The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning, and fisheries

Promotor: Prof. Dr. J.W.M. Osse
Hoogleraar Algemene Dierkunde

Co-promotor: Dr. F.A. Sibbing
Universitair Hoofddocent Functionele Diermorfologie
aan de leerstoelgroep Experimentele Dierkunde, departement Dierwetenschappen

Leo Nagelkerke

The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning, and fisheries

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit te Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op dinsdag 7 oktober 1997
des namiddags te half twee in de aula

Abstract

Nagelkerke, L.A.J. 1997. The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning, and fisheries. Doctoral thesis, Experimental Animal Morphology and Cell Biology, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands

ISBN: 90-5485-755-2

Subject headings: *Barbus* / biodiversity / cyprinids / ecomorphology / feeding / food partitioning / lakes / species flock / sustainable fisheries

The rediscovery of a unique species flock of cyprinid fish, its taxonomy and its feeding-biology are described. Fourteen species of barbs (*Barbus* spp, Cyprinidae, Teleostei) were found in highland (1800 m) Lake Tana, in northwestern Ethiopia. Lake Tana is an isolated fresh-water system, because its only outflowing river, the Blue Nile, of which it is the source, drops over 40 m high waterfalls only 35 km from the lake. The carplike barbs in the lake are unique and show a wide variety of discrete, and consistent types, widely differing in 1) size and shape, 2) feeding behaviour, and 3) spatial distribution. Together with 4) the early morphological divergence of juvenile barbs, 5) the reproductive segregation of the adults, and 6) part of their genetic characters, this diversity was decisive in our description of fourteen endemic species, seven of them new to science. Lake Tana was formed by volcanic blocking of the Blue Nile and subsequent flooding of the Lake Tana basin. The *Barbus* species probably evolved within the lake itself from one common ancestor, very similar to the present-day, riverine *B. intermedius*, making it a unique species flock. The driving force of their evolution most likely involved radiation into the new lacustrine trophic niches that became available when Lake Tana filled up. The presence of this group of very closely related fishes provides a unique opportunity to study the evolution of adaptation, and the relation of morphology and ecology: it forms a 'natural laboratory'. By using an ecomorphological approach, based on properties of fish foods, and functional morphological studies of the relations between fish parameters and their significance in dealing with food properties, predictions on the diets and food partitioning of the barbs have been made. These predictions were based on a large set of characters (33), which made the method robust and allowed for accurate resolving power. Testing of the predictions with field data revealed that individual diets, but especially food partitioning can be well predicted. This new method provides insights into the dynamic trophic interactions among species without the need for an extensive ecological sampling programme, and could be instrumental in predicting shifts in fish fauna composition, due to environmental impact, such as overfishing or the introduction of new species. The understanding and prediction of such shifts will help in developing a strategy towards sustainable fisheries and the protection of biodiversity.

This research was supported by:
NWO-WOTRO, project number W88-176
Interchurch Foundation Ethiopia/Eritrea (ISE), Urk
Interchurch Coordination Commission for Development (ICCO), Zeist,
Fisheries Resources Development Department of the Ministry of Agriculture, Addis Ababa
Bureau of Agriculture of theAmhara National Regional State, Bahar Dar
Ethiopian Orthodox Church (EOC/DICAD), development department
Agricultural University Wageningen

Cover: Lake Tana with Great white pelicans (*Pelecanus onocrotalus*) and Black kites (*Milvus migrans*) at Bahar Dar in the rainy season: photograph by G.J.M. van Snik.
Cover design: Wim Valen.

Caput Nili quaerere

("De bronnen van de Nijl zoeken": een zeer lastig karwei beginnen)

ቀስበቀስ እንቁላል በእግሩ ይሔዳል

("Langzaam maar zeker zal een ei pootjes krijgen en gaan lopen"; Amhaars spreekwoord)

Vlam

Schuimende morgen

en mijn vuren lach
drinkt uit ontzaggelijke schalen
van lucht en aarde
den opalen dag

(H. Marsman, Verzamelde Gedichten, 1938,
uitgeverij Querido)

voor Suus

Contents/Inhoud

Chapter 1

General introduction

Leo A.J. Nagelkerke[1]

[1] *Agricultural University, Wageningen Institute of Animal Sciences (WIAS), Experimental Zoology Group, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

In 1986, the Lake Tana Fisheries Resources Development Program (LTFRDP) was started by the Ethiopian Ministry of Agriculture, in cooperation with the Development Branch of the Ethiopian Orthodox Church (EOC). The project was supported by the Interchurch Foundation Ethiopia (ISE) from Urk, The Netherlands. At this time, hardly anything was known about the identity and dynamics of the Lake Tana fish resources. Therefore, Tesfaye Wudneh was assigned as fisheries expert, to investigate the fish stocks. One of the species in the lake, *Barbus intermedius* Rüppell showed such an immense morphological variability that it was suspected that there were at last several different populations of barbs in Lake Tana and possibly several species. The presence of different species or populations, and therefore of different units of fish stock complicates rational management of the resources. To investigate the identity and the evolution of the Lake Tana *Barbus* biodiversity and its role in the ecosystem, a research project was initiated. The results of that study are reported in this thesis.

Before I will evaluate the results of the research project, I will first introduce Lake Tana in a broad sense: its topography, climate, flora and fauna in general, and its fish in particular. Secondly I will describe the context and history of my research project, its aims, and its progress in answering the major questions. The latter is, of course, subject of the main body of this thesis and

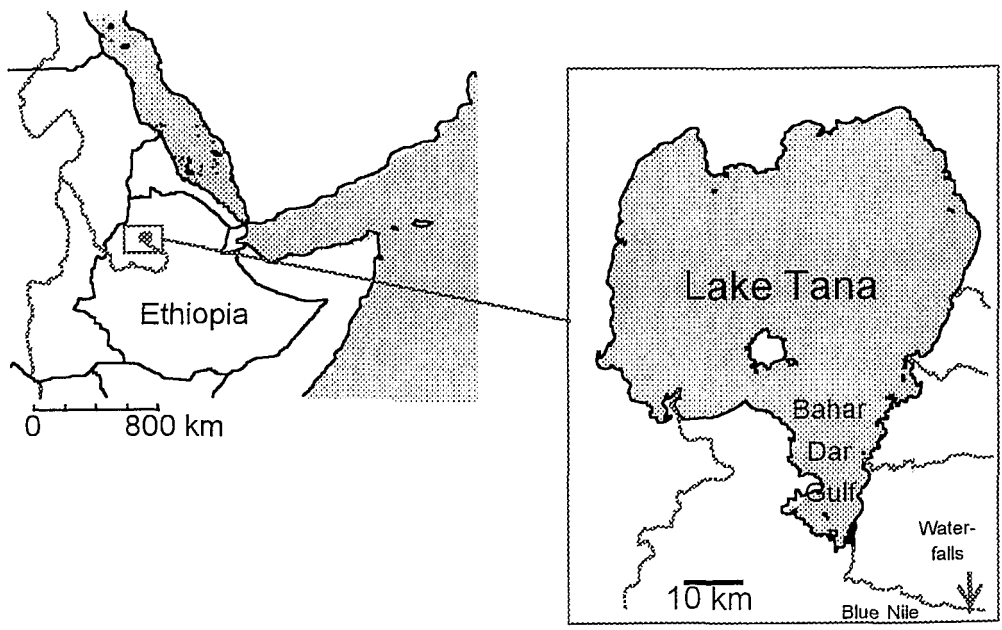


Fig.1.1. A map of Ethiopia and Lake Tana. The southern Bahar Dar Gulf is indicated, as well as the Blue Nile and the waterfalls in it.

every chapter will be discussed in short. Finally there will be a short general discussion in which I will try to come to a synthesis of the research until now. This involves addressing some preliminary results that are not presented in the following chapters, and making some generalizations. This also brings me to future research that still should be performed to come to an even better understanding of Lake Tana.

Short introduction to Lake Tana

Topography and geology

Lake Tana is situated in the north-western highlands of Ethiopia in the provinces of Gojjam and Gonder, at an altitude of approximately 1800 m (Fig.1.1). It is the source of the Blue Nile (or Abbay as it is called in Amharic, the chief language of this part of Ethiopia), and as such it has been a place that was searched for since the times of Julius Caesar and Alexander the Great. The first European to see the legendary source was the Portugese Jesuit Pedro Paez, in 1613.

The so-called Tana-rift, in which Lake Tana lies, is a shallow trough which is not connected to the main Eastern Rift Valley as such, but it certainly has some relation to it (Baker et al. 1972, Mohr 1962). The lake probably formed through volcanic blocking of the Blue Nile in early Pleistocene times (Mohr 1962). Subsequently the Lake Tana basin filled up. It now covers an area of approximately 3150 km^2, and is Ethiopia's largest lake. Four larger, permanent rivers tribute to the lake (the largest is Gelgel Abbay; the 'small Blue Nile'[1], which is *c.* 100 km), as well as many short, seasonal streams. The lake is shallow with an average depth of 8 m and a maximum depth of 14 m. Its bottom consists of volcanic basalts, usually covered with a muddy substratum with only little organic matter (1.2-2.3%: Gasse 1987). At some places volcanic peaks in the lake bottom form reefs, or even islands (Fig. 1.2). The lake is bordered by low plains in the north (Dembea), east (Fogera), and south-west (Kunzila) that are often flooded in the rainy season (forming extensive wetlands), and by (at some places steep) rocks in the west and north-west.

Most islands in Lake Tana are small, but two of them are larger (Dagà, and Dek, which used to be the seat of Ethiopian emperors). Both large and small islands usually contain ancient Ethiopian Orthodox churches. At the southernmost tip, in the city of Bahar Dar ('Sea Shore'), the Abbay flows out of the lake, only to drop over 40 m high waterfalls, 35 km from its origin, at Tissisat ('the smoking waters', Fig. 1.3). This effectively isolates Lake Tana and its tributaries from the rest of the Blue Nile basin and other fresh-water systems.

Climate

The Lake Tana area has a tropical highland climate, with moderated temperatures, because of the altitude. The climate is strictly seasonal and dominated by the dry season (*begà*) from October-November until May-June, and a rainy season (*kiremt*) with maximum monthly rainfall

[1]Amharic words (including local dialect) other than geographical names are italicized; some literal translations are indicated between apostrophs.

Fig.1.2. One of the smaller Lake Tana islands: Kibran, in the Bahar Dar Gulf.

Fig. 1.3. The Tissisat ('smoking water') waterfalls over which the Blue Nile drops, only 35 km from its outflow from Lake Tana.

(up to 500 mm, approximately one third of the total annual rainfall) in July (cf. Chapter 4, Nagelkerke & Sibbing 1996). Occasionally the dry season is interrupted by a 'small' rainy season (*belg*) in March, but the frequency of the latter is diminishing over the years (Wudneh pers. comm.).

Minimum air temperatures range from 7°C (December 1990) to 16°C (May 1992), maximum air temperatures range from 23 to 31°C (August 1992 and May 1990 respectively; all data from Wudneh, 1997, cf. Table 1.1). Winds are predominantly southerly (force 2-3 Beaufort) from January until July, and mostly northerly (force 2-2.5 Beaufort) from August until November (Gasse 1987).

Table 1.1. Some climate and water parameters of Lake Tana

	Minimum	Maximum	Average	Source
Climate				
Minimum air temperature	7°C (Dec '90)	16°C (May '92)		Wudneh 1997
Maximum air temperature	23°C (Aug '92)	31°C (May '90)		Wudneh 1997
Rainfall			c. 1500 mm/year	Addis Ababa, Meteorology Office
Water				
Chlorophyll a	3.7 mg m^{-3}	6.2 mg m^{-3}		Wood & Talling 1988 (min), Admasu 1986 (max)
Salinity			143 mg l^{-1}	Wood & Talling 1988
Biomass			129 mg C m^{-2}	Wudneh 1997
Temperature	18.3°C	26.2°C	22.3°C	pers. obs.
Conductivity	136 µS cm^{-1}	234 µS cm^{-1}	194 µS cm^{-1}	pers. obs.
pH	7.86	8.87	8.43	pers. obs.
Oxygen content	3.3 ppm	10.8 ppm	6.5 ppm	pers. obs.
Transparency (Secchi-disk)	0.31 m	1.82 m	0.83 m	pers. obs.

Water

Lake Tana is usually characterized as an oligotrophic lake (Rzóska 1976, Admasu 1986, Wudneh 1997). The lake has low chlorophyll *a* concentrations (3.7 mg m^{-3}: Wood & Talling 1988; 6.2 mg m^{-3}: Admasu 1986), low salinity (143 mg l^{-1}: Wood & Talling 1988), and low mean biomass (129 mg carbon m^{-2}: Wudneh 1997).

The seasonal rains cause the lake level to fluctuate regularly with an average difference between minimum (May-June) and maximum (September-October) lake level of approximately 1.5 m. We measured water temperatures from 18.3 to 26.2 °C (average: 22.3 °C, n=216) in the entire sampling period from 1992 until 1995 (Table 1.1). Conductivity ranged from 136 to 234 µS cm^{-1} (average 194 µS cm^{-1}, n=92), pH from 7.86 to 8.87 (average 8.43, n=92) in the same period. The oxygen content of the water is usually high, ranging from 3.3 to 10.8 ppm in the water column (average 6.5, n=216). There is no anoxic layer, although close above detritus-covered bottoms the oxygen content can drop to near 0. Due to the shallow saucer-shape of the lake, and the fairly strong winds

that usually start after sunset, the water of the lake is well mixed. Transparency ranges from 0.31 to 1.82 m (Secchi depth), with an average of 0.83 m (n=218).

