportion of females compared to males) is dominated by females in both small barb species, especially in the larger size classes (62-82 mm FL, Fig. 6.2). Sex-reversal has never been reported for cyprinid fish (Devlin and Nagahama, 2002) and therefore is not a likely explanation. Most probably females grow faster than males (Fig. 6.2). Besides, the size class 50-67 mm FL is significantly more vulnerable to predation by large barbs than size class 67-82 mm (de Graaf, personal communication). This means that the mortality of males generally will be higher than in females, which will result in the observed female biased sex ratio progressively increasing with fish size. Size-dependent sex ratio was also reported for *Limnothrissa miodon* (Marshall, 1993) and *Rastrineobola argentea* (Wanink, 1998) as well as for marine clupeids (Millan, 1999).

6.4.5 Adaptation to lacustrine conditions

Big rains during July-September mark the breeding season for river-spawning 'large barb' species in Lake Tana (Nagelkerke and Sibbing, 1996). We expect that the riverine *B. humilis* follow the general *Barbus* pattern and spawn in shallow riverine backwaters during the rainy season. Extending lacustrine spawning in Lake Tana back in time, to the dry period with high zooplankton production, may well be an adaptive strategy of *B. humilis* developed after invasion of Lake Tana. It still is a benthic-littoral species, probably feeding on the same type of food organisms as his riverine conspecifics.

Barbus tanapelagius is an endemic species of Lake Tana that was never observed in the rivers and predominantly occupies the large open water area of the lake. The probably lake-born *B. tanapelagius* start prolonged multiple spawning already in March and seems, as an obligate zooplanktivore, fully adapted to lacustrine conditions.

It is unknown if *B. tanapelagius* evolved from the riverine *B. humilis* at all. Molecular analyses to investigate their phylogeny are underway. If the age of Lake Tana is 10.000 years (Chorowicz *et al.*, 1998), it is a relatively young lake. Since it has been isolated from other systems by 40 m high waterfalls since its origin, it is unlikely that

B. tanapelagius evolved somewhere else and migrated later to Lake Tana. Therefore, this species probably evolved not later than *ca.* 10.000 years ago.

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Chapter 7

Dynamics of cestode infection and its effects on small pelagic barbs (*Barbus humilis* and *B. tanapelagius*) in Lake Tana, Ethiopia

Environmental factors causing fluctuations in prevalence of plerocercoid larvae of tapeworm, *Ligula intestinalis*, and the effect of this parasite on its intermediate host, small cyprinid fish species (< 10 cm fork length (FL)), were investigated in Lake Tana (Ethiopia) from January to December 2000. Infection rate, averaged over all habitats, was significantly higher in *B. tanapelagius* (10 %) than in *B. humilis* (6 %), increasing up to respectively 90 % and 55 % for their largest size class (81-90 mm FL). The high infection rate in *B. tanapelagius* is explained by its specialized zooplanktivory, ingesting more copepods infected with tapeworm than *B. humilis*, a polyphagous bentho-pelagic species. Below a threshold of 48 mm FL the infection rate was zero in both species, probably due to poor preying capacity of such small fish on evasive copepods. The benthic *B. pleurogramma* and *Garra* species were not infected at all. For *B. humilis* two stocks are identified by a significant difference in infection by *L. intestinalis*: a stock from turbid areas without vegetation (low prevalence, 3 %) and a stock from clear shallow areas (prevalence 10 %), most probably due to higher activity of birds (the final host preying small fish and dropping tapeworm eggs) in clear shallow areas. For *B. tanapelagius* the prevalence of *L. intestinalis* was higher in shallow and intermediate depths (< 6 m, 13 %) than in deep offshore areas (7 %). This appears to depend significantly on the low density of cyclopoid copepods and birds offshore. High temperature may regulate seasonal infection patterns in *B. humilis*, possibly by activating their immune response. In all infected species *L. intestinalis* caused retardation in gonad development, early size at maturity and lower absolute fecundity, thus affecting their life history strategies. In this study it is demonstrated that parasitism can also cause the same changes in life-history traits as fishing pressure induce of commercially

exploited stocks.

7.1 Introduction

Most fish face a wide range of different enemies including competitors, predators and parasites. Parasites may induce shifts in species densities, size composition and affect commercially interesting stocks. Parasites can alter the size-specific schedules of reproduction and the mortality of their hosts. This may depend on vulnerability of species, habitats and seasonal factors.

Lake Tana is an oligo-mesotrophic shallow (< 14 m deep) lake in the Northwest highlands of Ethiopia (elevation 1830 m). With a surface area of 3200 km^2 Lake Tana accounts for half of the total freshwater area of the country. The Cyprinidae family (22 species) dominates the Lake's fish fauna, two other families (Cichlidae and Clariidae) are represented by a single species. Three species of small barbs (< 10 cm fork length (FL)) have been reported for Lake Tana: *B. tanapelagius* (de Graaf *et al.*, 2000a), *B. humilis* (includes the recently synonymised *B. trispilopleura* ecotype, Dejen *et al.* (2002)) and *B. pleurogramma* (Boulenger, 1902).

Barbus tanapelagius and *B. humilis* constitute the main link in the food chain between the primary consumers (zooplankton) and the top predators, the large piscivorous barbs (Nagelkerke and Sibbing, 2000; de Graaf *et al.*, 2000a,b). Despite their ecological importance, little is known of their distribution, standing biomass and biology. A high prevalence of tapeworm infection (*Ligula intestinalis*) in the two small barbs, which are a possible target for developing fisheries, made us prioritize this study of parasite-fish interactions.

Ligulids are important cestode parasites of cyprinid fish in lakes and reservoirs throughout the world (Kennedy, 1974; Dick and Choudhury, 1995; Bush *et al.*, 2001; Loot *et al.*, 2002). In Africa, infection by cestode larvae has been reported from fish of the Nile in Egypt and the Sudan and from the East African lakes (Paperna, 1980; Okedi, 1981; Ogwai, 1998). Quantitative data available from the Sudan Nile show infection prevalence ranging from 7-10 % in *Synodontis* spp. and 13-70 % in various siluroid fish and *Polypterus* spp. (Paperna, 1980).

Ligulids have a complex life cycle involving copepods as the first intermediate host, fish as the second intermediate host and piscivorous birds as the final host. Parasite eggs are deposited via bird faeces into water where hatching eggs release free-swimming coracidium larvae. The ciliated coracidium larva will survive 1-2 days in the water and its movement attracts predation by copepods. Development in the copepod produces a procercoid larva, which is infectious to fish, the second intermediate host, after eating the copepod. Within the fish, a large plerocercoid larva develops, which usually remains free within the body cavity of the fish host and grows, swelling the belly of its host and increasing its vulnerability to bird predation.

Plerocercoids may occupy the body cavity of fish for several years (Sweeting, 1976). Specifically, trophically transmitted parasites increase the vulnerability of the intermediate host to predation by the definitive hosts (Holmes and Bethel, 1972). Parasites have an impact on the ecology of host populations (Kennedy, 1974; Sweeting, 1976; Holmes and Bethel, 1972). *Ligula plerocercoids* hamper the gonadal development and causes sterilization of infected fish (van Dobben, 1952; Dick and Choudhury, 1995). According to (Okedi, 1981) the tapeworm seriously affects the stock of the small cyprinid *Rastrineobola argentea* in Lake Victoria by damaging internal viscera and retarding maturation of the ovary. (Wanink, 1998) reported that the mean weight of infected *Rastrineobola argentea* in Lake Victoria falls to 20 % below the value for healthy fish.

The high abundance of *B. tanapelagius* and *B. humilis*, their key role in the food web (de Graaf *et al.*, 2000a; Dejen *et al.*, 2002) and their potential as a target for fishery development in Lake Tana urges closer investigation of these resources. As part of the on-going fish and fisheries biology study, an assessment of the major causes of mortality such as parasitism and predation is required to understand the dynamics and potentials of Lake Tana's ecosystem and its resources. Fish parasites have direct impact on the population dynamics because they influence reproductive potential, predation and competition within and between species. The objective of the present study are: (a) to compare the prevalence of cestode infections in small barbs at different fish size, habitat and season, (b) to analyze the effect of *L. intestinalis* infection on the life-history of the fish, (c) to examine the effects of environmental factors on fish-parasite interactions.

7.2 Materials and methods

A total of 9841 *B. humilis* and 4319 *B. tanapelagius* was collected from January to December 2000 in four different mostly turbid habitats without vegetation (a-d, replicated in 16 sampling stations) and in one habitat with clear water and vegetation (e) (Table 7.1, Dejen *et al.* (2002)). The turbid habitats are characterized as (a) shallow littoral zone (*ca.* 2 m deep) with rocky bottom; (b) shallow littoral zone (*ca.* 2 m deep) with muddy/sandy bottom; (c) sub-littoral zone (*ca.* 6 m deep) and (d) pelagic deep water (*ca.* 10 m deep). Monthly samples (day and night) were obtained using benthic and pelagic multi-mesh monofilament survey gillnets type "NORDEN" (Lundgrens Company, Sweden) composed of 5 different randomly distributed meshsize-panels (5.0, 6.25, 8.0, 10.0 and 12.5 mm bar mesh). In addition a three-meter beam trawl was used during dusk and dawn.

Table 7.1: Sampling stations in the southern bay of Lake Tana: their local name, depth, substrate (m = mud; r = rock; s = sand), area border (fp = flood plain, temporary submerged vegetation; p = papyrus; t = tree; al = agricultural crop land; h = houses; ow = open water) and co-ordinates (each minute 1.8 km). The larger the depth at which a Secchi-disc can still be seen (Secchi-depth), the clearer the water. Secchi-depth range indicates change over seasons. Note that only station 'e' has large amounts of floating vegetation (mainly *Ceratophyllum*) (Dejen *et al.*, 2002).

Station	Local name	Depth (m)	Substrate	Border	Secchi-depth range (cm)	Co-ordinates Latitude	Longitude
a1	Mushe	1.5-3	r	p	40 - 70	11°, 44′	37°, 19′
a2	Gerima	1.5-3	r	p	45 - 80	11°, 37′	37°, 23′
a3	Blue Nile	1.5-3	r	r/t	60 - 75	11°, 37′	37°, 24′
b1	Menkir Dingaye	1.5-3	m	p	35 - 70	11°, 46′	37°, 19′
b2	Yigashu	1.5-3	m/s	fp	30 - 60	11°, 39′	37°, 25′
b3	Bosit	1.5-3	m/s	r/al	25 - 75	11°, 45′	37°, 26′
b4	Mebra	1.5-3	m/s	r/al	35 - 75	11°, 41′	37°, 25′
b5	Guma Tirs	1.5-3	m	fp	30 - 50	11°, 39′	37°, 25′
c1	East of Ambo	4-7	m	ow	45 - 65	11°, 45′	37°, 20′
c2	Airport	4-7	m	ow	45 - 75	11°, 38′	37°, 21′
c3	Boled	4-7	m	ow	30 - 60	11°, 43′	37°, 25′
c4	Debre Mariam	4-5	m/s	ow	40 - 75	11°, 38′	37°, 24′
d1	Mid Gulf	10-14	m/s	ow	50 - 75	11°, 45′	37°, 22′
d2	Mehale Zege	10-13	m	ow	40 - 70	11°, 42′	37°, 23′
d3	Kentefami	8-10	m/s	ow	45 - 65	11°, 39′	37°, 23′
d4	Kibran	8-10	m	ow	40 - 70	11°, 39′	37°, 21′
e	Bahar Dar town	0.5-3	r	p/t/h	70 - 145	11°, 36′	37°, 23′

Two stocks of *B. humilis* were collected from two distinct habitats; a) a stock with mostly three lateral spots from clear inshore shallow areas with rocky substrates and vegetation (station e) and b) a stock most often without spots from other areas with turbid water and no vegetation (stations a-d, Dejen *et al.* (2002)). The analysis was done separately for the two stocks. Fish were visually inspected for the presence of larval cestode infection in the body cavities (Fig. 7.1), and the cestodes were identified according to van Dobben (1952) as *Ligula intestinalis.* Data were analysed with respect to parasitic prevalence (proportion of infected fish). Length and fresh body weight of both fish (FL) and parasites were determined to the nearest mm and 0.1 g. The states of gonad maturity and sex were assigned by viewing the gonads at tenfold magnification through a microscope. Ovaries were staged in I - V maturity scales according to Nikolsky (1963). Stage I and II are immature stages, III-V are considered as mature.

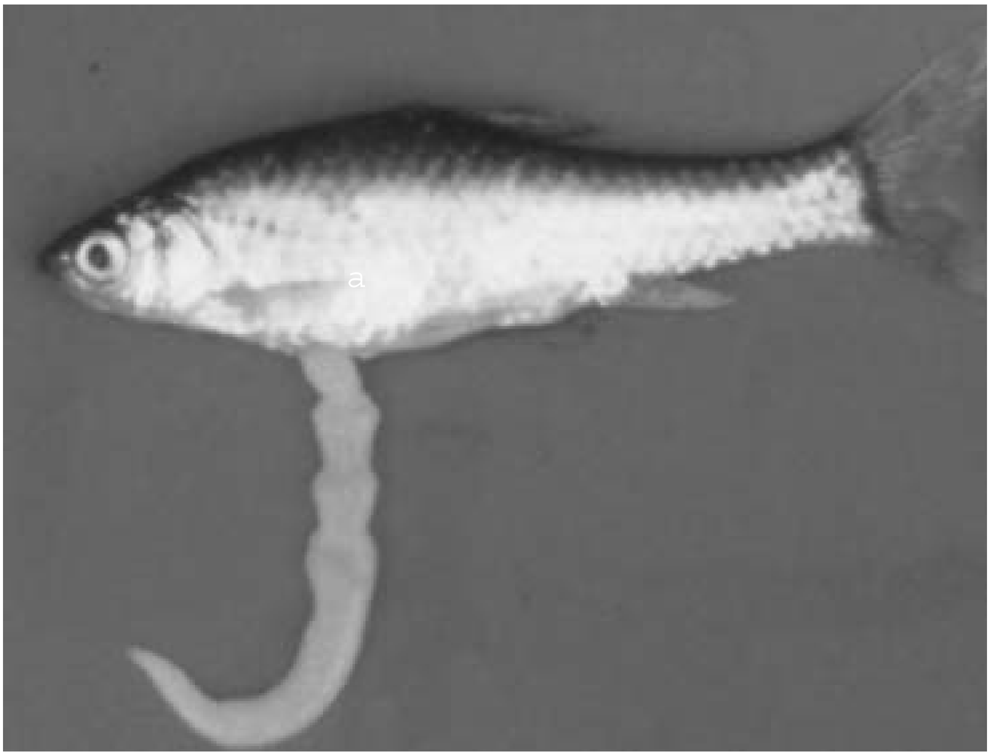

Figure 7.1: Plerocercoid stage of *L. intestinalis* in the body cavity of *B. humilis* (8 cm fork length) from the clear rocky habitat.

For the analysis of temporal distribution of parasite on fish, four seasons (Table 7.2) were identified in Lake Tana (Wudneh, 1998): a) hot dry season (March-May),

b) rainy season (June-August) c) wet, high water level season (September-November) and d) cool, dry season (December-February). Variations in parasite prevalence between fish species, seasons and habitats were statistically tested using non parametric statistics: Spearman's rank order correlation, Mann-Whitney U test and Kruskall-Wallis, and $p < 0.05$ was considered significant. SPSS 9.05 version for Windows software was used for the statistical analysis.

Table 7.2: Mean monthly rainfall (mm), average of daily maximum water temperature (°C) and mean zooplankton density (ind. l^{-1}) over four seasons from January to December 2000.

Season	Period	Mean monthly rainfall (mm)	Mean daily max. temperature (°C)	Mean zooplankton density (ind. l^{-1})
Cool/Dry	Dec-Feb	0	22	125
Hot/Dry	Mar-May	50	25	47
Rainy	Jun-Aug	323	23	37
High water level	Sep-Nov	144	22	32

7.3 Results

7.3.1 Environmental conditions

The daily maximum water temperature ranged between 21 and 26 °C and monthly rainfall between 0-517 mm for 2000 (Bahir Dar Meteorological Station). The main rainy season is from June to October, peaking in August. Average zooplankton densities (individuals per liter, ind. l^{-1}) over all stations showed a distinct seasonal variation. The highest densities were observed in the cool start of the dry season and lowest densities at highest water levels following the rainy season (Table 7.2. There was also a clear horizontal pattern in the average zooplankton distribution. On average over all seasons the zooplankton densities were highest in the sublittoral zone (mean 81 ind. l^{-1}), intermediate in the pelagic zone (mean 53 ind. l^{-1}) and lowest in the littoral zone (mean 38 ind. l^{-1}) (Dejen *et al.*, 2003b).

7.3.2 Cestode infection among 'small' cyprinids

Cestode larvae were absent in the three *Garra* species ($n = 420$) and in the small barb *B. pleurogramma* ($n = 389$). Between *B. humilis* and *B. tanapelagius* the infection rate was significantly different (Mann-Whitney U test $p < 0.05$): lower for *B. humilis* (6 %, $n = 9841$) compared with *B. tanapelagius* (10 %, $n = 4319$) (Table 7.2, Fig. 7.3).

Barbus humilis and *B. tanapelagius* below 48 mm fork length (FL) were not found infected with tapeworm. Above this threshold value, a highly significant positive correlation between FL and infection rate appeared for both fish species (Fig. 7.2) (Spearman Rank correlation for both species $p < 0.01$). Only one tapeworm was present in every infected fish. The average length and weight of the tapeworm was 60 mm and 0.55 g.

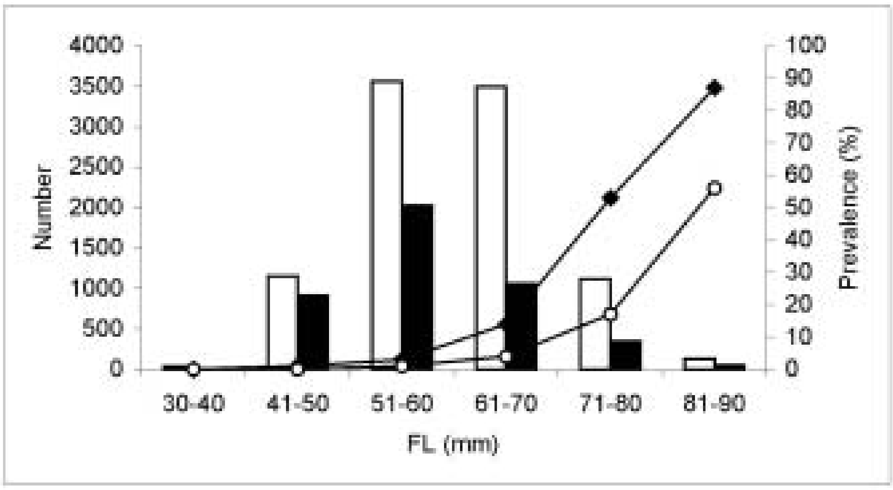

Figure 7.2: Prevalence of *L. intestinalis* (line) in relation to fork length of *B. tanapelagius* (dark diamonds, dark bars) and *B. humilis* (open circles, open bars). Bars show the number of specimens investigated.

7.3.3 Infection prevalence across habitats and season

Barbus humilis caught at the rocky clear water station 'e' showed conspicuously higher cestode infection prevalence (10 %) than the same species caught at turbid stations (0-3 %). For *B. tanapelagius* the infection prevalence reached its peak in the sublittoral (13 %) (Table 7.3). For each species, the infection prevalence rate across habitats was statistically significant (Kruskall-Wallis, $p < 0.05$).

For *B. humilis*, the samples collected from August through March revealed higher infection prevalence (5-11 %), than those collected from April to July (2-3 %). In the case of *B. tanapelagius*, higher infection prevalence was recorded from December to May (12-17 %) than from June to November (3-9 %) (Fig. 7.3). Statistical analysis of these results revealed that the variations in prevalence of *L. intestinalis* across months were significant for *B. tanapelagius* and *B. humilis* (Kruskall-Wallis, $p < 0.05$, $n = 12$).

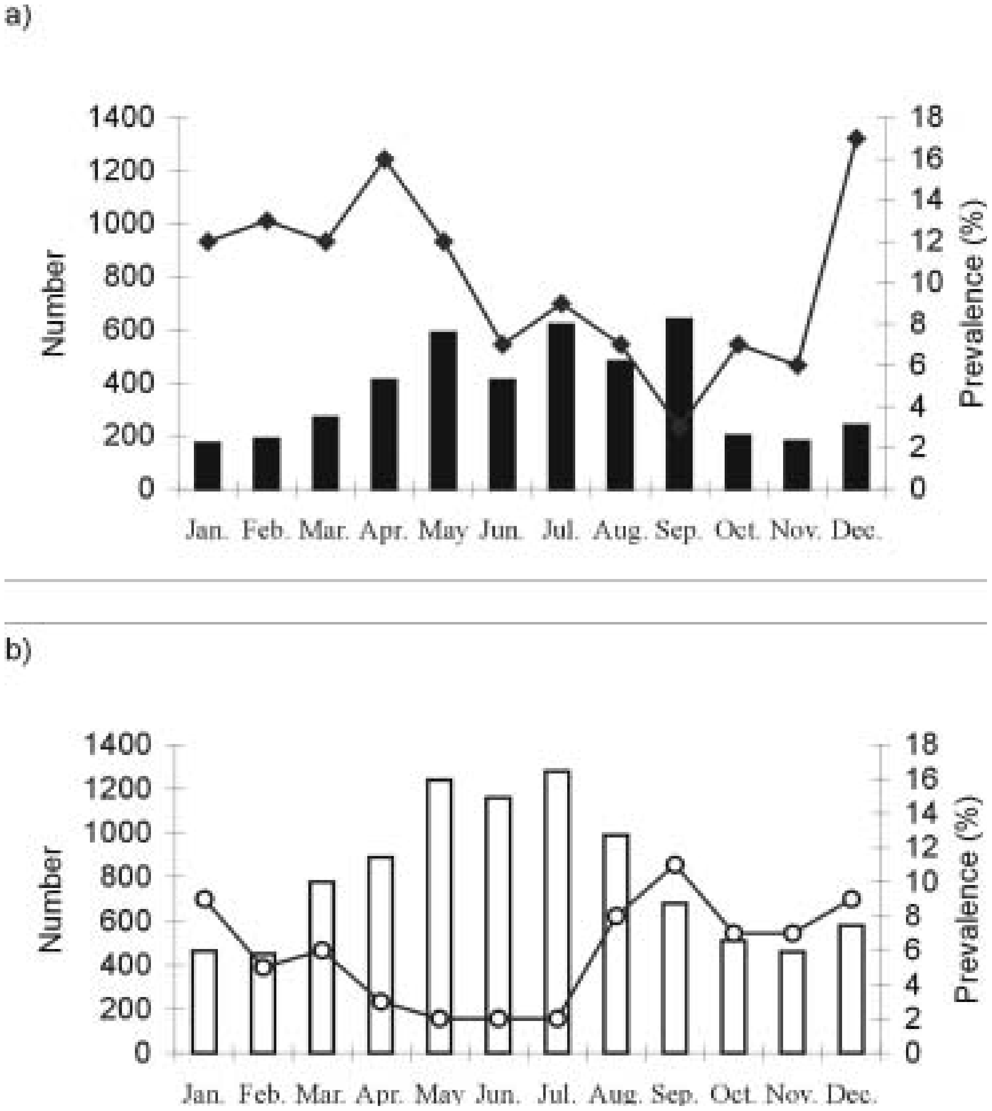

Figure 7.3: Monthly number of fish observations (bar) and prevalence of *L. intestinalis* (line) on a) *B. tanapelagius* and b) *B. humilis* from January to December 2000.

Only for *B. tanapelagius* was a decrease in infection prevalence apparently associated with a corresponding increase in the amount of rainfall (Spearman Rank Correlation, correlation coefficient =-0.61, $n = 12$, $p < 0.05$). A positive correlation between parasite prevalence and densities of zooplankton (Fig. 7.4) appeared only for *B. tanapelagius* ($R^2 = 0.26$, $n = 8$). A significant negative correlation ($R^2 = 0.37$, $p < 0.05$, $n = 11$) between water temperature and parasite prevalence was found only for *B. humilis* (Fig. 7.5).

Table 7.3: Tapeworm-infection rate (P, %) in *B. humilis* and *B. tanapelagius* across different habitats (depth between brackets), from surface and bottom. Sampling from January-December 2000. Number of fish investigated (N) is indicated for each station.

		B. humilis		*B. tanapelagius*	
Habitat	Station	N	P (%)	N	P (%)
Clear Water					
Littoral (0-3 m)	e	2860	10		
Turbid Water					
Littoral (0-3 m)	a, b	4996	3	120	3
Sublittoral (4-8 m)	c	1985	1	1676	13
Pelagic (8-14 m)	d			2523	7

7.3.4 The effect of parasite on reproductive strategies

Observations show that tapeworm infection caused a dramatic effect on gonad development. All fish infected, even larger specimens had immature gonads. *B. humilis* stock from turbid habitats have higher absolute fecundity than *B. humilis* stock from clear habitats (Table 7.4). Moreover in the same turbid habitats the absolute fecundity of *B. tanapelagius* is lower than *B. humilis*. At turbid habitats mean size at maturity (L_{50}, FL) of *B. humilis* was 64.5 mm, compared to 48.3 mm of *B. humilis* from clear habitat. Mean size at maturity of female *B. tanapelagius* was 58.5 mm. The sex ratio was skewed towards high proportion of females for both species. However, *B. humilis* from clear habitat has more females (87 %) than from turbid habitats (78 %) (Table 7.4).

Table 7.4: Absolute fecundity (average number of eggs per individual for length class 51-80 mm FL (mean ± standard error), length at 50 % maturity (L_{50}) of females and sex ratio of the *B. humilis* from turbid and clear habitats and *B. tanapelagius* in Lake Tana. Sample size is indicated in parenthesis (n).

Species/stock	Number of eggs	L_{50}(mm) females	Sex ratio Females:Males
B. humilis (turbid)	693 ±39 (162)	64.5 (4830)	0.78:0.22 (6971)
B. humilis (clear)	558 ± 24 (133)	48.3 (2329)	0.87:0.13 (2860)
B. tanapelagius	545 ± 19 (124)	58.5 (2877)	0.74:0.26 (4319)

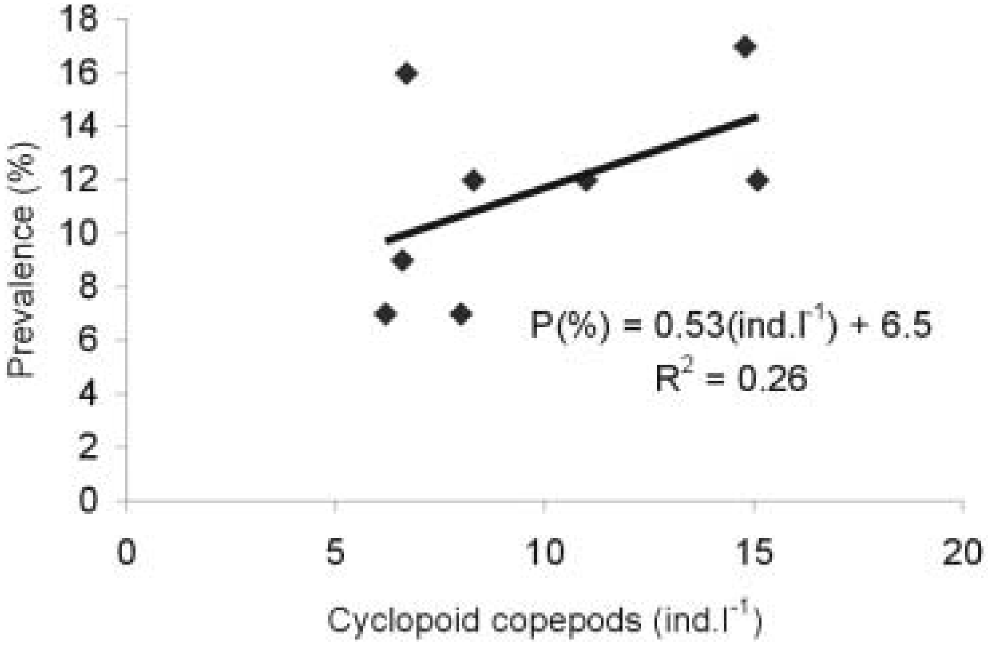

Figure 7.4: Correlation between monthly density of cyclopoid copepods (ind. l^{-1}) and monthly prevalence P (%) of *L. intestinalis* in *B. tanapelagius* in Southern Gulf of Lake Tana ($n = 8$)

7.4 Discussion

7.4.1 Fish species and size class sensitivity

An important aspect of species susceptibility to parasites are the changes in demographic characteristics of populations that parasitism might induce. High adult mortality appears to lead to short-term plastic changes in age and size at maturity of the victim population (Rochet, 1998).