Flora

The phytoplankton is dominated by diatoms of the genus *Melosira* (Gasse 1987, Wood & Talling 1988). The rather abundant blue-green algae are represented mainly by *Microcystis* and *Anabaena* species. Green algae are less abundant: *Pediastrum* and *Straurastrum* species are the usually most frequent (Gasse 1987), but sometimes *Volvox* abounds (Dumont 1986).

The eastern and southern shores of Lake Tana are covered with swamps, especially near river mouths, dominated by papyrus (*Cyperus papyrus*, Cyperaceae). *Typha latifolia* (Typhaceae) and waterlilies (*Nymphaea* spp., Nymphaeaceae) are also abundant here (pers. obs.). Sometimes we saw large chunks of vegetation, torn away from the shore and forming floating islands, up to 20 m across. In the open water, especially *Ceratophyllum demersum* (Ceratophyllaceae) and *Vallisneria spiralis* (Hydrocharitaceae) are abundant. They are only loosely rooted and can also be found in large quantities, sometimes floating freely in the water-column. *Pistia stratiotes* (Araceae) is a conspicuous plant, because it floats freely on the surface. Two species of trees should be mentioned here, as they often grow close to the shore: *Ficus sycomorus* (Moraceae), the fig tree, or *warka* (in Gojjam dialect) that is often the only tree left in agricultural areas after deforestation[2], and *Milettia ferruginea* (Leguminosae), the *berberra*, of which the dried and crushed seeds are used as a fish poison (cf. Chapter 4, Nagelkerke & Sibbing 1996).

Fauna

Most aquatic invertebrates are rotifers (14 species, of which *Keratella* and *Brachionus* species are most abundant: Wudneh 1997), molluscs, crustaceans, and insects (especially their larvae). Benthic life is poor (as was already remarked by Bini 1940). The large bivalve *Unio abyssinica* is relatively frequent in the lake (pers. obs.), as well as the smaller *Aspatharia rubens* (pers. obs.), and *Corbicula fluminalis* (Gasse 1987). Gastropods are usually found near the littoral vegetation and include the endemic subspecies *Bellamya unicolor abyssinica* (Viviparidae), *Lymnaea natalensis* (Lymnaeidae), *Anisus natalensis* (Planorbidae), and *Bulinus* spp. (Planorbidae), host to *Schistosoma haematobium*, the cause of bilharzia (Brown 1965). Some very large ostracods (probably of the family Cypridae) up to more than 1 mm are very conspicuous in the benthos, especially if detritus was present (pers. obs.). Midges (e.g. *Chironomus*, Chironomidae),

[2]Despite the limited direct human influences on Lake Tana, the area around it has been cultured for centuries, and consequently much of the original forest has disappeared. Deforestation has intensified over the last decades with the increasing human population. This might have resulted in an increase of the amount of silt that is transported into the lake by the rivers in the rainy season. It is unknown what the effects of this indirect human influence on the lake ecosystem are.

mosquitoes (e.g. *Chaoborus*, Chaoboridae, and *Culex* and *Anopheles* [malaria mosquito], Culicidae), May-flies (Ephemeroptera), stone-flies (Plecoptera), caddis-flies (Trichoptera) and dragon-flies (Odonata, 14 species, Dumont 1983) are the most abundant insect larvae (pers. obs.). Small oligochaetes (up to 3 cm), probably of the family Naïdidae were regularly found.

Cladocerans, and copepods (both cyclopoid and calanoid) are the most abundant crustaceans in Lake Tana and are the largest group of pelagic invertebrates (biomass). *Bosmina longirostris* and *Diaphanosoma excisum* are the most abundant cladocerans; *Daphnia*, *Ceriodaphnia*, and *Moina* species are much rarer (Wudneh 1997). The calanoid copepod *Thermodiaptomus galebi* and the cyclopoid *Thermocyclops* species are on average just as abundant as the most frequent cladocerans, while the cyclopoid *Mesocyclops* species are less often encountered (Wudneh 1997). The largest crustaceans are freshwater crabs of the genus *Potamonautes*, but they are fairly rare. A very conspicuous pelagic invertebrate is the hydrozoan *Limnocnida indica* (order Trachylina) a clear Palearctic influence in the lake (Thiel 1973).

Amphibia, especially anurans are present in the lake (especially in the marshy shore-areas) but rather inconspicuous. Crocodiles are absent from Lake Tana, but are present upstream from the Tissisat waterfalls. This situation has not changed since Cheesman reported this in 1936, and like him I have wondered why they have never invaded the lake.

The largest Lake Tana reptiles are the Nile monitor (*Varanus niloticus*)[3], and a python species (*Python sebae*). The latter is rarely seen. The most diverse vertebrate group is that of the (aquatic) birds. Piscivorous species include residents such as Little grebe (*Tachybaptus ruficollis*), Great white pelican (*Pelecanus onocrotalus*), Great and Long-tailed cormorants (*Phalacrocorax carbo*, and *P. africanus*), Darter (*Anhinga rufa*), many species of heron (*Ardeola* spp., *Egretta* spp., and *Ardea* spp.), Hammerkop (*Scopus umbretta*), and African fish eagle (*Haliaeetus vocifer*). Egyptian goose (*Alopochen aegytiaca*), Spur-winged goose (*Plectropterus gambensis*), and Pygmy goose (*Nettapus auritus*) are the most conspicuous non-piscivorous aquatic birds. Palearctic migrants that depend on the lake 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*)(all pers. obs.).

There are not many aquatic mammals. The local fishermen told me they sometimes caught otters in their nets (especially along the rivers), but I have never seen one. Hippopotami ('gumare') however, were always present in small numbers, despite the fact that Cheesman (1936) already feared their extinction.

Fish

The Lake Tana ichthyofauna is still relatively undisturbed by human influence. Modernized fishing has only started since 1989 and there have been no successful introductions of exotic

[3]Which is sometimes called *azu*, i.e. crocodile, by the local population. This can cause some confusion.

species (although in 1938, during Italian occupation, it was tried to introduce northern pike, *Esox lucius*, and *Gambusia holbrooki*, for lake stocking and mosquito control respectively[4]).

Greenwood (1976) described the Lake Tana fish fauna as very truncated, i.e. very poor in species and families. There is one cichlid: *Oreochromis niloticus*. This is the most widespread tilapia species in Africa, although the Lake Tana population has recently been described as the separate subspecies *O. niloticus tana* on the basis of its genetic structure (Seyoum & Kornfield 1992). Boulenger (1902, 1911) mentions three catfish species of the genus *Clarias* (Clariidae), one of them endemic to the lake (*C. tsanensis*). However, all three have been synonimized to the most common member of the genus: *C. gariepinus* (Teugels 1986).

The obscure *Nemacheilus abyssinicus* (Balitoridae) was, until recently, only known from a single 4-cm specimen from Lake Tana, and it was wondered whether it was really from the lake or that it was a result of a museal mix-up (Beadle 1981), especially because this loach is the only species from this Palearctic family known from Africa. In 1993 it was rediscovered in small streams close to Lake Tana, and since then in large parts of the Ethiopian high plateau (Dgebuadze et al. 1994). However, only one specimen was found by us in Lake Tana itself, from a depth of 14 m on October 3rd, 1993.

The largest fish family in the lake is the Cyprinidae, represented by three genera: *Garra*, *Varicorhinus*, and *Barbus*. Boulenger (1907, 1911) mentions the species *Garra quadrimaculata* and *G. dembeensis* for Lake Tana, but we have found that the descriptions are inconsistent and the taxonomic position of the Ethiopian *Garra* populations is unclear. *Varicorhinus beso* was described by Rüppell (1836), and is a very distinct, large cyprinid. Nowadays, the phylogenetic relationships between the genus *Varicorhinus* and the genus *Barbus* are being discussed, as the former seems to be very closely related to some 'large' barbs (Howes 1987).

The genus *Barbus* is a taxonomic wastebasket: more than 800 species have been included, from East-Asia to South-Africa, diploids, tetraploids, and even hexaploids, with adult sizes of 4 cm and of 100 cm (Howes 1991). African barbs are usually subdivided into (evolutionary diploid) 'small' barbs, and (evolutionary hexaploid) 'large' barbs (Golubtsov & Krysanov 1993). These two groups can, among others, be distinguished by adult size (maximum of 10 cm v. maximum of 100 cm) and scale characters. Boulenger (1902, 1907, 1911) mentions three 'small' barbs for Lake Tana: *B. pleurogramma*, *B. humilis*, and *B. trispilopleura*. The first species has a strongly serrated spine, and is probably very much related to the widespread African *B. paludinosus*. *B. humilis* and *B. trispilopleura* are difficult to distinguish, and might be conspecific. The exact relationship between these two is unclear. The three 'small' barbs were considered to belong to the subgenus *Barbus (Enteromius)* by Bini (1940). These species have diverging striae on the exposed parts of their scales, in contrast to the 'large' barbs with parallel striae.

The 'large' Lake Tana barbs are the focus of this study. They were first described by Rüppell (1836). He described 5 *Barbus* and 1 *Labeobarbus* species. Boulenger (1902, 1907) lumped two of Rüppell's species, synonimized the genus *Labeobarbus* with *Barbus*, and added a further 5 Lake

[4]Ministry of Agriculture, Addis Ababa, internal report

Tana species. Bini (1940) described a total of 10 species with 23 subspecies of 'large' barbs. He considered them to belong to the separate subgenus *Labeobarbus*, which is corroborated by recent work (Berrebi 1995).

The published descriptions and keys of the 'large' barbs of East-Africa (not only Lake Tana) were inadequate for accurate identification. This was one of the reasons for Banister (1973) to revise this group. He concluded that he was dealing with one, very variable species, synonymous with *B. intermedius* Rüppell 1836. He distinguished two subspecies: *B. intermedius australis*, and *B. intermedius intermedius*, the latter containing all Lake Tana forms.

When this research project started, Banister's work formed the (widely accepted, cf. Greenwood 1976) state of the art, concerning the Lake Tana barbs. The reasons for reconsidering his conclusions are (among other things) explained in the next section.

The project

History and settings

When the Lake Tana Fisheries Resources Development Program (LTFRDP) was started in 1986 hardly anything was known about the fish resources. Four commercially interesting fish species were recognized at the time: the tilapia *Oreochromis niloticus* (*korosso*), the catfish *Clarias gariepinus* (*ambaza*) and the cyprinids *Varicorhinus beso* (*bezo*) and *Barbus intermedius* (*nech assa*: 'white fish'). The morphological differences among the barbs however, were so striking that it was likely that there were at last several different populations, or even distinct *Barbus* species in Lake Tana. Moreover, local fishermen distinguish different barb types at least since Rüppell's time, and probably already for centuries [5](Rüppell, 1836, cf. Chapter 4).

It is essential for rational management to know what the units of fish stock (viz. different populations or even species) are (Law & Grey, 1988 Wudneh 1997). Unbalanced exploitation of fish stocks will lead to cascading effects in the ecosystem, especially if different fish stocks play different ecological roles. Shifts in fish composition or more dramatic deleterious influences could be the result, endangering the biodiversity of the system, which could lead to decreased and less stable productivity of the resources.

A research project was initiated to identify the taxonomic status and the ecological role of the different barbs in the functioning of the ecosystem. These basic biological results could provide fishery biology with data that are needed to study population dynamics and productivity of the system, which in their turn can be translated to the fisheries and management practice.

[5] The mysterious *Sorz* was searched after by both Cheesman (1937) and Bini (1940). They both concluded it was a mythical fish. However, I found that any fish that was too large to be carried by one man was called *Sorz*, either barb or catfish. The largest barb I have seen weighed 12 kg and was 85 cm long, the largest catfish was 1.28 m, with a weight of 28 kg. The latter one could have been a real *Sorz*, especially for a small fisherman.

Aims of the project

The main aims of the project were:

1. assessment of the *Barbus* biodiversity
2. assessment of the significance of the biodiversity for the functioning of the ecosystem
3. study of the evolutionary origin of the *Barbus* group of Lake Tana.

ad 1. to investigate the taxonomic status of the different *Barbus* morphotypes: are they phenotypic morphs of one very polymorphic species (morphotypes), or are they reproductively isolated populations, i.e. biological species (*s.* Mayr 1942)?
ad 2. a) to investigate the ecological (especially trophic) role the *Barbus* morphotypes play in the ecosystem: are the morphotypes also ecotypes? This question will be tackled using an ecomorphological approach which argues that a species' feeding (in)abilities can be predicted from its morphology. This predicted diet has to be tested against the actual food. If derived and actual diets match, this method has predictive value in case of a changing environment (e.g. overexploitation of certain species, introductions of exotic species; Sibbing et al. 1994). Direct scoring of gut contents of fish, without an ecomorphological analysis does not have such predictive value.
b) to reconstruct a food web of Lake Tana, in which the dynamic interactions between the different *Barbus* morphotypes/species, other fish species and the resources are well described. Such a food web reconstruction provides important insights into the system and the effects of its exploitation, which is important for rational management and the protection of biodiversity.
ad 3. to develop hypotheses about the selective forces and evolutionary mechanisms which led to the origin of the Lake Tana *Barbus* morphotypes/species. Adaptive radiation of feeding characters and disruptive selection is thought to play an important role in this.