Ligula intestinalis was found in the two small barbs *B. humilis* and *B. tanapelagius*, but not in *B. pleurogramma* and the three *Garra* species. Host resistance and behavior are the most important factors dictating variation in intensity of infection and parasite loads (Tanguay and Scott, 1992; Quinnell *et al.*, 1995). Of the four examined fish species during the present study, only *B. tanapelagius* and *B. humilis* were found to feed on zooplankton. Among the zooplankters, mainly cyclopoid copepods, are intermediate hosts for *L. intestinalis.* The higher infection prevalence in *B. tanapelagius* may be explained by being a specialized zooplanktivore, hence encountering and ingesting tapeworm more frequently than *B. humilis*, a polyphagous bentho-pelagic species. Host specificity of *L. intestinalis* among the examined fish species of Lake Tana appears largely attributable to the difference in food type. Infection rate for the 81 - 90 mm size classes was 55 % in *B. humilis* and 90 % in *B. tanapelagius* (Fig. 7.2). The overall prevalence and parasite weight increased with fork length of fish ($>$ 48 mm). The 48 mm FL infection threshold may be due to a low ability of small fish in catching (in their scale) large and evasive copepods with parasites. In other fish species, also nematode infections increase with age and length of the fish (Wotten and Waddell, 1977; Ismen and Bingel, 1999).

7.4.2 Habitat variability

Feeding segregation often very much depends on spatial segregation and by consequences the infection rate for cestode larvae. The two small barbs show a clear segregation in spatial distribution pattern. *Barbus tanapelagius* is restricted to the surface layers of deep offshore waters, whereas *B. humilis* prefers the shallow inshore lake habitats and the benthic areas of some deep water (de Graaf *et al.*, 2000a; Dejen *et al.*, 2002). *Barbus humilis* is a generalist feeder preferably dwelling near the benthos and *B. tanapelagius* feeds on zooplankton in the upper part of the water column (Dejen *et al.*, 2002). This difference in habitat and trophic position provides an opportunity for comparing and understanding species-specific parasite-host interactions.

A third factor required for high infection rates is birds dropping parasite eggs with their faeces. For *B. humilis* the highest parasite prevalence was found in the clear water habitat (station 'e'). This station is near the town of Bahir Dar where fish wastes are dumped attracting many fish-eating birds, which concentrate at this shore to feed on fish discards. These birds can easily detect *B. humilis* in the clear water, and by eating them become the primary hosts for *L. intestinalis*. At the same time birds will infect this and to less extent more offshore areas, by dropping faeces with parasite eggs. Although the zooplankton density is low in the littoral zone, its distribution pattern overlaps with both coracidium larvae and *B. humilis*, rendering a peak infection rate for this species. A higher prevalence of *L. intestinalis* was found in *B. tanapelagius* in the sublittoral areas. This is most likely dependent of both zooplankton density and the abundance of the cestode coracidia developed from eggs dropped in the birds' faeces.

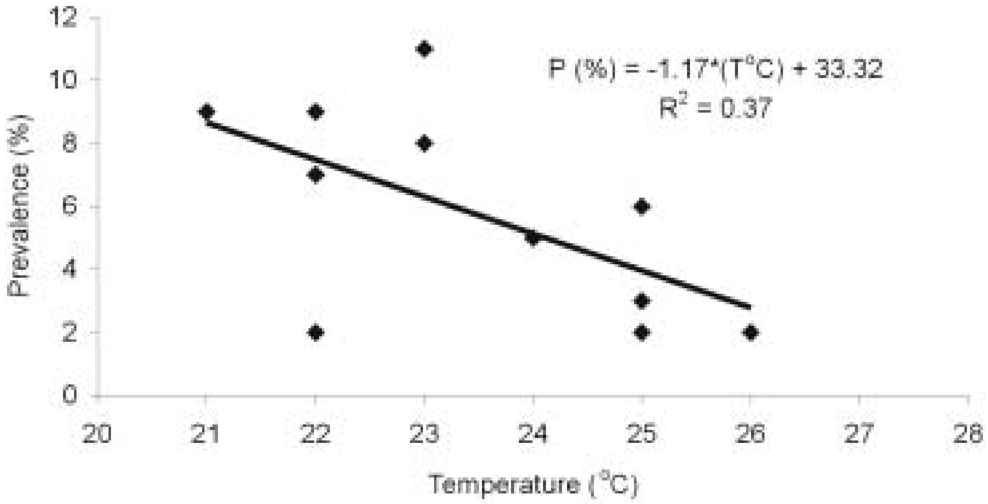

Figure 7.5: Correlation between maximum monthly daily water temperature T (°C) and monthly prevalence P (%) of *L. intestinalis* in *B. humilis* Southern Gulf of Lake Tana ($n = 11$).

7.4.3 Seasonal effects on parasite prevalence

Significant seasonal variation in the *L. intestinalis* infection was observed in both *B. tanapelagius* and *B. humilis* during this study. Season-related host feeding patterns, availability of infected intermediate hosts, immunological and hormonal changes, and temperature are the most frequently suggested causes for seasonal fluctuation in prevalence and abundance of parasitic infections (Kim *et al.*, 2001). In the current study, low prevalence of *L. intestinalis* was found in both *B. humilis* and *B. tanapelagius* during the breeding season. Temperature-dependent host rejection response has been reported in some helminth species (Eure, 1976) and is only significantly correlated for *B. humilis* (Fig. 7.5), prevalence decreases with increasing temperature. The spawning season for *B. humilis* ranges from March to August and one month later for *B. tanapelagius* (Dejen *et al.*, 2003a). This corresponds well with the period of low prevalence of *L. intestinalis* on both species. Therefore spawning related hormonal changes might also influence the seasonality of *L. intestinalis.*

7.4.4 Parasite induced reaction norms on life-history strategies

An important aspect of high adult mortality is the changes in demographic characteristics of populations. Life history traits like size at maturity are expected to be affected by changes in adult mortality rate due to fishing (Rochet, 1998; Chen and Mello, 1999). These changes in life history may influence population dynamics. *Ligula intestinalis* affecting the adult population of the small barbs might cause similar reactions norms on life-history traits of small barbs as exploited fish stocks induced by fishing pressure.

If we look at the effects of the parasite on fish populations, the present study shows that the parasite caused retardation in female gonad development especially at adult population. As a response *B. humilis* from clear habitat (relatively high parasite prevalence, 10 %) has lower length at first reproduction and lower absolute fecundity than *B. humilis* from turbid habitats (Table 7.4, Dejen *et al.* (2003a)). Most probably the high parasite prevalence of adult fish in clear water induced a shift in reproductive strategy towards high reproductive effort starting at small size for *B. humilis* from clear habitat. The highest proportion of females for *B. humilis* stocks from clear habitats might be also a strategy to increase fecundity by having more females in the population. Trade-offs between early maturation and fecundity has been clearly expressed between the two stocks of *B. humilis* exposed to different parasite prevalence. *B. humilis* from clear habitat benefit by maturing earlier that will increase survival to maturity because of shorter period as juvenile. Whereas *B. humilis* from turbid habitats delay maturity that will increase fecundity with size.

The consistently higher prevalence of *L. intestinalis* in *B. humilis* from the shallow clear rocky habitat may suggests that it is a separate stock from the *B. humilis* that dominates in shallow and intermediately deep turbid areas without vegetation. Indeed, Boulenger (1902) considered these two stocks as a separate species. However, recently Dejen *et al.* (2002) found that they are not separate species, but a single biological species with continuous phenotypic plasticity in pigment patterns induced by transparency of water increasing the risk for predation by birds.

In conclusion, this study shows the impact of *L. intestinalis* parasite on small barbs, differentiated over season and space. Apart from increasing the predation risk for parasitised fish, *L. intestinalis* plerocercoids render the intermediate host infertile, reducing reproductive capacity of the breeding stock. In most studies changes in demographic characteristics of population were mainly associated with increasing fishing pressure (*e.g.*, Rochet (1998); Chen and Mello (1999)). However, in this study it is demonstrated that parasitism can also induce changes in life-history traits in the same dimension as fishing pressure. Most parasites with indirect lifecycles (meaning more than one host is required to complete their lifecycles) seems to be able to increase the intermediate hosts susceptibility to predation, there by improving their chances of entering their definitive hosts (Lass and Bittner, 2002). Further detailed studies are needed on the biology of the parasite, the role and activity patterns of birds in the total lifecycle of the parasite. Moreover, the multiple effects of the parasite and the predators on the population dynamics of the host should be investigated.

Acknowledgements

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Chapter 8

Biomass and production of pelagic small barbs (*Barbus humilis* and *B. tanapelagius*) in Lake Tana, Ethiopia: assessing potential for fishery

Growth, mortality and productivity of two small barbs (*Barbus humilis* and *B. tanapelagius*) in the Southern Gulf of Lake Tana were investigated. We used 26 consecutive months length-frequency data together with FiSAT software to study individual growth and mortality. Fitting the von Bertalanffy growth function to the length-frequency data gives the following growth parameters: $L\infty$ and K values of 91 mm and 1.2 year^{-1} for *B. humilis* and 76 mm and 1.65 year^{-1} for *B. tanapelagius*. Total mortality coefficient (Z) was estimated 3.94 and 3.88 year^{-1} for *B. humilis* and *B. tanapelagius* respectively. The total biomass over the whole lake area was 5 kg ha^{-1} (470 tons) for *B. humilis* and 9 kg ha^{-1} (2,000 tons) for *B. tanapelagius*. Annual production of *B. humilis* was 16.8 kg ha^{-1}, whereas for *B. tanapelagius* it was 32.4 kg ha^{-1}. Production to biomass ratio (annual P/B) for *B. humilis* was 3.36 and 3.60 for *B. tanapelagius*. The biomass of small pelagic fish in Lake Tana compared with small pelagics in other African lakes is low. Nevertheless, because of the large pelagic area of the lake (*ca.* 2,205 km^2) we suggest that there is a potential for a subsidiary fishery on *B. tanapelagius* in pelagic zone. The annual maximum sustainable yield of *B. tanapelagius* was 3,850 ton.

8.1 Introduction

The fishery on small pelagics is often commercially important for small-scale or artisanal inland fisheries (see Marshall (1984) for a review). Small-scale fisheries in the tropical region provide almost half of the total annual fish catch, twenty-fold more employment opportunities than the industrial fisheries, and have low-capital intensity (Laggis, 1993). Moreover, artisanal fisheries supply fish and fisheries products cheaply to the final consumer even in remote and isolated localities. In most African lakes and reservoirs small pelagic fish species, which grow rapidly and reproduce prolific, have become object of flourishing and sustainable fisheries (Marshall, 1984). Fishermen use light attraction techniques at night in combination with lift nets in some East African waterbodies (Wanink, 1999). The pelagic fish thus harvested provide cheap high protein food accessible as a supplementary diet to the poorer segments of the market. No records of commercial exploitation of small pelagics exist in Ethiopia.

Lake Tana is the largest freshwater body in Ethiopia (3150 km^2) and source of the Blue Nile river. An endemic flock of 15 large *Barbus* spp. (Cyprinidae), *Oreochromis niloticus* (Cichlidae), *Clarias gariepinus* (Clariidae) and *Varicorhinus beso* (Cyprinidae) are commercially important fish species in Lake Tana. In addition, three 'small barb' species ($<$ 100 mm fork length), *B. humilis*, *B. pleurogramma* and *B. tanapelagius* and some species of the genus *Garra* (Cyprinidae) have been reported in this lake. Serious decline of the stocks of endemic 'large barbs' in Lake Tana (de Graaf *et al.*, 2000b) raises the question if shifting fishery efforts to the 'small barb' (a subsidiary small-meshed fishery). The feasibility of such a fishery largely depends on the annual production of 'small barbs'. Prior to experimental fisheries testing gear and fishing techniques, the biomass and production of the small barbs must be investigated. The most important requirement for the development of a new fishery is the existence of adequate quantities of fish that can be harvested. Population dynamic parameters like recruitment and mortality, and production parameters like individual growth are key inputs to estimate fisheries potential (Sparre and Venema, 1998)

In the present study, we estimated from a two year continued sampling programme, the biomass and production of the two small barbs in Lake Tana and used this information to estimate their potential sustainable yield. The potential for a sustainable fishery on small barbs without a negative impact on the current fisheries of larger fish species is discussed.

8.2 Materials and methods

8.2.1 Study area

Lake Tana is the largest lake in Ethiopia with a surface area of 3150 km^2, a maximum length and width of 78 and 68 km respectively, a maximum depth of 14 m and a mean depth of 8.9 m. The shallow littoral zone (depth 0-4 m) is relatively small, *ca.* 10 % (315 km^2) of the total surface area of the lake. The sublittoral intermediate zone contains no macrophytes and occupies *ca.* 20 % (630 km^2) of the lake area (depth 4-8 m), whereas as the pelagic deep offshore zone is 70 % (2205 km^2) of the lake surface area and relatively deep (depth 8-14 m).

8.2.2 Sampling sites and collection

Fish were sampled from October 1999 to November 2001 in the Southern Gulf of Lake Tana at three different habitats, replicated in 12 sampling stations (Fig. 8.1). It consists of A) shallow littoral zone (average depth 2 m) with muddy/sandy bottom, some stations bordering temporary flood plains with submerged vegetation, others exposed to agricultural crop land and B) a sub-littoral zone, *ca.* 6 m deep, with sandy/muddy bottom and finally C) an open water zone, *ca.* 10 m deep with sandy/muddy bottom.

A bottom trawl was used during dusk and dawn. Trawling speed was 1.0 m s^{-1} and trawl hauls lasted for 15 minutes each. The mouth opening of the trawl (3 m wide and 1 m high) was kept open with a 3 m beam. The bar-mesh in the cod-end was 5 mm. Per fish species total fresh weight and number of catch and fork length to the nearest 1 mm were measured from a sub sample (half of the weight of the catch depending on the size of the catch).

8.2.3 Data analysis

Monthly length-frequency distributions of *B. humilis* and *B. tanapelagius* were collected for 26 consecutive months. Growth parameters and mortality were estimated using the FiSAT II (FAO-ICLARM Stock Assessment Tools) computer package (Gayanilo *et al.*, 2002). Growth was assumed to be described by the von Bertalanffy growth function (VBGF):

$$L_t = L\infty(1 - e^{-k(t-t_0)}),$$

where L_t is length at age t, $L\infty$ is the asymptotic size, K is a growth constant and t_0 is the hypothetical age at length zero.

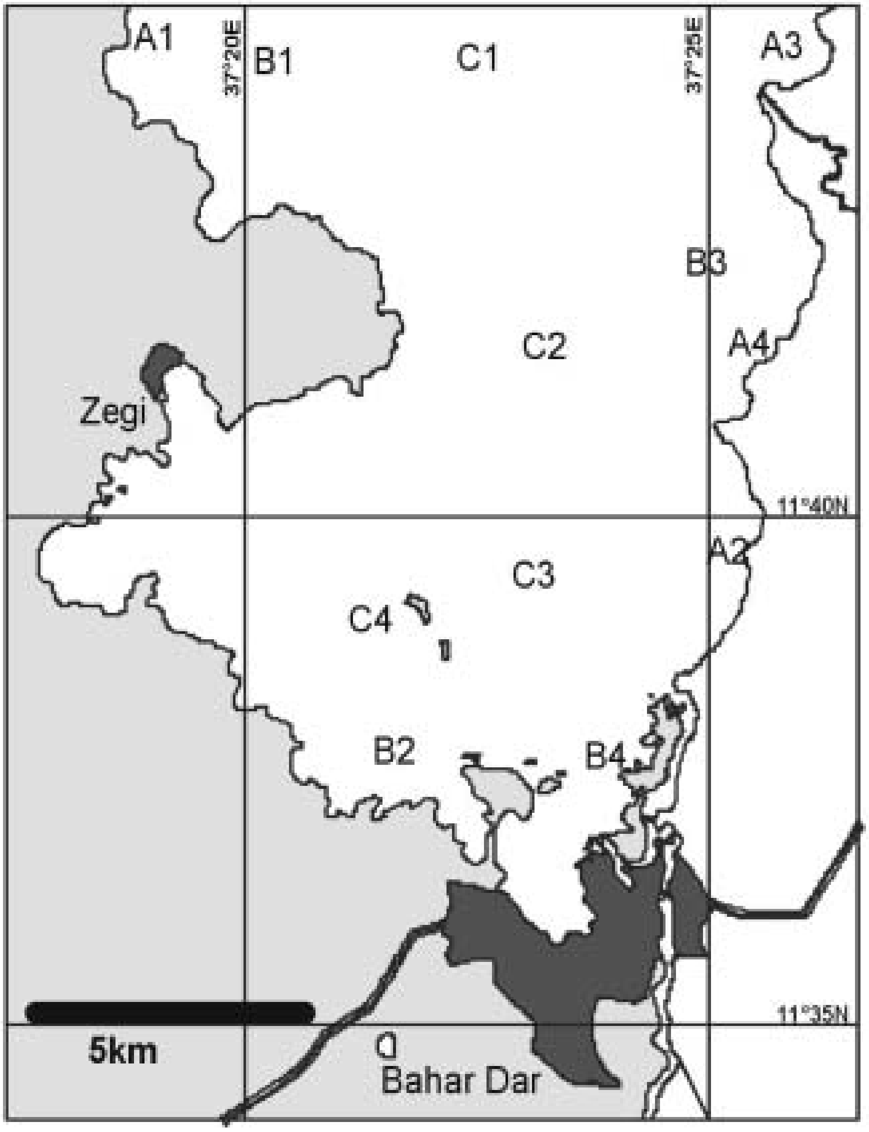

Figure 8.1: Sampling stations. Three macrohabitats: littoral (A1-A4), sublittoral (B1-B4) and pelagic (C1-C4).

Total mortality rate (Z) was estimated from a length-converted catch curve using pooled length-frequency samples, and is defined by the equation (Pauly, 1984):

$$ln(N_i/\Delta t'_i) = a + bt'_i,$$

where N_i is the number of fish caught in a given length class i; t'_i the relative age corresponding to length class i and $\Delta t'$ is the average time needed, on the average by the fish to growth through length class i.

The Pauly and Munro (1984) relationship was used to calculate the index of overall growth performance Φ:

$$\Phi = 2 Log L\infty + Log K$$

and the potential longevity t_{max} was estimated from the relationship (Pauly, 1980):

$$t_{max} = 3/K$$

Additional information on growth rate was measured experimentally from the outdoor basin. For *B. humilis* ($n = 99$, seven length class 18-80 mm FL) we managed to estimate mean length increment from outdoor basin observation (the water directly comes from the lake to the basin without any filtration and we didn't add any food in the basin).

Biomass (B) was estimated by swept area method (Sparre & Venema, 1998) from samples taken with bottom trawl. The swept area, a, is estimated from:

$$a = V^{*}WS$$

where v is velocity of the trawl over the ground when trawling and WS is wing spread (the width of the swept or mouth opening of the trawl). For the estimation of biomass we use the catch per unit area. It is estimated by dividing the catch by the swept area (the area of which the length of the trawl travelled times the width of the trawl).

Barbus humilis is a bottom and littoral species and the bottom trawl we used is appropriate to get realistic biomass estimate. For *B. tanapelagius* the catch from the bottom trawl was very low, because this species is found mainly at the surface of the water column (0-8 m deep) whereas the bottom trawl in sublittoral and pelagic habitats was carried out at 1-2 m above the bottom. Therefore we used the proportion of surface and bottom gillnet catch taken at the same time for two years to correct the underestimated biomass for *B. tanapelagius* from the bottom trawl. We found that surface gillnet catch in weight is 4× the bottom gillnet catch and therefore multiplied the bottom trawl catch by 4.

Production (P) was estimated using the following equation (Huryn & Wallace, 1987).

$$P = G * B$$

where G = annual instantaneous growth rate.

$$G = b * K((L\infty/L_{mi}) - 1)yr^{-1}$$

Where b is the exponent of length-weight relationship, K is a growth constant from the von Bertalanffy growth function, $L\infty$ is asymptotic length (mm) and L_{mi} is mean length in class i.

8.3 Results

8.3.1 Population structure

Both species are small (< 100 mm FL) and the females grow to a larger size than the males. The maximum length recorded was 96 mm and 89 mm fork length (FL) for *B. humilis* and *B. tanapelagius* respectively. Mean length (FL) and standard deviations ($\pm SD$) from length-frequency data was 63.2 ± 8.5 mm (females, $n = 4852$) and 55.6 ± 6.6 mm (males, $n = 1401$) for *B. humilis* specimens and 58.6 ± 7.9 mm (females, $n = 2925$) and 53.3 ± 5.5 mm (males, $n = 1041$) for *B. tanapelagius*.

8.3.2 Growth parameters

The FiSAT program estimated $L\infty$ and K values of 91 mm and 1.2 year^{-1} for *B. humilis* and 76.0 mm and 1.65 year^{-1} for *B. tanapelagius* respectively. Fig. 8.2 and Fig. 8.3 show the length-frequency data with one recruitment peak from September-November for both species. The value of growth index (Φ) were 3.99 and 3.98 for *B. humilis* and *B. tanapelagius* respectively. The longevity of *B. humilis* was 2.5 year and for *B. tanapelagius* was 1.8 year.

The correctness of FiSAT to estimate growth was confirmed by the similar results obtained through the direct measurement of growth in the outdoor basin for *B. humilis*. In this observation *B. humilis* growth coefficient K was 1.44 year^{-1} and $L\infty$ was 85 mm FL (Fig. 8.4)

8.3.3 Estimation of Mortality

Length-frequency data from experimental trawl were used to apply length-converted catch curve analysis for the two small barbs. For these species the estimated total mortality was equal to the natural mortality since the fishery does not exploit them. Total mortality (Z) was 3.94 and 3.88 year^{-1} for *B. humilis* and *B. tanapelagius* respectively (Fig. 8.5).

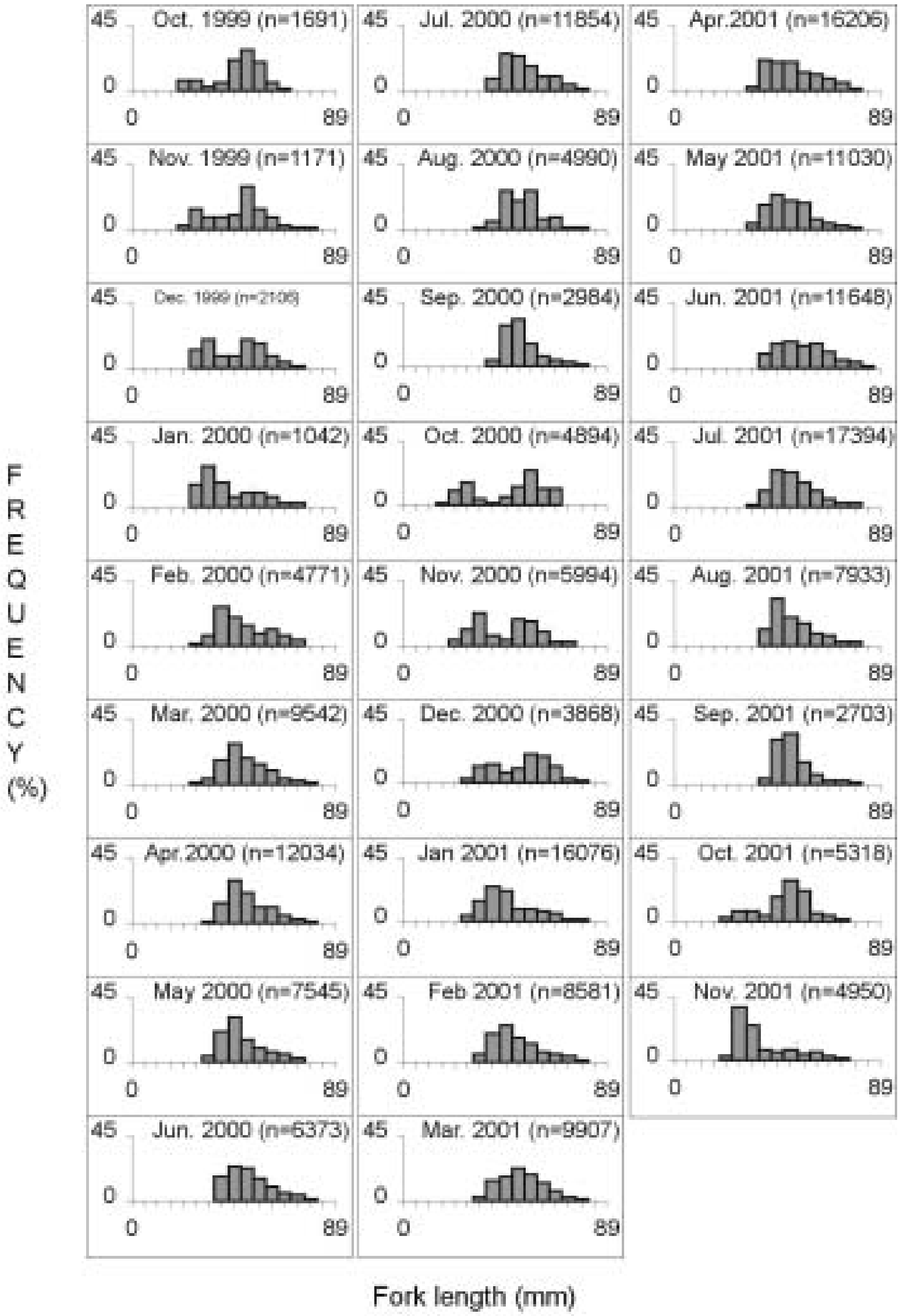

Figure 8.2: Length frequency distribution of *B. humilis* from October 1999-November 2001.