Stages of the project

In this section I will discuss the subsequent chapters and present their major conclusions within the framework of the project. As explained before, the initial questions about the Lake Tana fish came from the fisheries practice. There was hardly any knowledge of the resources, and before fishery biology could analyse the stocks and population dynamics, some basic questions about the biology of especially the barbs first had to be solved. The most urgent question was the definition of the variety of barbs. Our initial null-hypothesis was that there was only one stock of *Barbus* in the lake, as described by Banister (1973). The alternative hypothesis was that there were more barb populations. The investigation of these hypotheses was the goal of the initial pilot study, described in Chapter 2.

Chapter 2; Pilot study: a unique species flock?[6]

In October-December 1990 a ten week field trip at Lake Tana resulted in the distinction of 13 discrete morphotypes: Acute (Ac), Barbel (Ba), Bighead (Bh), Bigmouth big-eye (Be), Bigmouth mini-eye (Mi), Bigmouth small-eye (Se), Carplike (Ca), Dark (Da), Intermedius (In), Lip (Li), Troutlike (Tr), White hunch (Wh), and Zurki (Zu). Intermediates between morphotypes were rare (<10%) and our initial distinction, based on general habitus, was confirmed by canonical discriminant analysis on a set of 17 morphometric characters. This result falsified our initial null-hypothesis that there was only one *Barbus* population in Lake Tana.

The morphotypes were also found to be ecologically different. They were distributed unevenly over water depths (e.g. Tr and Bh usually in shallow water; In and Be in deep water) and substratum types (Li mostly over rock; Ac preferring sandy or muddy substrate). The barbs had considerably varying diets: Zu was found to be primarily herbivorous, Ca was molluscivorous, and Ba, In, and Li benthivorous. One of the most striking discoveries was the large number of morphotypes (8 of the 13) that had an important amount of fish in their diets. Cyprinids do not have oral teeth or discrete stomachs, and are therefore not well adapted for piscivory. Probably it can only develop among cyprinids in the absence of more specialized piscivores (Sibbing, 1991a). In Lake Tana the only other piscivore is *Clarias gariepinus*, but this species is an opportunistic feeder and is not specialized in eating fish. Piscivory in the barbs was strongly correlated with certain morphological characters: piscivores had larger, and more terminal oral gapes, and shorter barbels, intestines, and protrusion lengths.

The uniqueness and distinctness of the morphotypes, together with their ecological differentiation, and the presence of many piscivorous types suggests that the Lake Tana barbs evolved inside the lake, radiating into the different available food niches. We hypothesized that the common riverine *Barbus intermedius* was present in the Blue Nile at the time the lake was formed by volcanic blocking, and is the ancestor of all large Lake Tana barbs. If this is true we are dealing with an endemic and undamaged cyprinid species flock, unique in the world (Greenwood 1984, Kornfield & Carpenter 1984).

Chapter 3; Early morphological divergence[7]

Mina et al. (1993) suggested that the morphological diversity we found among the barbs of Lake Tana was largely caused by phenotypic plasticity. They argued that most *Barbus* morphotypes only start diverging from a common pool of young barbs when they reach a length of 20 to 25 cm, and that only of fish larger than 25 cm, 90% can be assigned to particular morphotypes. However, in this study we showed that 11 of the 14 morphotypes (an additional morphotype: Shorthead [Sh] was defined) can already be distinguished from fork lengths of less than 12 cm. In the length class of 10-15 cm we could already reliably assign more than 80% of almost 4000 specimens to one of

[6]Published in Environmental Biology of Fishes 39: 1-22, 1994.

[7]Published in Netherlands Journal of Zoology 45: 431-454, 1995.

the morphotypes. Of three morphotypes (Ca, Mi and Tr), juveniles could not be found. By morphometric analysis (both univariate and multivariate) we showed that the young barbs are distinguished on the same grounds as larger specimens of the same morphotypes. According to age estimates by Mina et al. (1993) this means that the barbs attain their adult morphology already in their first year.

We consider the early divergence of separate morphotypes as additional evidence that we are not just dealing with phenotypic plasticity, although it is no absolute proof. The fact that there are so many morphotypes (14) makes it unlikely we are dealing with polyphenism, which is usually described for two or three alternative phenotypes, triggered by some clear environmental factor (Dgebuadze 1995, Witte et al.1990).

We divide the Lake Tana barbs in three groups: 1) a group of 11 morphotypes which can already be distinguished when they are c. 10 cm; 2) a group of three morphotypes for which no juveniles have been found (Ca, Mi and Tr): the juveniles may be rare or living in papyrus beds or far up the rivers, or they may not have been recognized as such because they belong to a phenotypically plastic group ; 3) a group of fishes that do not belong to any of the described morphotypes, usually caught near the shore: they may be new, as yet undescribed morphotypes, but they could also form a phenotypically plastic group. The existence of these three groups suggests that different morphotypes could be in different stages of speciation. We propose a hypothetical evolutionary history of the Lake Tana *Barbus* morphotypes. When the Blue Nile was blocked by volcanic activity, in early Pleistocene times, a highly variable barb was present in the river. This barb probably was similar, or the same as the riverine *B. intermedius*, that is still abundant in the Ethiopian highlands. The Lake Tana basin filled up, presenting a range of new lacustrine environments to the barbs. Adaptive radiation into new (trophic) niches, and disruptive selection drove the diversification, and finally the speciation of the barbs. The morphotypes that have radiated into the new open water environment (most unlike their original riverine habitat), are the most aberrant from their riverine counterparts, and the most distinct of all morphotypes. The barbs that live near the shore (shore-complex), a habitat resembling riverine circumstances (shallow water, terrestrial influences) are still most alike to the highly variable riverine *Barbus intermedius*.

Chapter 4; Reproductive segregation[8]

Additional evidence of the specific status of at least four *Barbus* morphotypes, came from molecular genetic studies. Dixon et al. (1994, 1996), working in the immunology research group of our department, studied certain genes of the major histocompatibility complex (MHC). MHC-genes are the most polymorphic genes known in vertebrates and the cell-membrane proteins they produce are involved in the specific recognition of antigens. Therefore it is anticipated that these genes will evolve rapidly when organisms radiate into new environments and meet new antigenic agents. This provides a marker for evolutionary divergence among populations/species which can be interpreted functionally. It was found that alleles of the class II β-chain encoding MHC genes were shared

[8]Published in Journal of Fish Biology 49: 1244-1266, 1996.

among specimens of the same morphotypes, but not between different morphotypes, suggesting that these morphotypes form separate gene pools. However, segregation of the spawning stocks would be the ultimate proof of reproductive isolation, and therefore of the presence of several species.

To investigate this we interviewed local fishermen about the migration of fish in the rivers, their aggregation, and the presence of young fish. We also performed experimental fishing in the river mouths and upstream. In this way we got an impression of the occurrence of fish that were running (i.e. about to spawn), and we could analyse whether the different morphotypes differed in their preferred rivers, the localities within the rivers (upstream and downstream), or spawning time. The size at first spawning was also investigated.

We found some differences among the different rivers, and some small temporal differences among the four most abundant morphotypes (Ac, Be, In, and Sh). The biggest differentiation however, was between the species composition upstream and downstream. Upstream, Ac and Be were completely missing, while they contributed > 20% to the downstream catch. In contrast, Tr, which is relatively rare in the downstream catch (c. 1%) was abundant upstream (c. 20%). Of course these spatial differences in frequencies can be caused by temporal spawning differences. If Ac and Be migrate upstream later than Tr, the same distributions could be the result. However, there are no signs that this actually happens, and there are other signs that the spatial component is very important. Zu was almost and Bh completely absent from the catches in the river mouths and upstream reaches. Running specimens have, however, incidentally been found in the lake itself. Zu was found close to the river Gelda mouth, but Bh was found far from any river. This suggests that there is a spatial pattern with lake spawners (Bh and Zu), river mouth spawners (Ac and Be), upstream spawners (Tr), and morphotypes that spawn in the whole river (In and Sh). The almost complete absence from the catches of some, usually rather abundant, morphotypes (Ba, Da, Li, and Zu) could mean that they also spawn at different sites and/or times.

Next to the spatial and/or temporal segregation there is a marked difference in the size of first spawning among the morphotypes (e.g. the smallest running male was 12 cm fork length for Sh, and 28 cm for Se). These differences suggest different life-history traits, such as age of first spawning, life span and growth rate, which could be instrumental in speciation events (Crawford & Balon 1994). The cumulative evidence of 1) discrete morphologies of the morphotypes, 2) their early divergence, 3) genetic differences, 4) segregation during spawning, and 5) essential differences in spawning size, is so convincing that, from now on, we will consider the morphotypes are separate biological species.

Chapter 5; Revision and description of seven new species[9]

The cumulative evidence that the different Lake Tana *Barbus* morphotypes are real biological species, as listed at the end of the preceding section is so convincing that we decided to assign species names to them. There is also a pragmatic side to this decision, because further delay would

[9]Accepted: Zoölogische Verhandelingen, Leiden.

produce a body of papers that only refer to the trivial names (cheironyms), which cannot be checked properly.

In order to assign the species names we first had to investigate the relation between our morphotypes and previous species and subspecies descriptions. After comparison of our specimens with the available type-specimens and original descriptions, we concluded that seven morphotypes were synonymous with previous descriptions, viz. *B. acutirostris* (Acute), *B. dainellii* (Bighead), *B. gorgorensis* (Carplike), *B. gorguari* (Dark), *B. macrophtalmus* (Bigmouth big-eye), *B. nedgia* (Lip), and *B. surkis* (Zurki), and that the other seven were new species viz. *B. brevicephalus* (Shorthead), *B. crassibarbis* (Barbel), *B. longissimus* (Bigmouth mini-eye), *B. megastoma* (Bigmouth small-eye), *B. platydorsus* (White hunch), *B. truttiformis* (Troutlike), and *B. tsanensis* (Intermedius). We gave descriptions of all 14 species, as well as an identification key.

The species *B. intermedius* was not redescribed. After study of the type specimen we decided that it belonged to the variable group of barbs from the shore-area (cf. Chapter 3), which we expect to be very close to the ancestral riverine barbs. The Intermedius as morphotype does not belong to the shore-complex, and was described as *B. tsanensis* (this is rather confusing; it was an unfortunate choice to call this morphotype Intermedius). We suspect that the *Barbus* species that were described for Lake Tana by previous authors, but that were not found by us, also belong to the shore-complex. Most of their fishing activities must have taken place close to the shore, while we had the opportunity to sample the open water extensively. Most of our new species are open-water species, explaining why they were not described earlier.

Berrebi recently (1995) suggested that all large, hexaploid barbs belong to the subgenus *Barbus (Labeobarbus)*. We suggest to re-elevate *Labeobarbus* from subgeneric to generic rank again, as this group supposedly is monophyletic, and adding species to the large and paraphyletic genus *Barbus* hardly seems meaningful.

Chapter 6; Trophic segregation: predicting diets, using an ecomorphological approach

The presence of several, morphologically distinct *Barbus* species has been convincingly proven in the previous chapters and is not just of academic importance. Rational multispecies management of the Lake Tana ecosystem will be more complicated than the management of a single *Barbus* species. If only one, variable species is present, and e.g. the piscivorous morphs are selectively caught in commercial fisheries, this will not easily lead to overfishing since the piscivores will be replaced by new specimens from the common pool of juveniles. If the piscivores are separate species however, such replacement will not take place, and overfishing will more easily occur. Therefore, the identity of the different Lake Tana barbs is also of interest for rational management of fisheries.

An additional condition for improving rational management of the Lake Tana ecosystem is the understanding of the dynamic interactions among fish stocks and their environment (Sibbing et al. 1994). By sampling gut contents of fish it is possible to get an impression of resource partitioning as it is at the moment, but this method has no predictive value as how to interactions shift, once circumstances change (as they do under the influence of e.g. fisheries or dam construction).

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 the options as to how an organism feeds, and what challenges, imposed on it by a food item, it can meet effectively. If certain feeding strategies are really of importance for survival and reproduction, then natural selection will favour constructions to execute such feeding behaviour efficiently. Each fish parameter (e.g. gape size) matches a food parameter (e.g. food size). Accumulating such fish parameters (e.g. a fish has both crushing teeth and a high density of taste buds) will further specify the food that can be processed efficiently (e.g. large benthic snails). Hence, the more parameters are taken into account, the more precisely and accurately diets can be predicted (Sibbing 1991*a*, Sibbing et al. 1994)(if some boundary conditions are met, such as knowledge about the occurrence of a certain food type in the environment).

We defined the challenges that different types of aquatic food impose on cyprinid fishes by investigating their velocity, size, habitat and chemical and mechanical properties. We hypothesized what structural solutions cyprinids could develop to meet these challenges for a large set of parameters (33), which were proven from functional morphological studies to be critical in the sequence of feeding actions (from detection to digestion). Each structure in an organism has multiple functions. The eventual size and shape of a structure will reflect a trade-off among these different functions. If only one or a few parameters are considered to predict the ability of an organism to deal with a certain food type, these other functions can obscure the prediction. If many parameters are taken, all of which are important for food processing, each individual parameter will also be influenced by other functions, but these will not be the same for each individual parameter. A large cumulative parameter set will therefore give a trend reflecting the importance for food-processing more accurately than a small parameter set. Therefore we used a multivariate approach, using many (33) characters.

These parameters were measured in a large collection of Lake Tana barbs of all morphotypes. The correlations between the set of structural parameters that were predicted to be necessary to deal with certain food types and the set of actual measurements of these parameters in the fish were used as quantitative predictions for the diets (within species) and food resource partitioning (among species) of the Lake Tana *Barbus* species.

The results suggest that there are five trophic groups among our barbs: 1) *B. acutirostris*, *B. dainellii*, *B. gorguari*, *B. longissimus*, and *B. megastoma*, associated with fish and macro-insects; 2) *B. platydorsus*, and *B. truttiformis*, also associated with fish and macro-insects, but less exclusively, 3) *B. crassibarbis*, not clearly associated with any food type; 4) *B. macrophtalmus*, associated with filter-feeding on zooplankton, and 5) *B. brevicephalus*, *B. gorgorensis*, *B. nedgia*, *B. surkis*, and *B. tsanensis*, associated with benthic food types, plants, sessile algae, and plankton. One of the remarkable things is that animal and plant foods do not cluster as separate groups. From the 'fish's viewpoint' some animal foods are more alike to some plant foods than to some other animal foods (e.g. zooplankton is more like phytoplankton for the feeding fish than the former is to larvae/worms, and seeds and molluscs are both perceived as stiff and strong, sedentary foods).

Chapter 7; Trophic segregation: testing predicted against actual diets and food partitioning

In this chapter the quantitative predictions of diets and resource partitioning that were developed in Chapter 6 are tested against actual gut contents data that were collected over a two year period at different locations, habitats, times and seasons. Both frequency of occurrence and volume-percentages of the gut contents give a similar picture of actual food resource partitioning, largely consistent with the five trophic groups that were predicted. We find three large groups with a total of five subgroups: 1) piscivores, with 1a) *B. acutirostris*, *B. dainellii*, *B. gorguari*, *B. longissimus*, *B. megastoma*, and *B. truttiformis*, which are rather strict piscivores; 1b) *B. platydorsus* which is a less specialized piscivore; 2) *B. macrophtalmus*, intermediate between piscivores and non-piscivores; 3) non-piscivores with 3a) the benthivores *B. nedgia* and *B. tsanensis*, 3b) the macrophyti-molluscivorous *B. gorgorensis* and *B. surkis*. *B. brevicephalus*'s position is not consistent within the non-piscivorous group: it was predicted to be linked with the benthivore group, but it mainly feeds on zooplankton. *B. crassibarbis* is the most aberrant species, since it was predicted to be intermediate between piscivores and non-piscivores, and is found to be benthivorous.

It was more difficult to predict the diets of individual species accurately. One of the main reasons for this is that the food types are not evenly distributed over the environment and the gut contents of fish will reflect the availability of food rather than its (in)abilities to utilize particular food types. The following complications for effective diet and food partitioning predictions are discussed: 1) the uneven distribution of food types; 2) the food fish model which describes the mechanistic (not just the correlative) relation between food properties and the morphology of the fish is not always understood completely; 3) food quality differences and competition for food resources: if there is no competition for food, predictions will not work, since then opportunistically feeding fish will take the food that is readily available, especially if it is of high quality; 4) some food types are sometimes difficult to distinguish in the gut contents; 5) the methodology is complex and involves many steps, which could cause information to get lost or distorted. We have tried to avoid this by having continuous feed-back with the original data.

In short, the predictions of food partitioning work especially well when there is 1) a competitive situation, in which 2) food is overall scarce, and for 3) food types that are equally available to all species in the comparison, that are of 4) relatively high quality, and of which 5) the feeding mechanism is well understood

In conclusion, we believe that the ecomorphological method can be a useful tool in predicting the trophic niches of a group of fish species, in a comparative context. Resource partitioning is better predictable than the individual diets of fish, due to differences in abundance and availability of food types. The method works best with closely related species, but the underlying principles of challenges of food types that have to be met by the predator are universal and most probably cross phylogenetic boundaries (Wainwright & Richard 1995). The method could be applied in evaluating and predicting the effects of environmental changes on size and species composition in ecosystems, such as overfishing, the introduction of new species or the building of dams.

The peculiarities of the Lake Tana system, such as its low productivity (Wudneh 1997) and its large number of piscivores (8) led us to a hypothesis about the driving force behind the evolution of the Lake Tana barbs. Most primary production in Lake Tana is phytoplankton. This is not eaten by the barbs since it requires extreme adaptations to retain such small particles, and a specialized phytoplanktivore is already present. Most of the phytoplankton energy gets transferred into zooplankton, which is a difficult food for cyprinids once they grow larger. The most effective zooplanktivore is the small *Barbus trispilopleura* which lives virtually everywhere in Lake Tana. This small fish (< 8 cm) appears to be the most abundant food resource in the lake which is readily available to large barbs (especially in the pelagic regions). As there were no specialized piscivores present in the lake it paid off for the barbs to specialize for this relatively abundant and high quality food type, even if cyprinids are poorly equipped for piscivory. We called this phenomenon the 'zooplankton bottleneck' and hold it responsible for the large number of barbs that eat other fish. It could also explain why the differentiation of feeding characters seems to be most elaborate in the anterior parts of the fish's heads. It appears that the first interface with the prey, i.e. the capturing mechanism was under a stronger selective pressure than other structures in the head and have therefore evolved faster. The capturing, rather than diminution or digestion is especially critical in eating fish.

Chapter 8; Threats to the spawning stocks[10]

When we first started investigating the spawning behaviour of the barbs to clear their taxonomic status (cf. Chapter 4), we focused our study on the larger rivers flowing into Lake Tana, as we knew from local fishermen and a pilot study, that the barbs migrated towards and/or upstream the rivers in the spawning season. We found that during the 1993 and 1994 spawning seasons enormous catches of ripe barbs were taken by the fishermen. This situation was very alarming, because 90% of the fish that were caught were ripe (i.e. about to spawn). Fish on spawning migrations are particularly vulnerable to overfishing as the whole population concentrates in a small area (Craig 1992). Overfishing of spawners can, in extreme cases lead to a decrease in the number of recruits (Gabriel et al. 1989), which endangers the future fish stocks. There are signs by now that recruitment overfishing is already taking place (GOPA-consultants 1996*b*). We also signalled a further threat to the spawning stocks of Lake Tana barbs: the traditional fish poisoning with the dried and crushed seeds of the *berberra* tree (reported in Chapter 4). This method has an adverse effect on the fish stocks as it not only kills the spawners, but also the young fish. In the light of the vulnerability to overfishing of the spawning stock and the increasing number of fishermen in the area that employ this method, some kind of regulation is necessary[11].

---

[10]Published in Bioscience 45: 772-775, 1995.

[11]Measures to ban fish poisoning completely, and to close fishing near and in the rivers during June to September have now been proposed to the authorities by GOPA-consultants (1996*b*), who, according to their references, mysteriously managed not to notice our work on this subject.

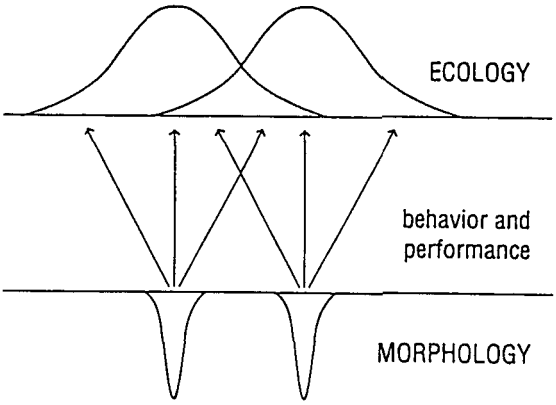


Fig. 1.4. The relation between morphology and ecology. The bottom axis reflects morphological variance, the top axis reflects variation in an ecological trait (such as diet). Morphology and ecology are connected through an intervening variable: behaviour and performance: note that the variation in ecology is larger than that of morphology (after Ricklefs & Miles 1994).

These observations urged us to warn the involved authorities and the scientific community to increase knowledge on freshwater ecosystems and especially on Lake Tana, as they are often undervalued, underexplored, and exceptionally vulnerable to the deleterious influences of human activities (Bruton 1990). As a practical measure, we suggested that the spawning areas should be closed for fisheries during spawning time[11].

Endemic species flocks form natural laboratories for studying evolutionary processes (Coulter et al. 1986). In that respect, Lake Tana forms a unique opportunity, because it is relatively undamaged. Sustainable fisheries can only be achieved if there is a strategy balancing exploitation and conservation of the biodiversity. This should be implemented locally and requires knowledge of the ecosystem. Without local expertise and responsibility neither sustainability nor conservation will be accomplished.

General discussion

The ecomorphological method

Ecomorphology studies the relationships between morphology and ecology. The underlying assumption is that morphology limits the use of ecological space through an intervening variable, such as behaviour or performance. In other words: behaviour covaries with morphology and affects the ecology of an organism (Ricklefs & Miles 1994, Fig.1.4). Therefore, morphology is correlated with ecology in a predictable way. Each morphology is mapped onto a point in ecological space with greatest efficiency. This makes it possible to use clearly defined and repeatable measures to determine a species' niche instead of elaborate and extensive sampling of e.g. gut contents.

However, because an individual's morphology is fairly constant, it is impossible to say something about its niche-breadth. Moreover, the morphology of a species does not readily change with short-term temporal changes of the environment. This means that the pattern we see now between morphology and behaviour is not necessarily adaptive. If, for example a fish species developed some adaptation for competing for the relatively scarce food organism 'a', it could still be able to utilize food organism 'b' (although less efficiently) . If, during the evolutionary history of the fish species the environment changed and food organism 'b' appeared in the ecosystem and became very abundant, it could be more profitable for the fish species to switch to this new food type, although the fish species was not structurally optimized for it. The morphological structures we see now can be the shadow of adaptations to past environmental circumstances. Another complicating factor is phylogenetic differences. Morphological differences do not only reflect ecological importance, but also the phylogenetic history of a taxon. It is important to take this history into account when using the method. In our particular case of the Lake Tana barbs we are dealing with very closely related species (probably each other's closest relatives) and have largely avoided this problem. Moreover, particular (usually rather extreme) adaptations to particular food types probably cross phylogenetic boundaries (Wainwright & Richard 1995).

In this study we have shown that it is possible to predict resource partitioning among the Lake Tana *Barbus* species fairly accurately, while predicting their individual diets is somewhat less successful. However, in general, the method does predict the ability of the species to utilize a particular food type well. This strongly suggests that the environmental factors that drove trophic and morphological differentiation are still present. We expect that the overall low productivity of Lake Tana and the scarcity of food, causing permanent trophic competition among the barb species are the most important of these factors, as was explained in Chapter 7 in the section about the 'zooplankton bottleneck'.

In our ecological research we have mainly focused on food resources until now. However, distribution differences of the species are also a very important ecological factor segregating species. Also these ecological characters can be predicted using the ecomorphological method, provided that the right characters can be defined. Until now we found that the species have different preferences for depths and substratum types (Chapter 2), leading to a preliminary distribution pattern (example in Fig.1.5). Most data were obtained from the southern Bahar Dar Gulf of Lake Tana, but an expedition to the northern parts of the lake has produced a similar picture of species distributions, suggesting that the results of our studies can be extrapolated for the whole lake.

The evolution of the Lake Tana Barbus *species flock*

An evolutionary scenario of the Lake Tana *Barbus* species flock can be developed from the cumulative, and different types of information, gathered in the subsequent chapters. It will be discussed in short, as well as some of its consequences.

Lake Tana was formed by volcanic blocking of the Blue Nile, probably in early Pleistocene times (c. 2 million years ago: Mohr 1962), although it has been suggested that it could be much younger. When the Blue Nile was blocked it probably contained most of the widespread (riverine)

fish species of the Ethiopian high plateau, among which was the ancestral *Barbus* stock, probably very much like the present day riverine *Barbus intermedius*. The ichthyofauna of Lake Tana could develop in isolation, because only 30 km from the outflow of the Blue Nile from the lake it drops over the 40 m high Tissisat waterfalls, and there are only small and few rivers that tribute to Lake Tana. It is highly likely that the Lake Tana barbs evolved sympatrically from one ancestral species, and not in allopatry. Lake Tana is shallow (maximally 14 m) and regularly saucer-shaped without separate basins that could have been isolated during droughts. Moreover, there is no geological evidence for such droughts. It is also unlikely that the Tana-barbs stem from several ancestral species. The Lake Tana basin only occupies a small part of the Ethiopian high plateau, and all riverine barbs of the whole plateau are considered to belong to one, highly variable (pers. obs.) species: *B. intermedius*. It seems unlikely that at the time of the origin of Lake Tana the situation was so different that many species of riverine barbs inhabited the region, that have since gone extinct without leaving clear traces in the rivers.