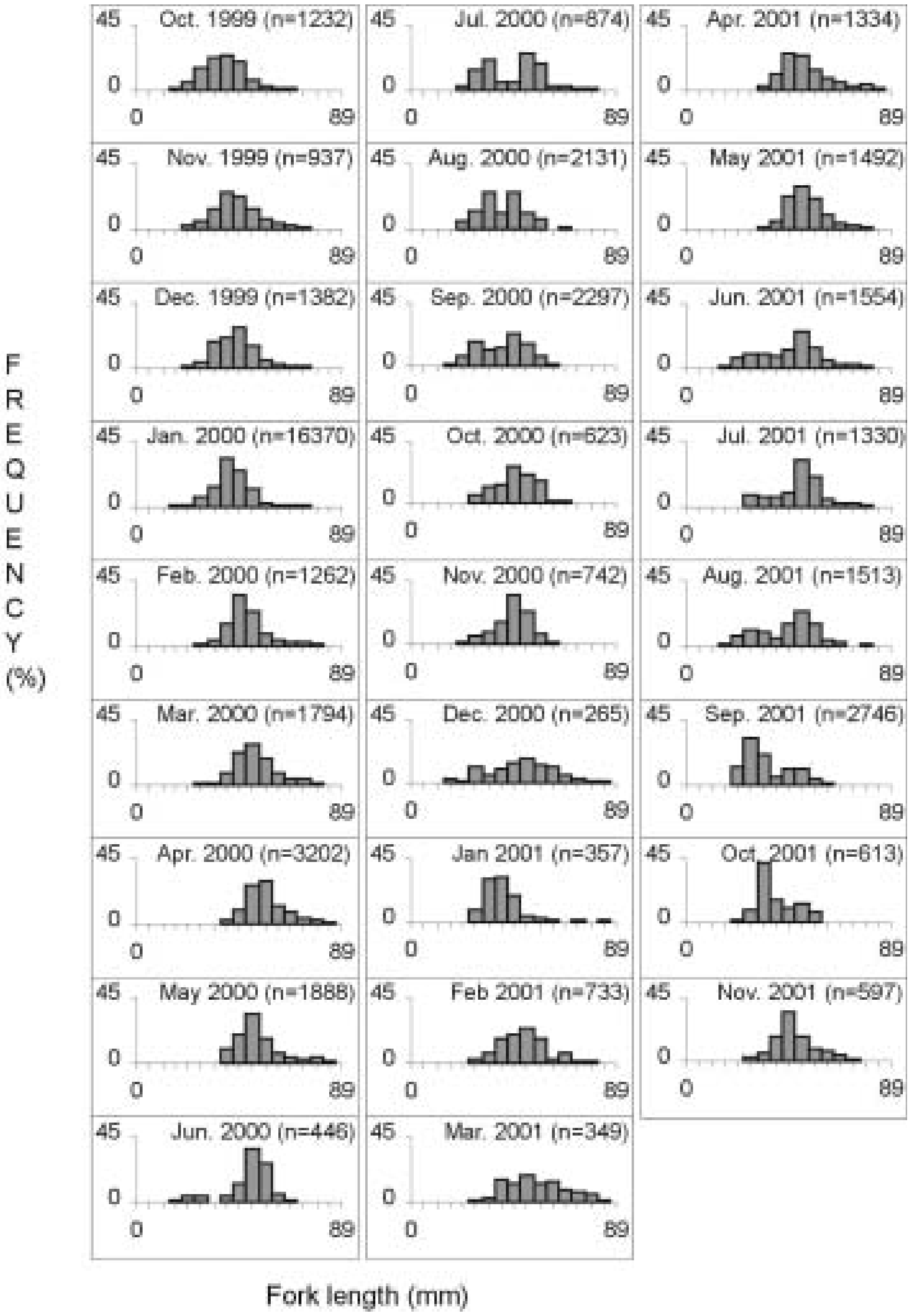

Figure 8.3: Length frequency distribution of *B. tanapelagius* from October 1999-November 2001.

8.3.4 Biomass and production

Length-weight relationships (FL in mm; fresh weight (W) in gram) were calculated for *B. humilis* (W=1.97 * $10^{-5}FL^{2.898}$; N=4886; r^2=0.92), and for *B. tanapelagius*

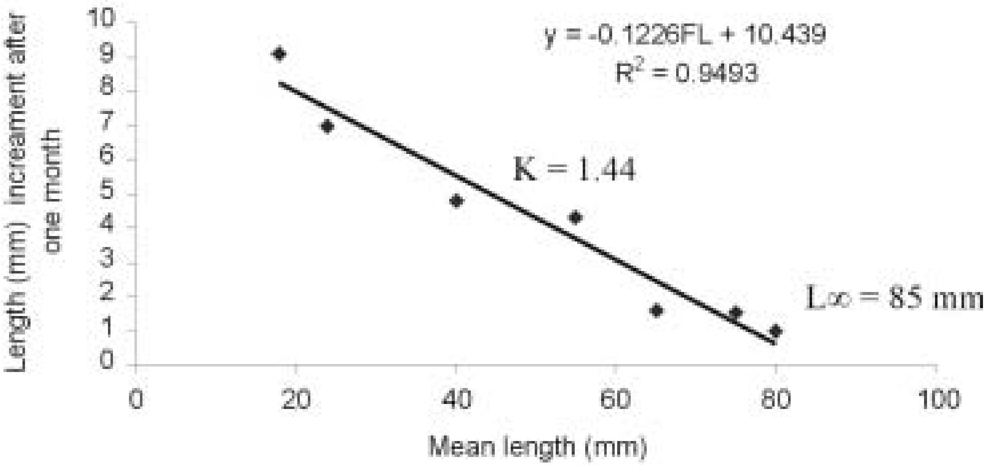

Figure 8.4: Outdoor basin growth measurement on *B. humilis.* Mean length change in mm over one month (n=99, seven length classes 18-80 mm FL).

(W=1.54*$10^{-5}FL^{2.919}$; N=2926; r^2=0.91).

Biomass estimated for *B. humilis* was 5 kg ha^{-1} (Fig. 8.6). *Barbus humilis* was absent in the pelagic habitat. Biomass estimated for *B. tanapelagius* was 9 kg ha^{-1}. The total biomass contributing to its littoral and sublittoral habitats for *B. humilis* was 470 ton whereas for *B. tanapelagius* it was estimated *ca.* 2,000 ton (sublittoral and pelagic habitats). Annual production of *B. humilis* was 16.8 kg ha^{-1}, whereas for *B. tanapelagius* it was 32.4 kg ha^{-1}. Production to biomass ratio (annual P/B) for *B. humilis* was 3.36 and 3.60 for *B. tanapelagius.* The annual production over the whole lake area (315,000 ha) was estimated on basis the relative surface areas of shallow littoral (10 %), intermediate sublittoral zone (20 %) and deep offshore pelagic (70 %). Total annual production was 1600 tons for *B. humilis* and 7,200 tons for *B. tanapelagius.*

8.4 Discussion

Growth of fish may be studied using annuli on hard parts like otoliths, mark recapture experiments or by analysing length-frequency data (Sparre and Venema, 1998). Here, we used length-frequency analysis because annuli on hard parts of these specimens were rather unclear and because of logistic constraints we were unable to examine daily rings.

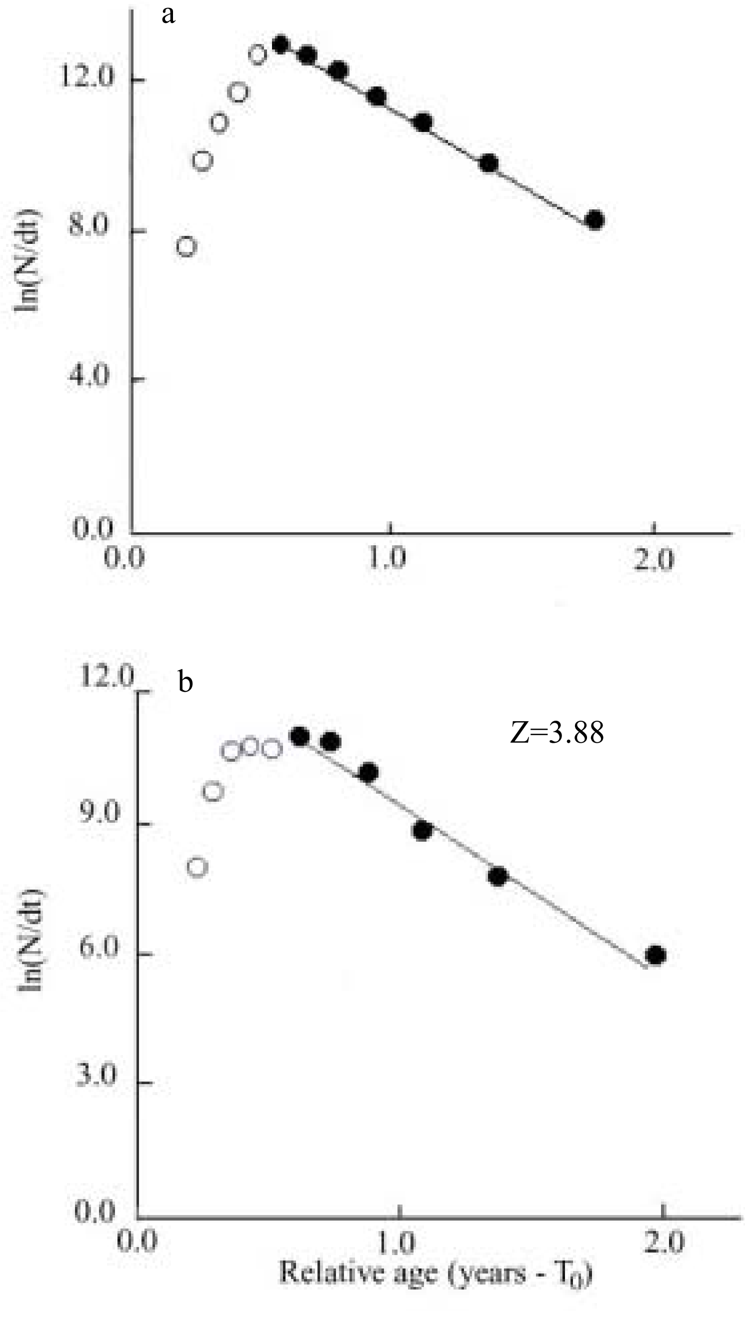

Figure 8.5: Length-converted catch curve analysis to estimate total mortality (Z) for a) *B. humilis* and b) *B.tanapelagius*.

There are no other populations of *B. humilis* and *B. tanapelagius* except from Lake Tana for comparison of their growth and mortality estimates. However, a similar growth index has been observed for the small cyprinid (*Rastrineobola argentea*) from

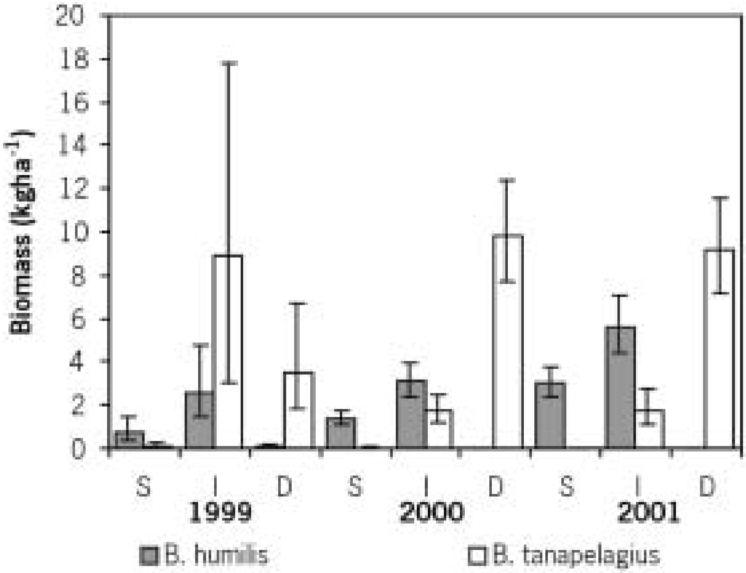

Figure 8.6: Mean biomass (kg ha^{-1}) for the two small barbs (*B. humilis* and *B. tanapelagius*) at three habitats (Shallow (S), Intermediate (I), Deep (D)) in three successive years (1999-2001).

Lake Victoria, with a Φ-value of 3.58 (Table 8.1). On the other hand, *Barbus* species from the eutrophic Tissawewa reservoir in Sri Lanka have relatively higher Φ-value than the cyprinids from Lake Tana and Lake Victoria. Compared with the fresh water sardines of Africa, the two small barbs in Lake Tana and *Rastrineobola argentea* have lower growth index and lower P/B ratios (Table 8.1). The mortality rate was similar for the two small barbs in Lake Tana.

The breeding period data suggested that the two small barbs have one extended breeding peak during March-August (Dejen *et al.*, 2003a). The two small barbs appear to have one cohort each year. This is evidenced from the length-frequency data that the recruitment episode starts in October/November for *B. humilis* and September/October for *B. tanapelagius.* Taking into account that *B. humilis* reach 20 mm in around 2 months at juvenile stages (outdoor basin observation), the recruitment peak detected in this study corresponds to the spawning peak of July-August. For *B. tanapelagius* the spawning time is in May/June.

With regard to the two small barbs annual production and P/B ratio, no previous estimates were available, so we had no idea of the general levels to be expected. Therefore, we applied three methods (swept area, carrying capacity of zooplankton and prey

Table 8.1: Parameter estimates (asymptotic length ($L\infty$), growth constant (K), growth index (Φ), total instantaneous mortality (Z)) and annual production: biomass ratio (P/B) ratio of small pelagic fishes in African Lakes and Asian Reservoir.