The ancestral *Barbus* stock was probably also highly variable in morphology, just like the present day *B. intermedius* and the Lake Tana barbs that live in the shore areas (the 'shore-complex'). This is explained by the habitat along the shores, which resembles riverine circumstances more than the open water (e.g. because of stronger terrestrial influences). The high variability of the barb population will have enabled some individuals to radiate into the new lacustrine habitats (such as deep, open water), especially when food was available (such as *B. trispilopleura*) in this low productivity lake. The 'zooplankton bottleneck' can have played an important role in the drive towards the open water. These incipient morphotypes therefore radiated into new niches (adaptive, or initially, exaptive radiation when some individuals already had behavioural or structural characters that made them suitable for food types they never encountered before: exaptation or 'pre-adaptation'), using other, or specializing to use specific food sources.

The only way in which (genetically based) morphological variation can have become fixed in morphotypes, followed by speciation is by assortative reproduction, i.e. specimens of an incipient morphotype have a higher probability of reproducing with specimens of that same incipient morphotype. This process of disruptive selection can result in different populations, and finally in speciation. However, if all barbs migrate towards the rivers to spawn, it is unlikely that assortative mating will develop. We found that there is reproductive segregation, and we hypothesized that spawning triggers will reach different species at different times. When fish feed in the open water it will be triggered later, because potential spawning triggers (such as changes in pH, conductivity, temperature) are first noticeable in the rivers. This could produce temporal spawning segregation. If all fish only migrate up a certain gradient difference, the ones living in the open water will not migrate so far up the rivers, as the shore-dwellers, possibly accounting for spatial differences. This hypothesis is rather speculative, but it is corroborated by the fact that open water feeders, such as *B. acutirostris* and *B. macrophtalmus* are found running almost exclusively in the river mouths.

The variability of the ancestral barb species provided the 'raw material', and could have been a *conditio sine qua non* for speciation in Lake Tana. The much smaller variability of *Varicorhinus beso*, *Clarias gariepinus* and *Oreochromis niloticus* is consistent with the fact that they do not

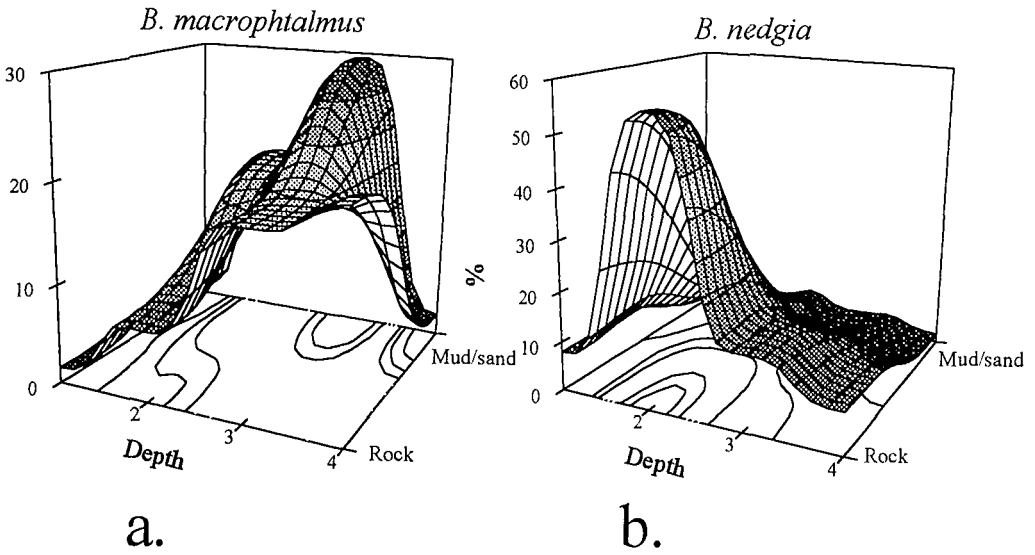


Fig. 1.5. An example of different distribution patterns of barb species in Lake Tana over depths and substrate types. The Y-axis indicates the percentage of specimens caught at a particular depth and substrate. Depth categories are: 1: 0-3 m; 2: 3-6 m; 3: 6-9 m; 4: 9-14 m. *B. macrophtalmus* (**a**) is mainly found in deep water over muddy/sandy substrate; *B. nedgia* (**b**) is found primarily over rocks in shallow water.

belong to species flocks. The lack of variability in *Varicorhinus* and *Oreochromis* can be related to their very specialized feeding behaviour, which does not allow for much flexibility, if feeding is to be efficient. *Varicorhinus* especially eats epilithic diatoms and has specialized scraping jaws. *Oreochromis* is a specialized phytoplankton eater and has a very fine filtering apparatus and a long intestine. *Clarias* appears to be an opportunistic feeder, and we have no clear explanation for its lack in variability. The *Garra* spp. of Lake Tana are not well studied. They do show large variability in size, shape and colour and at least three morphotypes, with different distributions can be distinguished (Mina pers. comm., pers. obs.). Most specimens cannot be identified with the descriptions of *G. quadrimaculata* or *G. dembeensis* that were described for the lake by Rüppell (1836) and Boulenger (1907, 1911). A second species flock might be present in Lake Tana!

Future research

Several aspects that were outside the scope and/or feasibility of this project will be discussed next. Study of these aspects would further increase our knowledge of Lake Tana, both for evolutionary studies, and rational management. They can be divided in phylogenetic/ evolutionary, and ecological/ecomorphological aspects.

Phylogenetic/evolutionary aspects

First of all there are the still unsolved phylogenetic questions. Resolving of the phylogeny of the Lake Tana barbs could clear whether it is a real monophyletic group, and what the relations with the riverine *B. intermedius* and other barbs from the Blue Nile basin are. In this way an independent test of our evolutionary scenario would be performed. At present a study of the mitochondrial genome and of microsatellites is being performed to clear the phylogeny. The mitochondrial DNA does not appear to have significant differences among the *Barbus* species (D. Siebert, pers. comm.). Earlier work on a certain gene of the major histocompatibility complex (Dixon et al. 1994, 1996) did show consistent differences. *B. acutirostris*, *B. nedgia*, *B. truttiformis*, and *B. tsanensis* shared alleles of the gene among specimens of the same species, but not between species. This suggests genetic isolation, but the differences were small and indicate a recent origin for the species. The relationship of the Lake Tana barbs with other 'large' barbs could also give insights in the status and evolution of the genus *Barbus* in general, and the subgenus *Barbus (Labeobarbus)* in particular.

Secondly, the status of the small *Barbus(Enteromius)* species is unclear: are *B. humilis* and *B. trispilopleura* different or synonymous?; is the (endemic) *B. pleurogramma* synonymous with the widespread East-African *B. paludinosus*?

Finally, the *Garra* morphotypes should be examined, because they might well form a small second species flock in Lake Tana, increasing the lake's value as a natural laboratory.

Ecological/ecomorphological aspects

The distribution of the different *Barbus* species in time and space have only been studied to a very limited extent. Many more data are present and will be analysed shortly. Distribution differences can give insight into resource partitioning of the different species. The fact that all piscivorous barbs mainly feed on *B. trispilopleura* raises the question how competition can be avoided. Spatial (depth/ substratum/habitat) and temporal (diurnal) differences in e.g. foraging time and differences in hunting strategies can be mechanisms for this. A research program for studying resource partitioning among piscivores is anticipated.

The 'zooplankton bottleneck' suggests that the role of *B. trispilopleura* is extremely important for the conversion of primary production into fish. This is interesting from an ecological and evolutionary viewpoint, but also from a management viewpoint, because the large piscivorous barbs are the most popular for human consumption. A study on the biomass and productivity of *B. trispilopleura* is therefore urgently needed.

We tested the ecomorphological method using a group of closely related species in a low productivity environment. Both factors probably increase the chance of success for the method, but

we hypothesized that it should also work with less closely related species, even if their phylogenetic relationships are not well known. This should be especially true when food types that pose extreme challenges to fish are taken into account. To test this latter hypothesis an aquatic ecosystem containing species that are not all closely related should be examined in the same way as the Lake Tana barbs. Preferably this should be done several times, using low and high productivity systems, both temperate and tropical. The least such a study can yield is insights as to why this ecomorphological method cannot work in certain circumstances; in the best case it provides us with a generalized method for quickly and accurately reconstructing trophic hierarchies within food webs.

Chapter 2

The barbs (*Barbus* spp.) of Lake Tana: a forgottten species flock?

Leo A.J. Nagelkerke[1], Ferdinand A. Sibbing[1], Jos G.M. van den Boogaart[1], Eddy H.R.R. Lammens[2] & Jan W.M. Osse[1]

[1] *Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

[2] *Limnological Institute, Vijverhof Laboratory, Netherlands Institute for Ecological Research, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands*

Published in: *Environmental Biology of Fishes* (1994) **39**: 1-22.

ABSTRACT

In October-December 1990, the large barbs (*Barbus*) that contribute more than 60% of the catch in Lake Tana (northern Ethiopia) were studied. Previous authors (Rüppell 1836, Boulenger 1902, 1911, Bini 1940) described from 6 to 23 (sub)species for the lake. Banister (1973) lumped all of these into one subspecies: *Barbus intermedius intermedius* Rüppel, 1836. We found that the Lake Tana *Barbus* could be readily categorized in at least 13 discrete morphotypes, some of which were already distinguished by local fishermen. None of the known descriptions are adequate to distinguish the barbs unambiguously, which is important for monitoring and management of developing fisheries. Intermediates between morphotypes were rare (<10 %). By applying canonical discriminant analysis on a set of 17 morphometric characters (including some directly associated with feeding) our initial morphotype-distinction was confirmed. Also, differences between the morphotypes in distribution, related to depth and substratum were found, as well as differences in intestinal contents, a key to the food-niche. The high number of piscivorous morphotypes (8 out of 13) was striking as piscivory is relatively rare among cyprinids. Piscivory was found to be highly correlated with morphological (feeding related) characters. The presence of discrete morphotypes, that also differ in food-niche and distribution, strongly suggests that several distinct populations exist, that may be (partly or completely) reproductively segregated. Knowledge about these populations, that may represent separate units of fish stock, is of crucial importance for the management of sustainable fisheries and protection of the biodiversity in Lake Tana. It is possible that several species or even a unique cyprinid species flock are present, that urgently need protection.

INTRODUCTION

Lake Tana, the source of the Blue Nile, is Ethiopia's largest lake. It probably was formed during late Pliocene or early Pleistocene times (Mohr 1962). It now covers an area of about 3150 km^2 and has an average depth of 8 m, with a maximum of 14 m. It is situated at an altitude of 1830 m and can be characterized as an oligo-mesotrophic lake (Rzóska 1976, Admasu 1986) with a very truncated fish fauna (Greenwood 1976), i.e. it is poor in species and families.

There is only one representative of the family Cichlidae: Oreochromis niloticus (Linnaeus 1766), a very widespread species in Africa. The three species of *Clarias* Scopoli, 1777 (family Clariidae), that Boulenger (1911) describes for the lake (including the endemic *Clarias tsanensis* Boulenger 1902), have recently been synonimized to *Clarias gariepinus* Burchell 1822, the most common member of this genus (Teugels 1982).

The largest family in the lake is the Cyprinidae, which is represented by three genera: *Varicorhinus* Rüppell 1836, with one single species *V.beso* Rüppell 1836, *Garra* Hamilton 1822 (formerly *Discognathus*, Heckel 1842), for which Boulenger (1911) describes two species in Lake Tana: *G.quadrimaculata* (Rüppell 1836) and *G.dembeensis* (Rüppell 1836), and the least well

described genus of cyprinid fishes from Lake Tana: *Barbus* Cuvier & Cloquet 1816, which has been revised several times. Rüppell (1836), was the first to describe 5 *Barbus* and 1 *Labeobarbus* (later synonimized to *Barbus* as well). Boulenger (1911), mentions 10 large species (5 of which were described by him as new species in 1902) and 3 small ones, the latter not only being distinguished by their size, but also by scale and dorsal spine characters. Bini (1940) considered these small barbs as belonging to the subgenus *Enteromius* Cope 1869, and mentioned the same 3 species. He classified the large barbs in the subgenus *Labeobarbus* and described 23 (sub)species.

Boulenger's key to the species (1911) as well as the other known descriptions of the large Lake Tana barbs are inadequate to distinguish the species unambiguously. Bini's work does not solve this problem either. Banister (1973) lumped all the (sub)species of *Barbus* described for the lake by Rüppell, Boulenger and Bini in one extremely variable subspecies *Barbus intermedius intermedius* Rüppell.

In this paper, however, we will show that it is likely that several distinct populations of barbs are present in Lake Tana and that it is possible that a unique species flock is present, representing a great biodiversity most important for both evolutionary studies and fisheries management. This cyprinid species flock would make it the only one still intact, since the one in Lake Lanao on the Philippines, has virtually disappeared (Kornfield & Carpenter 1984).

In 1986, the Lake Tana Fisheries Resources Development Program (LTFRDP) was started by the Ethiopian Ministry of Agriculture in cooperation with the Development Department of the Ethiopian Orthodox Church. Within this project, investigations of the fish stocks were started by Wudneh (personal communication), accounting for the four (commercially interesting) species that were recognized for Lake Tana: *Oreochromis niloticus*, *Clarias gariepinus*, *Varicorhinus beso* and *Barbus intermedius*, the latter representing more than 60% of the commercial catch (Wudneh unpublished). The morphological differences that were encountered in the *Barbus* flock were striking (different morphotypes have already been recognized by the local fishermen for centuries (Rüppell 1836)). It was suspected that several populations of *Barbus* occurred in the lake, each with its specific (trophical) niche, thus representing different ecotypes. The existence of numerous ecotypes would make a reconstruction of a food web more complicated than with the four species that were recognized initially. Knowledge of such ecological interrelations of the fishes are, moreover, crucial for the monitoring and management of fisheries.