Species	$L\infty$ (mm)	K	Φ	Z	P/B	Reference
Clupeids						
Stolothrissa tanganicae (L. Tanganyika)	90 FL	2.52	4.31	5.50	4.25	Roest (1977)
Limnothrissa miodon (L. Tanganyika)	164 FL	0.96	4.41	9.80	4.25	Pearce (1988)
Limnothrissa miodon (L. Kariba)	81 TL	1.74	4.06	9.70	-	Marshall (1987)
Limnothrissa miodon (L. Kivu)	145 FL	1.20	4.40	7.40	-	Mannini (1992)
Cyprinids						
Engraulicypris sardella (L. Malawi)	138 FL	2.58	4.69	13.80	2.50	Rufli and van Lissa (1981)
Rastrineobola argentea (L. Victoria)	64 SL	0.94	3.58	3.28	3.25	Manyala (1992)
Barbus chola (Tissawewa, Sri Lanka)	120 FL	1.00	4.16	2.80	2.40	Pet (1988)
Barbus dorsalis (Tissawewa, Sri Lanka)	190 FL	0.85	4.49	2.50	2.40	Pet (1988)
Barbus sarana (Tissawewa, Sri Lanka)	260 FL	0.45	4.48	1.70	-	Pet (1988)
Barbus tanapelagius (L. Tana)	76 FL	1.65	3.98	3.88	3.60	This study
Barbus humilis (L. Tana)	91 FL	1.20	3.99	3.94	3.36	This Study

requirement of piscivorous barbs) to come up with reasonable estimates. Assuming a 10 % conversion efficiency from zooplankton production to fish production (Payne, 1986), Wudneh (1998) estimated that the zooplankton stock of Lake Tana could sustain an annual production of 73 kg ha^{-1} zooplanktivorous fish. The most important zooplanktivorous fish in terms of biomass and number are *B. tanapelagius*, *B. humilis* and the large barb *B. brevicephalus* (chapter 5). The most abundant large barbs is *B. brevicephalus* (29 % of the 15 large barbs species catch in weight) that accounted 4 kg ha^{-1}. Assuming P/B ratio of 3.0, the production level of *B. brevicephalus* is estimated *ca.* 12 kg ha^{-1}yr^{-1}. Therefore the total zooplanktivorous fish production from the two small barbs and *B. brevicephalus* will be *ca.* 60 kg ha^{-1}yr^{-1}, which is closer to the zooplankton carrying capacity estimate (73 kg ha^{-1}yr^{-1}) reported by Wudneh (1998).

We back-calculated the annual production estimate from top (piscivorous large barbs) to the bottom (two small barbs). Piscivorous large barbs accounted 12 % (4 kg ha^{-1}) of the total annual fish production (32 kg ha^{-1}) (Wudneh, 1998; de Graaf, 2003). Assuming a 10 % conversion efficiency, this production level of large piscivorous barbs needs 40 kg ha^{-1}yr^{-1} of prey fish (mainly the two small barbs which account 75 % of their diet). This agrees with the production estimate for the two small barbs by the swept area method (49 kg ha^{-1}yr^{-1}).

Biomass estimates on small pelagic fishes from other African lakes are mostly considerably larger than the two small barbs in Lake Tana. For example, 87 kg ha^{-1} *Rastrineobola argentea* in Lake Victoria, 100 kg ha^{-1} sardine (*Stolothrissa tanganicae* and *Limnothrissa miodon*) biomass in Lake Tanganyika (Pitcher *et al.*, 1996), 39-72 kg ha^{-1} for Lake Malawi and 59 kg ha^{-1} for Lake Kariba (Marshall, 1993; Pitcher *et al.*, 1996). All things being equal, intrinsically cyprinids yield lower than clupeids (Pitcher *et al.*, 1996). Cyprinids appear to have one to a few cohorts each year, whereas clupeids reproduction and recruitment is continuous. Moreover, cyprinids mature at second year and have lower relative fecundity, whereas clupeids mature at their first year and have higher relative fecundity (Dejen *et al.*, 2003a). Such a low biomass of small pelagics in Lake Tana may be attributed to the low productivity of Lake Tana compared to other East African lakes. However, low productivity is not a strong justification because Lake Tana has better productivity than several lakes with higher pelagic fish biomass. We compared the chlorophyll a content of Lake Tana with values given in the literature for other African lakes (Table 8.2). Compared with these lakes, Lake Tana's chlorophyll a content is lower than most lakes and higher than Lakes Kariba, Malawi and Tanganyika. Since these three lakes with low chlorophyll a content support pelagic fishery, Lake Tana with better productivity should support high pelagic fish biomass. We looked at possible correlation between pelagic fish biomass and lake characteristic (depth, altitude, chlorophyll a concentration and trophic status). Positive correlation ($R^2 = 0.42$, $n = 5$, Table 8.2) was found between pelagic fish biomass and depth, whereas negative correlation ($R^2 = -0.43$, $n = 5$, Table 8.2) with altitude. The biomass increase with depth is most probably explained due to the deep mixing layer so that primary and secondary production per m2 is much higher than in a shallow lake (Lake Tana). The pelagic biomass decrease with increasing altitude can be explained by the fact that it causes low water temperature as a result of which the growth of organisms will be slow. The other reason for low pelagic fish biomass could be that the plankton production is diverted into non-fish pathways (like sediments, benthos) in the pelagic food web. Sedimentation of plankton production, thereby enhancing detritivore production that may result in less being available for the planktivorous fish, *B. tanapelagius*.

The annual production per unit biomass (annual P/B) is a measure of productivity of a fish population. The higher the P/B, the higher the fishery mortality the population will be able to sustain (Vijverberg *et al.*, 2001). *B. tanapelagius* has a relatively high P/B ratio (3.60) compared with other small cyprinids (Table 8.1) and may be, therefore, more resilient to an increasing fishery mortality than most other small cyprinids.

Table 8.2: Small pelagic fish biomass (kg ha^{-1}), chlorophyll a content, mean depth (m) and altitude (m) for some African lakes.

Lake	Mean depth (m)	Altitude (m)	Chlor. concentration (mg m^{-3})	Sm. pel. biomass (kg ha^{-1})	Trophic Status	References
Tana	8.9	1830	6.4	13	Oligo-mesotrophic	Dejen *et al.* (2003b)
Awassa	10.0	1680	41		Hypertrophic	Mengistu and Fernando (1991a)
Chad	3.5	282	100		Hypertrophic	Lemoalle (1981)
George	2.3	913	200		Hypertrophic	Lemoalle (1981)
Malawi	290	500	1.0	72	Oligotrophic	Irvine and Waya (1999)
Naivasha	5.0	1890	40		Hypertrophic	Uku and Mavuti (1994)
Nakaru	2.3	1759	3600		Hypertrophic	Uku and Mavuti (1994)
Tanganyika	570	733	3.5	100	Oligotrophic	Salonen *et al.* (1999)
Turkana	3.12	360	1.2		Oligotrophic	Kolding (1993)
Kariba	29	485	2-11	59	Oligotrophic	Cronberg (1997)
Victoria	40	1134	8.4-24.5	87	Eutrophic	Mugidde (1992)

8.4.1 Fisheries management aspects

Conservation of the existing fisheries resources is the primary concern for managers of the Lake Tana fishery. One of the major problems at the moment is over-exploitation of the 'large barbs'. This problem could be averted by exploitation of the presently untapped resources of small pelagic cyprinids. Only few studies exist on the pelagic fish community of Lake Tana. A recent study on the two small barbs showed their ecological position in the food web, breeding season, size at maturity and fecundity (Dejen *et al.*, 2003a). We observed a high degree of habitat segregation between the juveniles of the 'large barbs' and the pelagic 'small barb', *B. tanapelagius*, whereas *B. humilis* habitat overlaps with the juveniles of large barbs in shallow littoral areas. Therefore targeting *B. tanapelagius* for subsidiary small-meshed fishery in the deep offshore pelagic habitat will most probably not have any adverse consequences on the stocks of the commercially important 'large barbs' (chapter 5). However, before recommending a fishery on the small pelagic barb, *B. tanapelagius* we need information about the potential sustainable yield of this species in Lake Tana. Therefore we estimated the virgin stock of *B. tanapelagius* about 1988 ton. The Maximum Sustainable Yield (MSY) can be estimated in the following way.

$$MSY{=}0.5{*}M{*}B$$

where M is natural mortality, B is virgin stock biomass estimated by swept area method (Sparre and Venema, 1998). In the case of *B. tanapelagius*, natural mortality is equal to total mortality because fishery mortality is zero. Accordingly, MSY of *B. tanapelagius* is 3,850 ton. The most important requirement for the development of a new fishery is the existence of adequate quantities of fish that can be harvested. With the observed substantial biomass, high productivity (high P/B ratio), high growth rate and short generation, fishery could be started on *B. tanapelagius* at pelagic habitats. In Lake Victoria, in spite of an intensified exploitation by man, Nile perch and piscivorous birds, the pelagic cyprinid *Rastrineobola argentea* population increased significantly (Wanink, 1999). Various explanations for this have been suggested, among which an increase in recruitment to the reproducing part of the population, a reduction in generation time, increased growth rate and reduction in size at maturity are the most probable (Wanink, 1999). *Barbus tanapelagius* has a relatively high growth rate, short generation time, high turnover rate (P/B ratio Table 8.1) than *Rastrineobola argentea.* Therefore, starting subsidiary small-meshed fishery might enhance the productivity of *B. tanapelagius* as evidenced from other East African lakes small pelagic fishery. The present study has shown the potential of having a fishery for small pelagics in Lake Tana. However, it must also be noted that our study considers only biological factors in suggesting the possibilities of starting a fishery. Ideally, proposal for promoting the sustainable use of fishery resources should be based on investigations of the biological and environmental, as well as the economic and social aspects. We therefore recommend further investigations on the viability, the magnitude, the fishing methods (night-fishery, lift net, trawl, gillnet) and operation time and management aspect for such a fishery.

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Samenvatting

Ethiopië, gelegen in Noordoost Afrika beslaat een oppervlakte van ongeveer 1,1 miljoen vierkante kilometer. In 1992, door de afscheiding van Eritrea, werd Ethiopië geheel door land omsloten en daardoor voor de aanvoer van vis als goedkope eiwitbron sterk afhankelijk van eigen zoetwatergebieden. Deze laatste bedekken slechts ongeveer 0,7 % van het totale oppervlak en bestaan uit tien meren. De meeste meren liggen in de Rift vallei en hebben een gezamenlijk oppervlak van circa 7.500 km^2. Verreweg het grootste buiten de Rift vallei gelegen zoetwatergebied is het Tana meer (3.150 km^2) dat op een hoogte van ongeveer 1800 m ligt in het noordwestelijk deel van het plateau. De visconsumptie per hoofd van de bevolking is laag in Ethiopië en is geconcentreerd in de grote steden, voornamelijk Addis Ababa en zijn omgeving. Door de grote afstand tot de hoofdstad is het Tana meer één van de minst geëxploiteerde meren.

Totdat omstreeks het midden van de 80-er jaren een visserij ontwikkelingsproject startte, ondersteund door Nederlandse non gouvernementele organisaties (ISSE, Urk en ICCO) werd de visserij als ambacht in het Tana meer bedreven door ongeveer 1000 personen. Die visserij was grotendeels beperkt tot de zuidelijke golf van het meer waar Bahar Dar ligt, de grootste stad van de streek. Deze traditionele visserij werd uitgevoerd met papyrus boten en exploiteerde vooral de vissen uit het kustgebied, Nijl tilapia, *Oreochromis niloticus* en grote barbelen, *Barbus intermedius*. De nieuw ingevoerde manier van vissen, waarbij gebruik wordt gemaakt van gemotoriseerde boten, bestrijkt een aanzienlijk groter deel van het meer, waarin de in open water levende typen grote visetende barbelen, van het genus *Barbus* en de Afrikaanse meerval *Clarias gariepinus*, voorkomen. De commerciële visserij richt zich tijdens het paaiseizoen (juli-oktober) op de in de rivier paaiende grote soorten barbelen, die zich aan het begin van die periode verzamelen in de monding van de rivieren. De introductie van de gemotoriseerde visvangst leidde tot een toename van de jaarvangst van 500 ton in 1988 tot 1.300 ton in 1997 en tot een aanzienlijke toename van de visconsumptie.

In 1999, tien jaar na de introductie van de nieuwe vistechnieken, rapporteerden vissers en onderzoekers een reductie van de populaties van grote barbelen. Verschillende maatregelen werden voorgesteld om het tij te keren. Een van deze voorstellen was om naast de bestaande een aanvullende visserij te starten met het gebruik van netten met kleine maaswijdte op de niet benutte kleine pelagische barbeelsoorten. Om de uitvoerbaarheid en de effecten van een dergelijke aanpak te bepalen en te adviseren over een duurzaam beheer, was onderzoek van de biologie en ecologie van de soorten kleine barbelen, ook behorend tot het geslacht *Barbus*, noodzakelijk.

Wij begonnen met het vaststellen van de aanwezige soorten van deze diploïde (i.t.t. de grote, hexaploïde) barbelen gezien de onduidelijke literatuur daarover en onderzochten daarna de soortspecifieke voedselvoorkeur, de voortplantingsbiologie, de individuele groei en de groei van populaties. Belangrijk was te bepalen hoe de natuurlijke hulpbronnen, vooral voedsel en ruimte, verdeeld waren tussen de soorten van kleine barbelen, de jonge exemplaren van de grote barbelen en een specifieke zoöplanktonetende soort grote barbeel, *Barbus brevicephalus*. Tenslotte werden de natuurlijke mortaliteit, de biomassa en de jaarlijkse productiviteit gemeten en bepaald. Deze gegevens vormen de grondslag van gemaakte schattingen omtrent het potentieel voor visserij op deze kleine barbelen.

In dit proefschrift komen de volgende onderzoeksvragen aan de orde; (1) Welke soorten kleine barbelen komen naast elkaar voor in het Tana meer en welke morfologische en ecologische diversiteit vertonen zij? (2) Met welke efficiëntie benutten deze soorten zoöplankton, zijn zij de dominante soorten temidden van het gilde van andere zoöplankton eters in het meer? (3) Welke sleutelkenmerken in structuur, functie, gedrag en ecologie maken deze soorten tot succesvolle zoöplankton eters, hoe valt de vergelijking uit met andere zoöplankton eters? (4) Vertonen de soorten kleine barbelen in het Tana meer een relatief hoge groeisnelheid, vruchtbaarheid en productivitet? In welke mate wordt groei en voortplanting beïnvloed door infecties met lintwormen? (5) Zijn de soorten kleine barbelen qua habitat onderling voldoende verschillend en ook verschillend van de grote commercieel belangrijke barbelen, zodat visserij op deze soorten zonder nadelige gevolgen voor de reeds bestaande visserij mogelijk is? (6) Vormen de kleine barbelen in termen van productiviteit sleutelsoorten in de gemeenschap van vissen van het meer? (7) Zijn de biomassa en de jaarlijkse productiviteit van deze vissoort(en) voldoende om duurzaam jaarlijks een voldoend hoge vangst te leveren, die interessant is voor een aanvullende commerciële visserij?

Vastgesteld werd dat er in het meer drie geldige soorten van diploïde kleine barbelen leven nl. *Barbus humilis*, *B. pleurogramma* en *B. tanapelagius*. *B. tanapelagius* is een nieuwe soort, endemisch voor het Tana meer. *B. pleurogramma* is een typische soort van de ondergelopen randzone van het meer en werd zelden in het meer zelf aangetroffen. *Barbus humilis* en *B. tanapelagius* zijn de algemene soorten in het meer. *Barbus trispilopleura* is een synoniem van *B. humilis*, en wordt beschouwd als een ecotype van die soort.

Uit cluster analyse blijkende morfologische verschillen, die ook bij oppervlakkige beschouwing onmiddellijk opvallen, uit verschillen in de onderzochte maaginhouden en uit de verschillen in habitat van beide soorten blijkt dat *B. humilis* en *B. tanapelagius* verschillende soorten zijn. Uit een recente moleculaire analyse (de Graaf, 2003) blijkt dat beide soorten nauw verwant zijn en dat de divergentie waarschijnlijk is opgetreden na de vorming van het Tana meer, of nadat het voor het laatst uitdroogde.

De productie en biomassa op hogere trofische niveaus is voornamelijk afhankelijk van de primaire en secondaire productie op lagere trofische niveaus. Hoewel vroegere studies het Tana meer als oligotroof en laag productief, aanduiden bleek uit deze studie dat de aanduiding meso-oligotroof juister is en dat de productiviteit hoger is (gemiddeld chlorophyl gehalte 6.4 μg/l) dan beweerd werd. De rivieren, die in het Tana meer uitmonden voeren zeer veel fijn sediment aan in de regentijd, waardoor de troebelheid van het meer zeer hoog is. Wij hebben significante tijdsafhankelijke verschillen gevonden in zooplankton dichtheid, de hoogste in het droge seizoen (november-april) wanneer de turbiditeit het laagst is. Turbiditeit bleek de omgevingsfactor, die de hoogste negatieve correlatie vertoonde met de zoöplanktondichtheid, dat gold speciaal voor *Daphnia* soorten. Voor het eerst werden de zoöplanktonsoorten nauwkeurig gedetermineerd en dit is essentieel om op langere termijn de status en de trends in de taxonomische samenstelling te kunnen volgen. Zo bleek uit ons onderzoek dat er vier soorten cladoceren, watervlooien, nl. *Diaphanosoma sarsi*, *Daphnia hyalina*, *D. lumholzi* en *Moina micrura* in het meer voorkomen, waarvan de aanwezigheid niet eerder was vermeld.

Morfometrie, uitgevoerd op structuren voor de voedselopname, toonde duidelijke specialisaties aan van *B. tanapelagius* (foeragerend op zoöplankton), *B. pleurogramma* (opzuigen van taai bodemvoedsel) en van *B. brevicephalus* (pompfiltratie van zoöplankton), terwijl *B. humilis* juist opvallend intermediair was in deze structuren. Dit wijst op het type generalist. Deze uit structuur- en ander onderzoek afgeleide hypothesen werden getoetst door darminhouden te analyseren. Hoofdbestanddeel van het voedsel van *B. tanapelagius* is zoöplankton (75 %), voor *humilis* en *brevicephalus* vonden we waarden van 40 % resp. 39 %. De voorspelde en de feitelijke voedselniche van de ondiep watersoorten, *B. humilis* en *B. pleurogramma* en de juvenielen van de 'grote' barbeelsoorten is breed en past bij de litorale en bentische gebieden met een diversiteit aan voedseltypen. Juvenielen van de grote barbelen eten veel detritus (34 %) en macrofyten (18 %), *B. tanapelagius* en *B. brevicephalus* daarentegen zijn gespecialiseerd op een paar voedseltypen en daarmee aangepast aan hun pelagische habitat, waarin weinig diversiteit aan voedseltypen bestaat. *B. brevicephalus* is aangepast aan het filteren van kleine deeltjes, hun dieet blijkt gedomineerd te worden door het grotere zoöplankton (0,8-1,3 mm) en verder te bestaan uit relatief grote volwassen dipteren, muggen en vliegen. Zowel de volwassen *B. tanapelagius* als de adulte *B. brevicephalus* selecteerden de grotere zoöplankton organismen uit de omgeving (>0,8 mm), de grotere *B. brevicephalus* at, zoals verwacht, de grootste.

De niches van de oever, ondiep water soorten, *B. pleurogramma*, *B. humilis* en de juvenielen van de grote barbelen overlappen elkaar in het litorale gebied. De beide open-water soorten, *B. tanapelagius* en *B. brevicephalus* vertonen een grote overlap in het sublitoraal en in het pelagische gebied. De trofische overlap volgt de ruimtelijke en is hoog binnen de kustgroep soorten en binnen de open-water soorten, maar gering tussen die twee groepen. De bezetting van de zooplanktivore voedsel niche werd zowel ruimtelijk als qua dieet vergeleken tussen de drie soorten kleine barbelen, de juvenielen van de grote barbelen en *B. brevicephalus*.

Langs de gradiënt litoraal-pelagisch vinden we *B. pleurogramma* in het meest ondiepe deel, dan volgen *B. humilis* en de juvenielen van de grote barbelen. *B. tanapelagius* en *B. brevicephalus* bezetten vooral het sublitoraal en het pelagische habitat.

Ten aanzien van hun voortplantingsstrategie lijken *B. humilis* en *B. tanapelagius* sterk op andere soorten met een korte levensduur, een kleine grootte bij geslachtsrijpheid, een hoge fertiliteit en herhaald paaien. Beide soorten hebben een lang paaiseizoen (van maart tot september). Het paaiseizoen van de grote barbelen,die in de rivier paaien, valt in de grote regentijd tussen juli en september. De beide soorten kleine barbelen beginnen te paaien in maart en benutten op die wijze de bloei periode van het zooplankton in de droge tijd. Tussen juli en november migreren de grote barbelen naar de rivieren om te paaien, waardoor het predatierisico van de kleine barbelen vermoedelijk kleiner wordt. Zowel de absolute als de relatieve vruchtbaarheid van *B. humilis* is groter dan die van *B. tanapelagius.* Deze hogere vruchtbaarheid van *B. humilis* wordt zowel toegeschreven aan de betere omstandigheden voor voedselorganismen in het litoraal, vergeleken met de pelagische zone als aan het brede voedselspectrum van *B. humilis* (volwassen insecten, larven van insecten, zoöplankton en detritus). Vergeleken met de kleine cypriniden en haringachtigen van andere grote Afrikaanse meren is de vruchtbaarheid van beide kleine barbeelsoorten uit het Tana meer (172-339 eieren per gram) laag (zie Tabel 6.2).

Van de vijf zoöplanktivore soorten, die bestudeerd zijn blijken alleen *B. tanapelagius* en *B. humilis* geïnfecteerd te zijn door de lintworm *Ligula intestinalis. B. tanapelagius* heeft de hoogste infectiegraad (>10 %)in zijn gehele leefgebied, terwijl de mate van infectie alleen hoog was bij *B. humilis* levend in helder water (circa 10 %) maar slechts 3 % bij dieren levend in troebel water. In alle besmette soorten leidt de aanwezigheid van de parasiet tot vertraging in de ontwikkeling van de gonade, tot kleinere afmetingen bij geslachtsrijpheid en tot lagere vruchtbaarheid. De belangrijkste reden voor verschillen in groei en vruchtbaarheid onder de kleine barbelen was de mate van infectie met deze lintworm, predatiedruk en voedseldichtheid zijn mogelijke neven factoren.

Om de individuele groeisnelheden van *B. humilis* en *B. tanapelagius* te schatten gebruikten wij lengte-frequentie analyse. Om deze groeisnelheden te kunnen vergelijken berekenden wij de index van algemene groeiprestatie Φ. Deze index bleek zeer vergelijkbaar bij de beide algemene soorten van kleine barbelen in het Tana meer, 3,99 en 3,98, resp. voor *B. humilis* en *B. tanapelagius.* Deze waarden werden vergeleken met groeisnelheden gevonden bij andere pelagische soorten in Afrikaanse en Aziatische meren en reservoirs (Tabel 8.1). De daar voorkomende kleine zoetwater haringachtige soorten hebben hogere groeisnelheden dan de kleine barbelen, maar dat geldt niet voor kleine cypriniden in eutrofe reservoirs in Sri-Lanka. De groeisnelheden van *B. humilis* en *B. tanapelagius* blijken sterk overeen te komen met waarden gemeten bij de kleine pelagische cyprinide, *Rastrineobola argentea*, uit het Victoria meer.

Voor beide soorten schatten wij de productiviteit (verhouding tussen productie en biomassa/jaar) door de jaarproductie (periode van 12 mnd) te delen door de gemiddelde biomassa in diezelfde periode. Jaar P/B verhoudingen waren 3,4 voor *B. humilis* en 3,6 voor *B. tanapelagius.* Deze waarden zijn relatief hoog vergeleken met die van kleine cypriniden in andere Afrikaanse en Aziatische meren, maar lager dan de gewoonlijk gerapporteerde waarden van kleine pelagische haringachtigen in Afrikaanse meren (Tabel 8.1). Gezien zijn hoge productiviteit vertoont *Barbus tanapelagius* de belangrijkste kenmerken van een echte kleine pelagische soort.

Groeiparameters en mortaliteit werden geschat met behulp van FiSAT II (FAO-ICLARM) Stock Assesment Tools) computer package. Hiervoor werden lengte-frequentie gegevens van 26 opeenvolgende maanden gebruikt. De totale coëfficiënt van mortaliteit (Z) werd geschat op 3,94 en 3,88 /jaar, resp. voor *B. humilis* en *B. tanapelagius.* De gemiddelde biomassa was 5 kg/ha in het litoraal en sublitoraal (470 ton voor het gehele meer) voor *B. humilis* en 9 kg/ha in het littoraal en pelagiaal voor *B. tanapelagius* (2.000 ton voor het gehele meer). De productie van *B. humilis* per jaar bedraagt 16,8 kg/ha in het litoraal en sublitoraal, die van *B. tanapelagius* is 32,4 kg/ha. De biomassa van kleine pelagische vis in het Tana meer is relatief klein vergeleken met die van de overeenkomstige fauna in andere Afrikaanse meren. Echter, gezien het grote oppervlak van het pelagiaal van het Tana meer (circa 2200 km^2) bedraagt de totale jaarlijkse productie 7.700 ton nat gewicht, hoog vergeleken met de andere vissoorten. *B. tanapelagius* staat daarmee voor ongeveer 50 % van de totale vis productie van het meer, *B. humilis* produceert ongeveer 25 %, de overige vissoorten, de grote barbelen, Nijl tilapia en de Afrikaanse meerval zorgen voor de overige 25 %. Deze grote fractie van het geheel toont aan dat *B. tanapelagius* de sleutelsoort is in het net van voedselrelaties tussen de organismen van het Tana meer.

De jaarlijkse vangst van commercieel belangrijke vissoorten in het Tana meer wordt geschat op 800-900 ton. Wij schatten dat de nu niet geëxploiteerde *B. tanapelagius* een maximale duurzame jaarlijkse productie kan leveren van circa 3.850 ton, 50 % van de biologische productie. Dit komt overeen met ongeveer vier maal de huidige commerciële jaarvangst. Dit nog voorlopige resultaat van ons onderzoek suggereert dat de jaarlijkse opbrengst van *B. tanapelagius* vier maal groter is dan de huidige gemiddelde totaalopbrengst van de visserij. Voordat een visserij op deze soort kan starten is voortzetting van het onderzoek nodig naar interacties tussen vissoorten, naar een geschikte vangmethode alsmede naar de socio-economische aspecten van een dergelijke visserij.

Commerciële vangst van *B. tanapelagius* zal niet direct de stand van de juvenielen van de grote barbelen aantasten, omdat er een strikte habitat scheiding is tussen *B.tanapelagius* in het pelagiaal en de juveniele grote barbelen in het litoraal. Er zijn echter vele indirecte effecten van een dergelijke visserij denkbaar. Aangezien de kleine barbelen een centrale positie bezetten in het ecosysteem van het Tana meer is het noodzakelijk eerst andere aspecten van de dynamica van het voedselweb te onderzoeken. De mogelijke gevolgen van een dergelijke visserij op de visetende grote barbelen en op de andere trofische niveaus van het voedselweb van het Tana meer worden in de discussie aan de orde gesteld.

Summary

Ethiopia, located in East Africa covers a total surface area of 1.1 million square kilometres. In 1992, the country became a land locked depending only on inland water resources for the supply of fish as a cheap protein source. Water bodies cover only 0.7 % of the area of the country and comprise of 10 lakes. Most of them are located in the Rift Valley, and together they have a total surface area of 7,500 km^2. By far the largest water body is Lake Tana (3,150 km^2), located outside the Rift Valley on the northwestern plateau. Fish consumption in Ethiopia is low and concentrated in the big cities, mainly Addis Ababa and its surroundings. Due to its distance from the capital city (500 km), Lake Tana is amongst the least exploited lakes.