To establish a rational management of fisheries, insights into the flock structure (what are the unit fish stocks?) are essential (Law & Grey 1988). Overexploitation of some flocks could cause dramatic shifts in the composition of the ecosystem. In order to establish sustainable exploitation of the fish resources and to protect the biodiversity of Lake Tana, which is still unaffected by large-scale fisheries and pollution, it is important to investigate whether the major part of the fish stock belongs to one panmictic population of *Barbus intermedius intermedius* or whether several morphotypes (or even species) exist.

Table 2.1. Trivial and abbreviated names of the thirteen morphotypes, together with the preliminary, qualitative descriptions, used in the field to distinguish each morphotype.

Trivial name	Abbrev-iated name	Qualitative description, based on general appearance
Acute	Ac	Head longer than body depth, tapering and narrow; terminal mouth; shallow body; silvery white
Barbel	Ba	Irregular, slightly concave dorsal head profile; both pairs of barbels very long, thick and dark-coloured; lower jaw directed obliquely upward; large, downward protrusion
Bighead	Bh	Head longer than body depth, with convex dorsal profile; large downward protrusion with a very large inferior gape; lips well developed, without lobes
Bigmouth big-eye	Be	Very large eye (diameter equal to snout length) lower jaw directed obliquely upward, often extending beyond the upper jaw; terminal mouth; nuchal hump
Bigmouth mini-eye	Mi	Head longer than body depth; terminal, wide gape; spindle-shaped, slender body; small eye (three eye diameters in snoutlength); greenish / yellowish
Bigmouth small-eye	Se	Lower jaw directed upward, extending beyond the upper jaw; very large terminal mouth; nuchal hump; two eye diameters in snout; slightly concave dorsal head profile
Carplike	Ca	Deep-bodied; usually a large anal opening; short, wide head (head-length 5 times in fork length, shorter than body depth); eye diameter at least two times in snoutlength; long barbels; small, inferior gape; golden-yellowish
Dark	Da	Conspicuous nuchal hump; large terminal gape; lower jaw directed obliquely upward, not extending beyond the upper jaw; straight dorsal head profile; very dark brown-reddish to black
Intermedius	In	No extreme characters; downward protrusion; medium-sized inferior gape; medium-sized barbels; headlength less than 5 times in fork length
Lip	Li	Well-developed lips, usually with large lobes on lower or upper jaw or on both; posterior barbels thick and long
Troutlike	Tr	Spindle-shaped, but relatively deep body; head shorter than body depth, straight dorsal profile; terminal mouth
White hunch	Wh	Nuchal hump (variable in size), body very wide in the pectoral area; wide head with slightly concave dorsal profile; lower jaw directed obliquely upward; jaws equal in length; gape (sub)terminal
Zurki	Zu	Deep-bodied; short head (head length 5 times in fork length, shorter than body depth); small barbels; small, inferior gape; dark green

If all variation found in the Lake Tana *Barbus* is due to extreme plasticity of one species, all intermediate morphs would be expected to occur. If discrete morphotypes are found, this would suggest that adaptive radiation has taken place in the past, resulting in several (partly) reproductively isolated populations.

In a general study of African cyprinids Matthes (1963) concluded that *Barbus* species are highly adaptable and that this large genus must have speciated explosively whenever the environment was suitable. According to his views the African species can be split into several distinct groups by investigation of their morphology in relation to feeding. Competition for food resources is an important factor in natural selection and thus in the adaptive radiation of species. Hypotheses about dominant selective factors in the adaptive radiation that led to the great diversity in Lake Tana *Barbus*, can be provided by relating the structural (morphological) differences to niche segregation and the different ways of exploiting a common habitat.

By studying functional morphology of the feeding apparatus we eventually aim at deducing the utilizable diets for the different morphotypes from the available food spectrum, as has already been demonstrated for common carp, *Cyprinus carpio* (Sibbing 1988, 1991*a*, 1991*b*, Sibbing et al. 1986). Such predicted potential food niches will be tested against the intestine contents selected from the available food spectrum. These actual feeding data should match the hypothesized feeding abilities and show the predictive value of this method in field research.

Knowledge of the interactions among different populations and their food niches makes it possible to reconstruct a food web that is not only essential for the rational management of fish stocks, but also potentially helpful for comprehending the evolutionary mechanisms of adaptive radiation.

This preliminary study focuses on testing our initial hypothesis that numerous, discrete morphotypes are present in the lake. This was based on a 10 week pilot study, during October-December 1990 at Lake Tana. After the initial identification of morphotypes, based on general appearance, morphometric characters were measured and analyzed. An initial analysis of collected intestine contents is also included.

MATERIALS AND METHODS

Fish collection

Some of the fishes were collected during two bottom-trawling programs of the fisheries project, during the first 5 days of November and December 1990, at the beginning of the dry season. Each program consisted of trawling 13 sampling stations in the southern bay of Lake Tana. These stations had sandy or muddy substrata and were trawled at daytime (between 0630 and 1100), for 30 min, using a bottom-trawl with a cod-end stretched mesh size of 40 mm. Rocky areas were not trawled. A total of approximately 500 kg of *Barbus* was collected in this way.

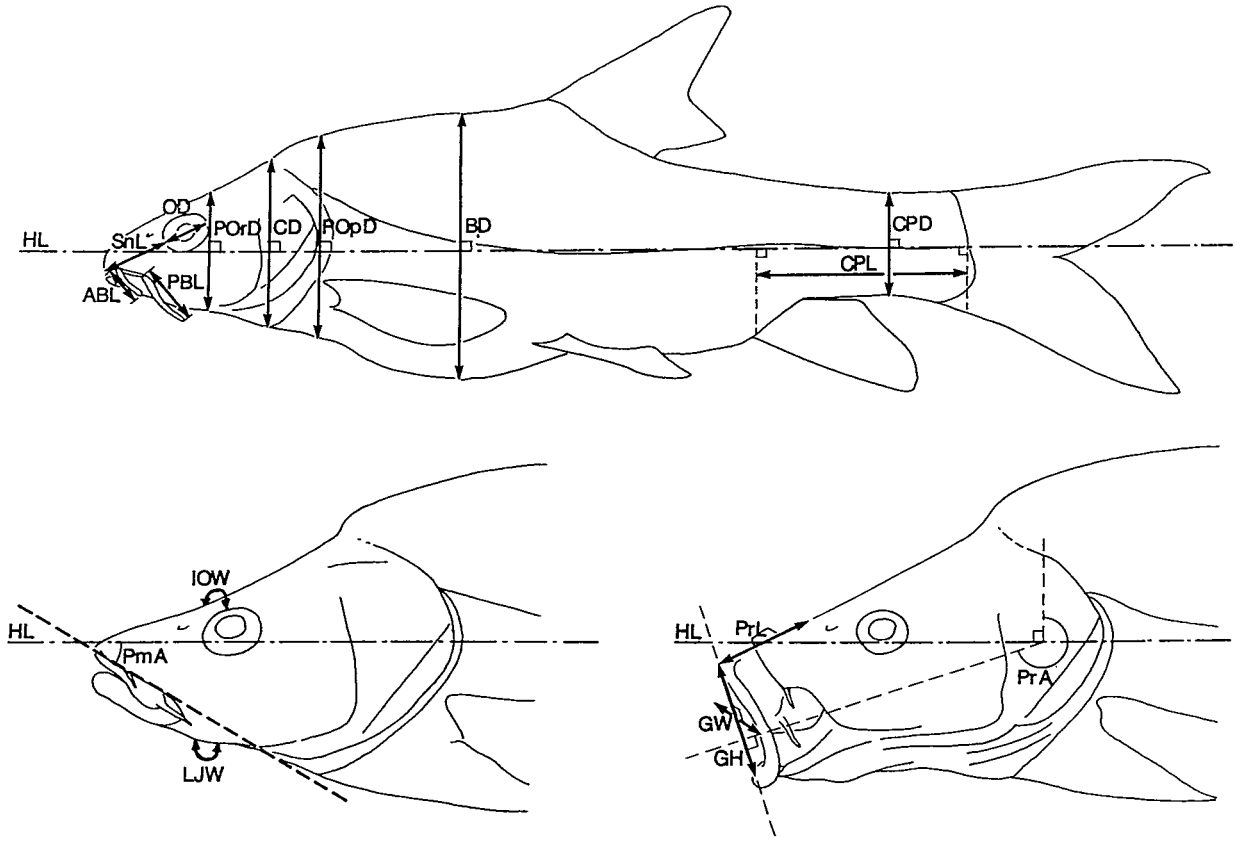


Fig. 2.1. Parameters used for the canonical variate analysis. Abbreviations and descriptions in table 2.2.

Table 2.2. The range of fork lengths (FL) of each morphotype, used for calculating the mass equation and the number of specimens is indicated. The utilized mass equation is: $M = a * FL^b$; with M = mass (g) and FL is in mm. R^2 is the correlation coefficient.

Trivial name	Fork length (mm)			n	Mass equation coefficients		
	Mean	Minimum	Maximum		a (*10^5)	b	R^2
Acute	291	140	482	37	0.345	3.215	0.99
Barbel	347	200	479	24	0.660	3.130	0.98
Bighead	370	251	490	16	2.05	2.909	0.90
Bigmouth big-eye	264	114	390	33	0.471	3.180	0.99
Bigmouth mini-eye	422	312	589	21	15.5	2.573	0.94
Bigmouth small-eye	375	170	499	25	0.669	3.093	0.98
Carplike	394	323	526	21	0.900	3.089	0.96
Dark	297	145	495	33	0.344	3.242	0.99
Intermedius	238	98	430	41	0.700	3.134	1.00
Lip	329	201	590	61	1.33	3.002	0.97
Troutlike	312	145	442	47	0.618	3.126	0.98
White hunch	326	194	476	32	0.615	3.152	0.98
Zurki	299	181	386	29	0.229	3.327	0.98
Beso	265	228	311	3	0.485	3.208	0.98

The commercial overnight gill-netting catch (near the bottom, with 80-100 mm stretched mesh size), was checked for *Barbus* morphotypes during 30 days (total of approximately 14,000 kg). During 12 of these days, the catch was completely sorted for species and morphotypes and fishermen were interviewed about the catch site (depth, substratum, shore or open water). Some additional gill-netting was performed, including small mesh-sized nets (10-100 mm stretched mesh) near the bottom and at the water surface.

Barbus-type distinction

At first, morphotypes were distinguished on general appearance, often in cooperation with local fishermen. Trivial names (often descriptive) were given (Table 2.1). Photographs of fresh fishes (Fig. 2.2) were taken in a later stage, using a perspex cuvette, as described in Barel et al. (1977), but modified for the larger size of the *Barbus* specimens (70x20x30 cm).

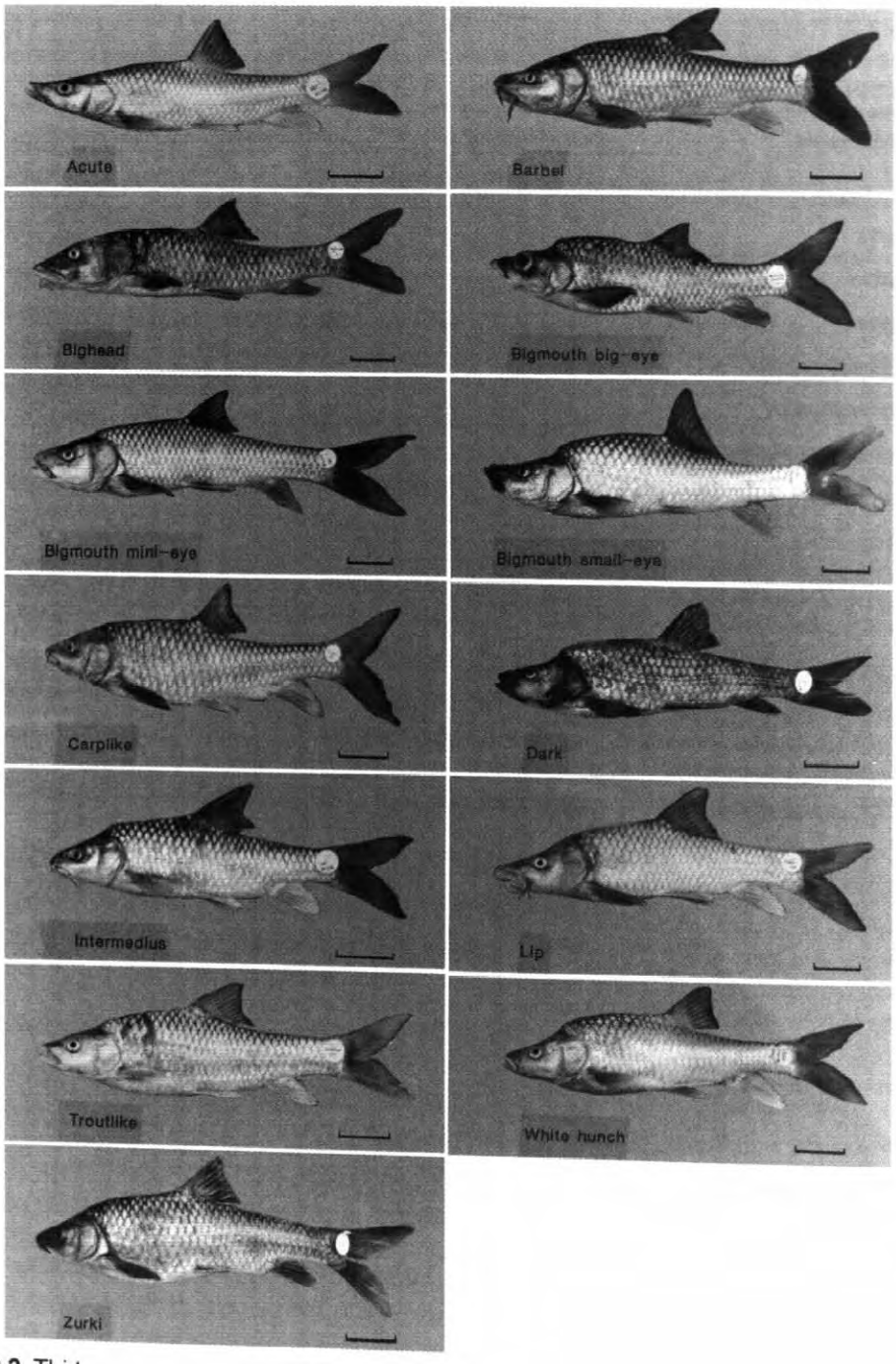


Fig. 2.2. Thirteen morphotypes of Lake Tana *Barbus*; specimens were freshly photographed. Bars indicate 5 cm.

On at least 6 specimens of each morphotype, ranging from 19 to 65 cm fork length (Table 2.2) 17 external characters were measured (Fig. 2.1, Table 2.3). Of each morphotype approximately equal numbers of males and females were measured. Most measurements were made, either parallel or perpendicular to the horizontal line, which was defined as the line running through the straight caudal part of the lateral line. Several other ways to determine this line (running through landmarks on the fish) appeared less satisfactory. Meristic counts, as used by Boulenger (1902, 1911), Bini (1940) and Banister (1973) showed extremely small variation and were not used in the eventual analysis. Some quite distinguishing characters, such as the presence of a nuchal hump, a concave or convex head or the development of lips were difficult to quantify and could not be taken into account in the mathematical analysis. However, they were very important in distinguishing the morphotypes on general appearance.

The 17 characters, for which complete data-sets were available, were log-transformed and used in a canonical discriminant analysis (James 1985). In this method canonical variates are constructed by making linear combinations of the original parameters. These combinations are chosen so as to maximize the quotient of the variance between (a priori chosen) groups and the variance within groups. The first canonical variate gives the best overall result, for all specimens, the second canonical variate gives the second best, etc. The loading factors of the canonical variates (See Table 2.3) show the correlation of the original parameter with the canonical variate. The a priori recognized morphotypes were used as groups. The group means of the canonical variates were clustered, using Ward's minimum variance method (Ward 1963), in which the distance between two clusters is the summed ANOVA sums of squares (over all variables) between them. This distance is expressed as a fraction of the total sums of squares (squared semipartial correlations). All multivariate statistics were performed using Statistical Analysis System (SAS) software (SAS Institute Inc., Cary, NC, USA).

Intestine contents analysis

A series of intestine contents was collected from fishes from both gill-netting and trawling, and preserved in 4% formalin. From all morphotypes, intestine contents of fishes ranging from 20 to 50 cm were analyzed. Volume-percentage and frequencies of each of six food-categories (fish, plant-material, molluscs, other benthos, zooplankton and detritus/substratum) were estimated. The collection of intestine contents was limited to a restricted sample (Fig. 9).

RESULTS

***Barbus* morphotypes**

When starting the fieldwork, a priori morphotypes were discriminated, based on general appearance (Fig. 2.2). Although these shapes were very different, the extreme homogeneity of meristic counts (such as the number of lateral line scales and the number of gill-rakers) was striking, as was already observed by Boulenger (1902). The characters that were initially used to discriminate the morphotypes were mainly of a qualitative nature (Table 2.1) and still preliminary;

they are useful for field characterization, but not very accurate. However, more than 90% of the fishes could be easily sorted into morphotypes. No continuum of intermediate forms was present in Lake Tana. In contrast, Banister (1973) concluded that the large barbs from the Ethiopian region, including Lake Tana, do constitute such a continuum.

Table 2.3. Characters used for the canonical discriminant analysis, their descriptions (see also Figure 2.1) and the loading factors of the canonical variates. Only loading factors of which the absolute value was larger than the mean of the absolute values are shown. The three largest loading factors for each canonical variate are bold-printed as well as the characters associated with these high loading factors.

Character	Description	Loading factors of canonical variates			
		Can1	Can2	Can3	Can4
Body Depth (BD)	Maximum dorsoventral dimension of the body			-0.175	
Post-orbital Depth (POrD)	Dorsoventral dimension of the head at the caudal edge of the orbit				-0.290
Cranial Depth (CD)	Dorsoventral dimension of the head at the rostral edge of the supra-occipital crista				-0.199
Post-opercular Depth (POpD)	Dorsoventral dimension of the body at the caudal, bony edge of the operculum				-0.207
Caudal Peduncle Depth (CPD)	Minimum dorsoventral dimension of the caudal peduncle			-0.221	-0.217
Caudal Peduncle Length (CPL)	Dimension between the insertion of the anal fin and the caudal end of the lateral line, parallel to the HL		0.172	**-0.262**	**-0.300**
Orbit Diameter (OD)	Maximum orbit diameter	0.345			
Snoutlength (SnL)	Minimum dimension between the tip of the premaxillae and the orbit		**0.462**		
Inter-orbital Width (IOW)	Minimum dimension between the two orbits	-0.276		**-0.351**	-0.200
Lower Jaw Width (LJW)	Maximum transversal dimension of the head between the retro-articular bones (mouth closed)	0.338	**0.314**		
Gape Height (GH)	Maximum dorsoventral dimension of the protruded mouth-opening	0.369	**0.331**		-0.170
Gape Width (GW)	Maximum transversal dimension of the protruded mouth-opening	0.428	0.256		
Anterior Barbel Length (ABL)	Maximum length of the anterior barbel	**-0.483**	-0.183	0.228	
Posterior Barbel Length (PBL)	Maximum length of the posterior barbel	-0.391		0.176	
Premaxillary Angle (PmA)	Angle between the HL and the line running along the caudal edge of the premaxillary bone	**0.642**			**-0.349**
Protrusion Angle (PrA)	Angle between the HL and the line perpendicular to the line connecting the rostral tips of the premaxillae and dentary bones, in protruded situation	**0.735**			
Protrusion Length (PrL)	Dimension between the rostral tips of the premaxillae and the rostral edge of the supra-ethmoid in the medial plain		0.270	**0.297**	**-0.300**

Eventually, 13 morphotypes were distinguished and used further for this study. Morphotypes were consistent over a considerable size range in both males and females. Therefore the differences between the morphotypes can not be accounted for by age or sexe. Their trivial and abbreviated names can be found in Table 2.1. From the canonical discriminant analysis of the 17 log-transformed measurements it was found that the first canonical variate accounts for 44% of the variance, the first four for 81% and the first seven for 97%.

Table 2.3 shows the character loadings for the first four canonical variates. Anterior barbel length, premaxillary angles and protrusion angles are the most important variables for discrimination along the first canonical axis; snout length, lower jaw width and gape height along the second; caudal peduncle length, interorbital width and protrusion-length along the third and caudal peduncle length, premaxillary angles and protrusion-length along the fourth canonical axis.

Figure 2.3 shows that with the first 4 canonical variates the groups can be well separated, except for the combination Ca, In and Zu, and the combination Da and Wh. Along the first canonical axis, two groups can be separated, one constituted of morphotypes Ba,Ca,In,Li,Zu and Bh and the other by Be, Mi and Ac,Se,Da,Tr,Wh; the second group has shorter anterior barbels and larger protrusion and premaxillary angles.

In the first group, Bh can be separated from Ba,Ca,In,Li,Zu along the second canonical axis, by having a larger gape height, a longer snout and a wider lower jaw. Ba and Li can be separated from Ca,In,Zu along the third canonical axis, the latter having a shorter protrusion, a longer caudal peduncle and a larger interorbital width. Ba can be separated from Li along the first canonical axis: Ba has a shorter anterior barbel and larger protrusion and premaxillary angles.

The second group (Be,Mi and Ac,Se,Da,Tr,Wh) can be split in three along the second canonical axis: Mi has the longest snout, the widest lower jaw and the largest gape height, Be is smallest in these characters, while the group Ac,Se,Da,Tr,Wh is intermediate. Tr can be separated from Ac,Se,Da,Wh along the third canonical axis, because it has a longer caudal peduncle, a larger interorbital width and a shorter protrusion. Ac and Se can be separated along the fourth canonical axis. Ac has a shorter caudal peduncle and protrusion and a smaller premaxillary angle. Da,Wh is intermediate for these characters and can also be separated from Ac and Se along the first canonical axis, because Da,Wh has longer anterior barbels and smaller protrusion and premaxillary angles.

Although the two groups Ca,In,Zu and Da,Wh cannot be split into different morphotypes by this analysis, they are still kept as valid morphotypes because there are qualitative characters, not included in the analysis, that can separate them. Da and Wh have discrete colours (Da is very dark, Wh is silvery white). Ca can be separated from In and Zu (and from any of the other morphotypes) by the robust pharyngeal jaws (Fig. 2.4). No intermediate forms of pharyngeal jaws between Ca and other morphotypes have been found. Zu is always dark green, while In is silvery white.

Using the the first 7 canonical variates, the morphotypes were clustered using Ward's minimum variance method (Fig. 2.5). The clustering shows that the morphotypes can be separated in two major groups, one containing morphotypes Ac, Ba, Be, Mi, Se, Da, Tr and Wh and the other containing Bh, Ca, In, Li and Zu.

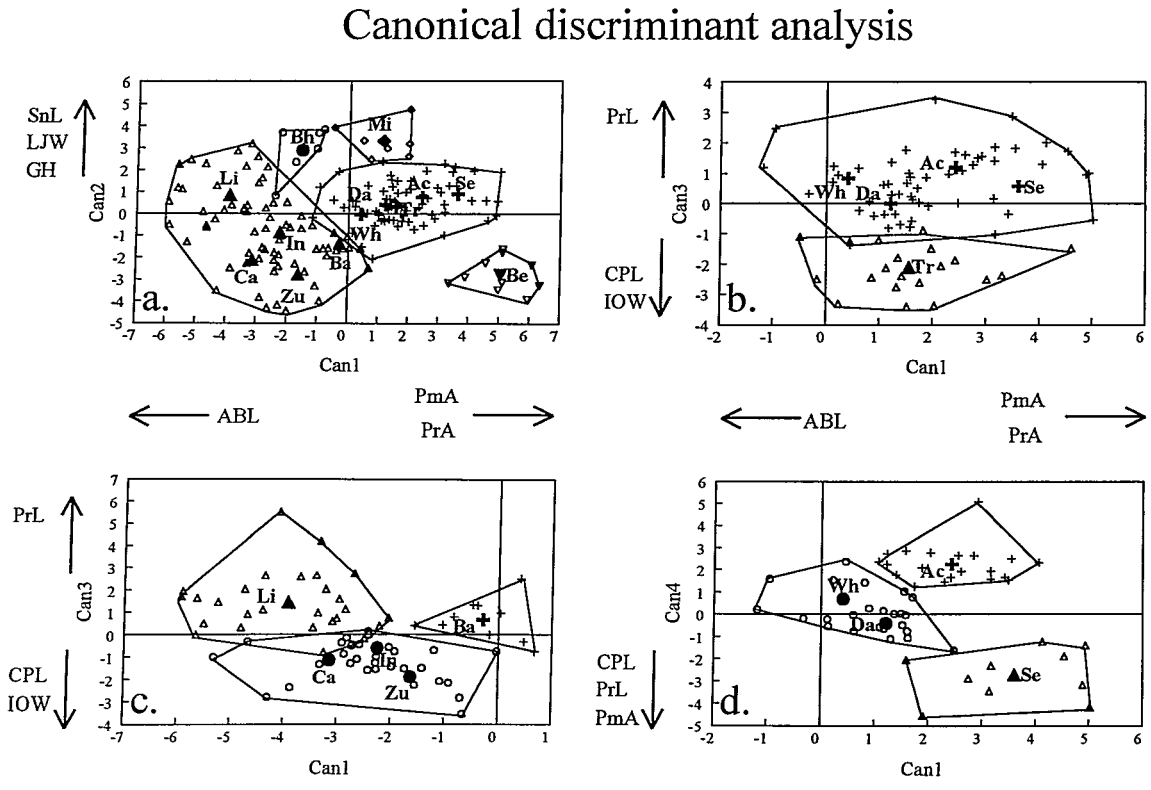


Fig. 2.3. Separation of the a priori morphotypes along the first 4 canonical axes. Bold symbols represent means of the morphotypes (indicated by their letter code). The abbreviations along the axes represent the 3 characters with the highest loading factors; arrows indicate in which direction these characters increase. For abbreviations and loading factors, see table 2.2.