Lake Tana fishery remained completely subsistent involving *ca.* 1000 persons, until a fisheries development project assisted by Dutch Non Governmental Organisations (ISSE, Urk and ICCO, Zeist) was launched in the mid 1980s. Fishery is mainly confined to the southern gulf (Bahar Dar, the largest town in the region). The traditional subsistence fishery using papyrus reed boats exploits the inshore fish community (Nile tilapia, *Oreochromis niloticus* and large barb, *Barbus intermedius*). The other type of fishery, motorised boat fishery, exploits a wider lake area including the open water fish community of the large piscivorous *Barbus* species and African catfish, *Clarias gariepinus.* The commercial fishery mainly targets the river spawning large *Barbus* species in the river mouths during their breeding period (July-October). The introduction of motorised fishery resulted in an increase of annual fish catch (from 500 tonnes in 1988 to 1,300 tonnes in 1997) and consumption during the first 10 years.

In 1999, a decade after the introduction of new fishing technology, fishermen and researchers reported a decline of the large *Barbus* stock. In order to avert this decline several management options were proposed. One of the proposed options was to start subsidiary small-meshed fishery on the unexploited small pelagic barbs. To know about its feasibility and effects, and to advise on sustainable management research had to be done on several aspects of the biology and ecology of the small *Barbus* species in Lake Tana. We started with their identification, their feeding biology and main food base (*i.e.* zooplankton) in the environment, their reproductive biology, their individual growth and productivity. Then we studied their resource partitioning among themselves and with the juveniles of the large barbs and a zooplanktivorous larger barb (*B. brevicephalus*). Finally we studied the mortality of small barbs, their biomass and production. On basis of the estimated biological production we were able to estimate the potential for fishery on the small barbs.

The following specific research questions were addressed in this thesis: (1) Which species compose the small barbs of Lake Tana and how morphologically and ecologically diverse are they? (2) Are the small *Barbus* species of Lake Tana efficient zooplankton feeders and are they the dominant zooplanktivores within the guild of zooplankton feeding fish? (3) Which key features in structure, functioning, behaviour and ecology would make small barbs successful zooplanktivores? How do these fishes compare to other zooplanktivorous species in Lake Tana? (4) Are the small *Barbus* species of Lake Tana characterised by a relatively high growth rate, fecundity and productivity? To what extent is growth and reproduction affected by cestode infection? (5) Is segregation in the habitat occupation between the small *Barbus* species of Lake Tana and the larger commercial fish species good enough to allow a fishery on small barbs without negative effect on the current fisheries on larger fish species? (6) Are the small barbs in terms of biological production key species of the fish community in Lake Tana? (7) Is the biomass and annual production of small barbs in Lake Tana large enough to ensure a sustainable yield that is high enough to make it interesting for the commercial fishermen to start a subsidiary fishery on small barbs? (8) What are the possible ecological effects of such a fishery on the structure of the Lake Tana food web?

Three valid small *Barbus* species (*Barbus humilis*, *B. pleurogramma* and *B. tanapelagius*) were identified in Lake Tana. We discovered *Barbus tanapelagius* as a new species, which is endemic to Lake Tana. *Barbus pleurogramma* was a typical species of the floodplains and was rarely found in the lake itself. *Barbus humilis* and *B. tanapelagius* are the most common small barbs in the Lake. *Barbus trispilopleura* is synonymised as an ecotype of *B. humilis*.

The morphological difference in cluster analysis, difference in feeding habits and habitat occupation of *B. humilis* and *B. tanapelagius*, suggest that *B. humilis* and *B. tanapelagius* belong to different species. However, most recent molecular analysis (de Graaf, 2003) suggest that *B. humilis* and *B. tanapelagius* are very closely related species that probably diverged in evolution after formation of Lake Tana, or its latest desiccation.

The production and biomass at higher trophic level (predatory fish) is mainly dependent on the primary and secondary production (lower trophic levels). Although previous studies reported that Lake Tana is very poor in productivity and characterised it as oligotrophic, our study revealed that it is rather oligo-mesotrophic and of higher productivity (mean chlorophyll-a content 6.4 μg l^{-1}) than previously reported. In Lake Tana, inflowing rivers carry a heavy silt load into the lake during the rainy season, which makes the lake very turbid. We observed significant temporal differences in zooplankton abundance, with highest densities during dry season (November-April) when water turbidity is low. Among the environmental factors, zooplankton abundance correlated most strongly with turbidity. Turbidity was negatively correlated with abundance, especially for *Daphnia* spp. Consistent identification of zooplankton species is essential for assessing the long-term status and trends in taxonomic structures of the assemblages. Our investigations showed four species of cladocerans (*Diaphanosoma sarsi*, *Daphnia hyalina*, *Daphnia lumholzi* and *Moina micrura*) that were not reported earlier for Lake Tana.

Morphometrics on feeding structures showed conspicuous specialisations for *B. tanapelagius* (cruising for zooplankton), *B. pleurogramma* (suction feeder on tough, benthic food) and *B. brevicephalus* (pump-filterfeeding on zooplankton), whereas *B. humilis* was conspicuously intermediate in most structures predicting a generalist feeding niche. The potential niches, set by fish size and other limitations, were tested by gut content analysis. Zooplankton constitutes the major component of the diet for *B. tanapelagius* (75 %), *B. humilis* (40 %) and *B. brevicephalus* (39 %). The predicted and actual feeding niches of the inshore-group *B. humilis*, *B. pleurogramma* and juvenile 'large barbs' is broad and fit into littoral and benthic areas with diversified food types. Juvenile 'large barbs' consumed a considerable amount of detritus (34 %) and macrophytes (18 %). In contrast, *B. tanapelagius* and *B. brevicephalus* are specialised on few food types, and adapted to their pelagic habitat which has little food diversity. Most of *B. brevicephalus* feeding characters are related to filtering small particles: their actual diet is dominated by the larger zooplankton (0.8-1.3 mm) and by relatively large adult dipteran insects. Both the adult *B. tanapelagius* and

B. brevicephalus showed positive size selective feeding and took the larger zooplankters from the environment (> 0.8 mm), but due to its larger size *B. brevicephalus* fed on slightly larger zooplankton items than *B. tanapelagius*. Based on niche overlap along the spatial dimensions, inshore dwelling groups: *B. pleurogramma*, *B. humilis* and juvenile 'large barbs' overlap at the littoral habitat. The two offshore dwelling species (*B. tanapelagius* and *B. brevicephalus*) showed high spatial overlap at the sublittoral and pelagic habitats. The trophic niche overlap followed the same dimension of spatial niche overlap, high within the inshore and offshore groups and a very small overlap between the two groups. The reproductive strategy of the two small barbs (*B. tanapelagius* and *B. humilis*) is similar with other short-lived species (small size at maturity, high fecundity and multiple spawning). Both species have a long breeding period (from March to September). Big rains during July-September mark the breeding season for river-spawning 'large barb' species in Lake Tana. Both small barb species start breeding in March, utilising the abundance of zooplankton, which peaks in the dry season. From July to November, the 'large' piscivorous barbs migrate to affluent rivers for spawning, which will reduce the predation risk for the small barb juveniles. Both absolute and relative fecundity of *B. humilis* was much higher than of *B. tanapelagius*. The higher fecundity of *B. humilis* may be attributed to the better food conditions in the littoral zone as compared with the pelagic zone in combination with the wide food spectrum of *B. humilis* (adult insects, insect larvae, zooplankton, detritus). The range of relative fecundity of the small barbs of Lake Tana (172-339 eggs per gram) was low compared with small lacustrine cyprinids and clupeids from other African lakes (6.2).

Of the five zooplanktivorous taxa studied only *B. tanapelagius* and *B. humilis* were infected by the cestode parasite (*Ligula intestinalis*) in Lake Tana. Infection rate varied according to species and habitat. *Barbus tanapelagius* showed the highest mean infection rate (>10 %) in all habitats, whereas in *B. humilis* infection rate was high (*ca.* 10 %) in clear water habitats but much lower in turbid water habitats (*ca.* 3 %). In all infected species the parasite caused retardation in gonad development, early size at maturity and lower absolute fecundity. A main reason for differences in growth and fecundity among the small barbs in Lake Tana was the level of infection with tapeworm, whereas predation pressure and food density are also possible co-factors.

We used length-frequency analysis to estimate the individual growth rates of *B. humilis* and *B. tanapelagius*. To enable a comparison of growth rates among species we calculated the index of overall growth performance Φ. The values of the growth index (Φ) were very similar for the two small barbs of Lake Tana, 3.99 and 3.98 for *B. humilis* and *B. tanapelagius*, respectively. We compared these growth rates with those of small pelagics in other African and Asian lakes and reservoirs (Tabel 8.1). Generally, the small freshwater clupeids have higher growth rates than the small barbs, with the exception of the small cyprinids in eutrophic Sri Lankan reservoirs. The growth rates of *B. humilis* and *B. tanapelagius* in Lake Tana are, however, very similar to the growth rate observed for the small pelagic cyprinid *Rastrineobola argentea* in Lake Victoria.

For both small barb species we estimated the productivity (annual P/B ratios) by dividing the annual production (12 month period) by the mean biomass over the same period. Annual P/B ratios were 3.4 for *B. humilus* and 3.6 for *B. tanapelagius.* These values are relatively high compared with the annual P/B ratios of other small cyprinids in other African and Asian lakes and reservoirs, but lower than values generally reported for small pelagic clupeids in African lakes (Tabel 8.1). *Barbus tanapelagius* because of its high productivity shows the main characteristics of a true small pelagic species.

Growth parameters and mortality were estimated using the FiSAT II (FAO-ICLARM Stock Assessment Tools) computer package. For these estimates we used 26 consecutive months length-frequency data. Total mortality coefficient (Z) was estimated at 3.94 and 3.88 year^{-1} for *B. humilis* and *B. tanapelagius* respectively. The mean biomass was 5 kg ha^{-1} in littoral and sublittoral (470 tons for whole lake area) for *B. humilis* and 9 kg ha^{-1} in sublittoral and pelagic (2000 tons for whole lake area) for *B. tanapelagius.* Annual production of *B. humilis* was 16.8 kg ha^{-1} in littoral and sublittoral whereas *B. tanapelagius* was 32.4 kg ha^{-1} in sublittoral and pelagic. The biomass of small pelagic fish in Lake Tana is relatively low compared with small pelagics in other African lakes. Nevertheless, due to the large pelagic area of Lake Tana (*ca.* 2200 km^2) the total annual production of *B. tanapelagius* is 7,700 tonnes fresh weight, which is high compared with the other fish species. *Barbus tanapelagius* represents *ca.* 50 % of the total fish production in the lake, *B. humilis ca.* 25 %, whereas the large barbs, Nile tilapia and African catfish together represent *ca.* 25 %. This relatively high contribution to the total production of the fish community as a whole shows that *B. tanapelagius* is a keystone species in the Lake Tana food web. In Lake Tana the annual fish catch from commercially important fish species is estimated *ca.* 800-900 tonnes. We estimated that the unexploited small barb, *B. tanapelagius* has a potential annual maximum sustainable yield of *ca.* 3,850 tonnes (50 % of the biological production). This corresponds with *ca.* four times the current annual commercial catch. This still preliminary result suggests that on average the potential yield of *B. tanapelagius* is four times the current total fishery yield. Prior to starting a fishery on *B. tanapelagius* it is necessary to continue research on interactions between the fish species, the fishing methods and the socio-economical aspects of such a fishery. Commercial fishing on *B. tanapelagius* in the pelagic zone will not directly affect the juvenile large barbs stocks as there is strict habitat segregation between *B. tanapelagius* (pelagic) and the juvenile large barbs (littoral). However, several indirect effects are possible. As these ‘small barbs’ occupy a central position in Lake Tana’s ecosystem, it is important to assess possible scenarios on the food web dynamics if a pelagic fishery on small barbs is established. The possible consequences of such a fishery on the piscivorous large barbs and the other trophic levels of the Lake Tana food web (*i.e.* phytoplankton, zooplankton) are discussed.

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Curriculum Vitae

Eshete Dejen Dresilign was born in Gondar, Ethiopia, on 30 June 1968. He attended elementary and secondary education at Addis Zemen School. In 1990 he obtained a Bachelor of Science (BSc) degree in Animal Sciences at Alemaya University of Agriculture (near Harar, Eastern Ethiopia) with distinction. In September 1990 he joined the Debre Zeit Agricultural Research Centre of the Alemaya University. He obtained in January 1995 a Master of Science (MSc) degree in aquaculture from the Department of Fish Culture and Fisheries of the Wageningen Agricultural University. The Netherlands Fellowship Programme sponsored the MSc study. The title of his thesis was 'A length-based simulation model to evaluate management options in a multispecies gillnet fishery of Lake Tana, Ethiopia'. From February 1995-May 1998, he served the Debre Zeit Agricultural Research Centre of the Alemaya University of Agriculture as assistant researcher, lecturer and assistant director to the Centre. In this period he organised and executed various smaller projects in the field of animal agriculture and fisheries. From May 1998-April 1999 he worked as associate researcher and assistant director at Debre Zeit Agricultural Research Centre of the Ethiopian Agricultural Research Organisation. In May 1999 he started his PhD at Experimental Zoology Group of Wageningen Institute of Animal Sciences. For this study he obtained financial support from Netherlands Foundation for the Advancement of Tropical Research, Interchurch Foundation Ethiopia-Eritrea (Urk), the Schure-Beijerinck-Popping Foundation, The International Foundation for Science (IFS-Sweden) and from Wageningen University. The field work was carried out from September 1999 to April 2002. The writing of the thesis was started early during this field work and more intensively continued from May 2002-May 2003 in Wageningen. He is married and has one boy.

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