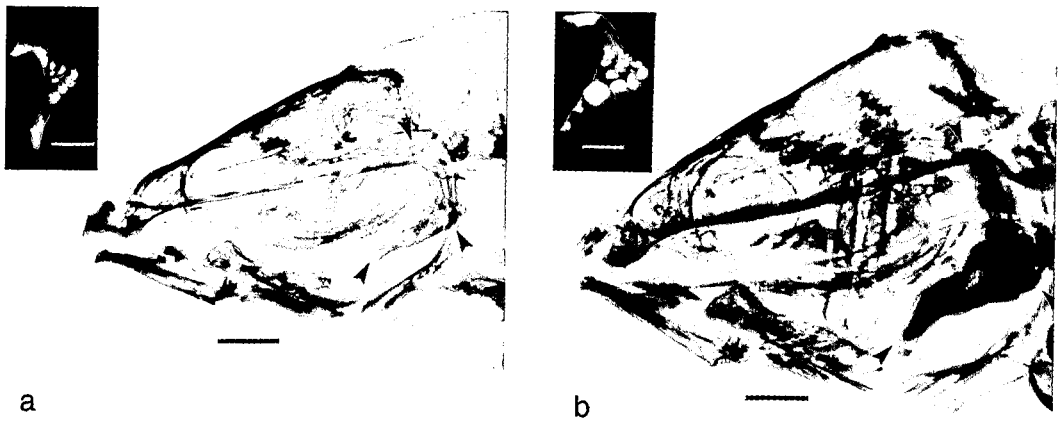


Fig. 2.4. X-ray photographs of 'intermedius' **(a)** and 'carplike' **(b)**, showing the differences in relative size and shape of pharyngeal jaws and teeth. Bars represent 1 cm.

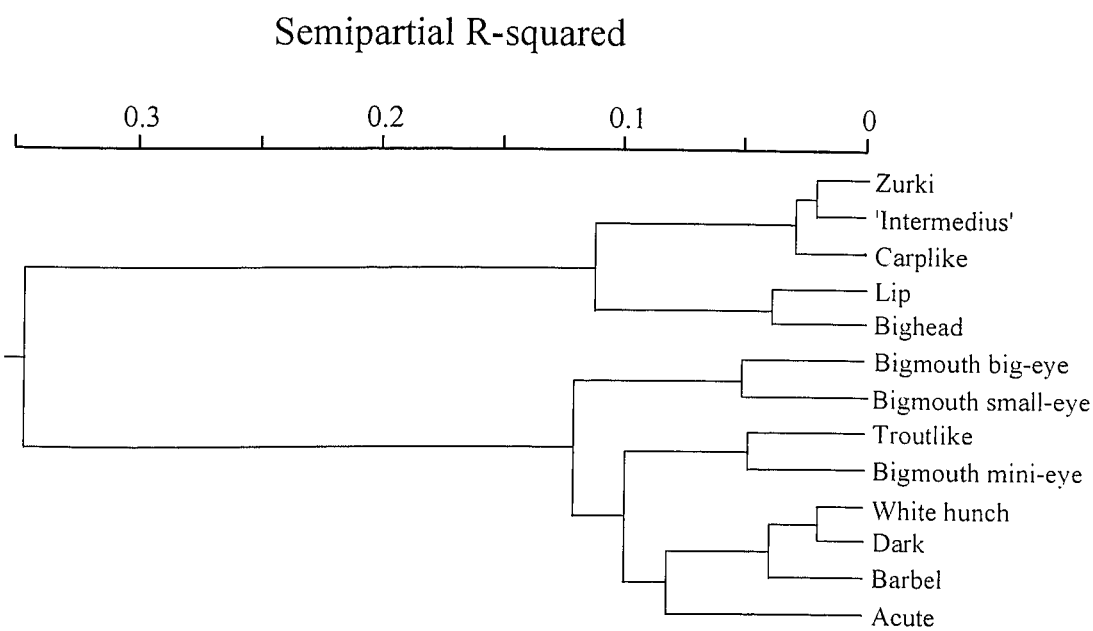


Fig. 2.5. Cluster diagram of the means of the first 7 canonical variates for each morphotype, using Ward's minimum variance method (see text).

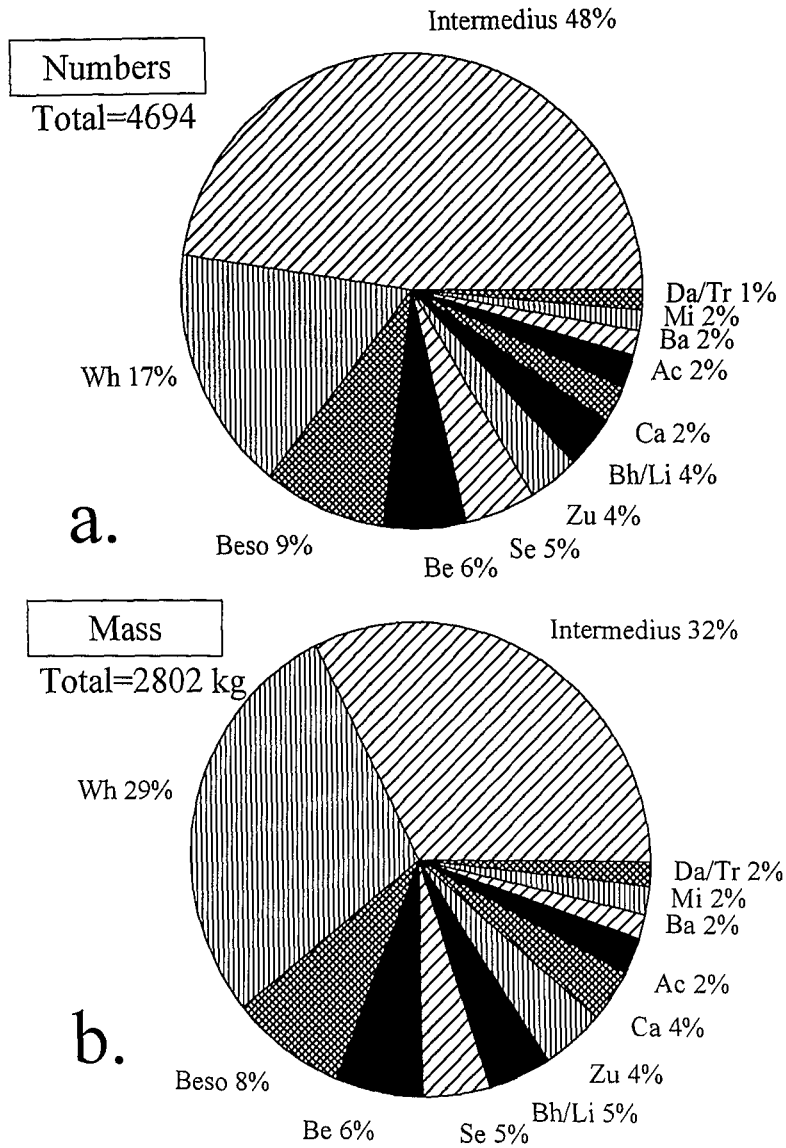


Fig. 2.6. Distribution of the morphotypes in the overnight, commercial gillnet catch during 12 days in October-December 1990. The distribution is given in numbers **(a)**. These numbers were used, together with length-frequency distributions and the mass-equations (Table 2.1), to reconstruct the distribution in kg **(b)**, showing the relative importance of the different morphotypes for fisheries.

Barbus morphotype occurrence

The numerical differentiation of the commercial cyprinid catch (which is an overnight catch of relatively large fishes: > 20 cm) in different morphotypes is shown in Figure 2.6*a*. 'Intermedius' is the most common barb (48%), followed by 'white hunch' (17%). *Varicorhinus beso* is the third most frequent cyprinid fish in the catch (9%). The other *Barbus* morphotypes each contribute little to the total catch (total 26%). By using the fish mass equations from Table 2.2 and the mean forklength of each morphotype in the catch, the mass-contribution of each morphotype to the total catch can be reconstructed (Fig. 2.6*b*). 'Intermedius' and 'white hunch' are now approximately equally important (32% respectively 29%), due to the larger size of 'white hunch'.

The morphotypes are not evenly distributed in the environment. There is a differentiation in depth distribution (Fig. 2.7) with 'Intermedius' and 'Troutlike', respectively, less than 10% and approximately 65% in shallow water up to 3 m depth, and in substratum distribution (Fig. 2.8) with 'Acute' and 'Lip' respectively 40 and 80% over rocks.

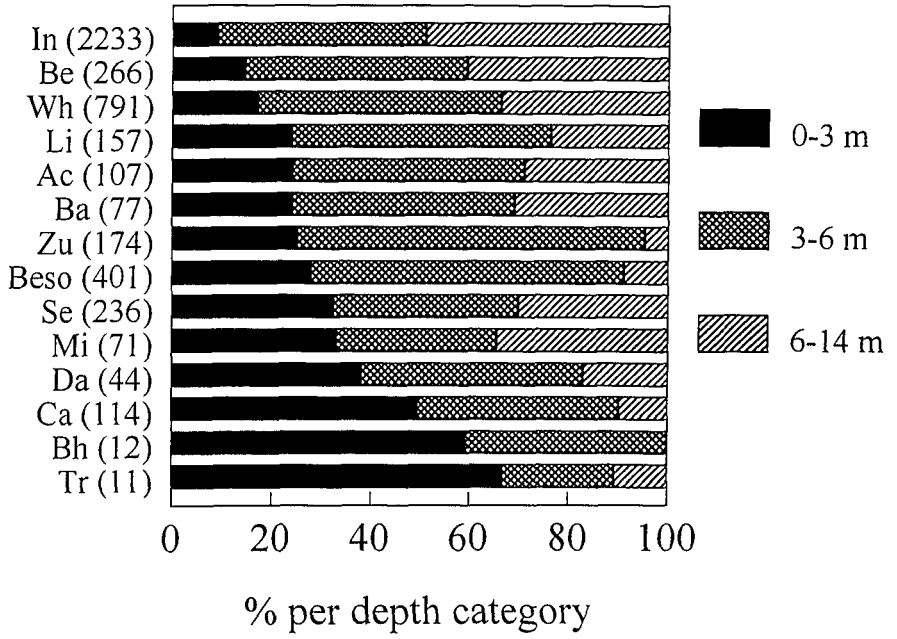


Fig. 2.7. Distribution of the morphotypes over 3 depth categories in the overnight, commercial gillnet catch during 12 days in October-December 1990. The percentage per depth category is given for each morphotype. The number of specimens per morphotype is indicated in brackets.

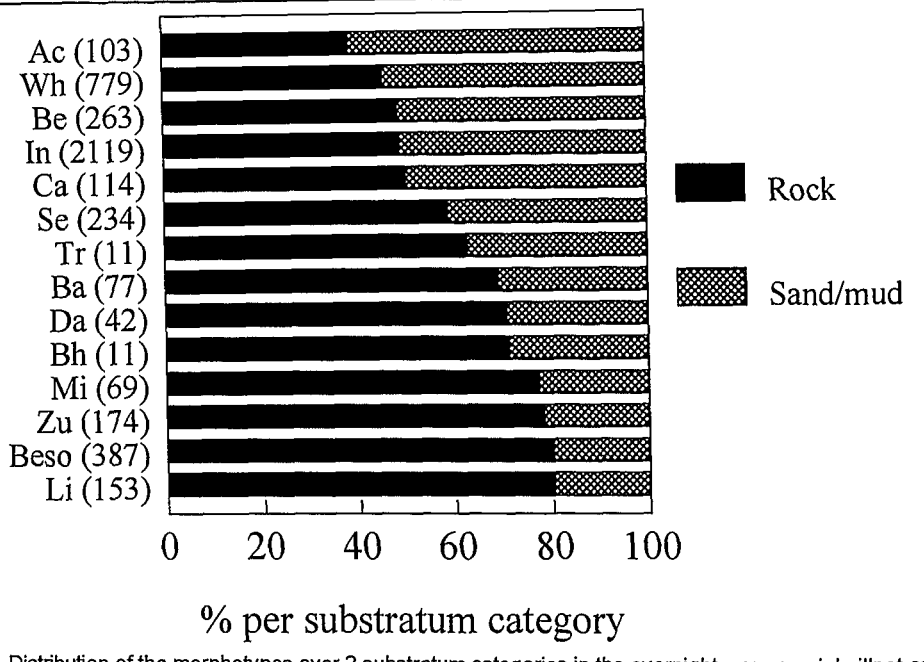


Fig. 2.8. Distribution of the morphotypes over 2 substratum categories in the overnight, commercial gillnet catch during 12 days in October-December 1990. The percentage per substratum is given for each morphotype. The number of specimens per morphotype is indicated in brackets.

Intestine contents

The frequency of occurrence of the specific food categories is different for the morphotypes (Fig. 2.9*a*). 'Intermedius', 'lip' and 'dark' appear most polyphagous. The mean volume-percentage of each food category is significantly dependent on the morphotypes ($p<0.001$, MANOVA). Although most morphotypes eat several or all food categories, some are found to be biased towards a single category, e.g. substratum and detritus in 'barbel', molluscs in 'carplike', plant material in 'zurki', and fish in 'white hunch', 'acute', 'bigmouth mini-eye' and 'bighead'. The large number of morphotypes in which fish is a substantial food item i.e. those morphotypes of which more than 20% of the individuals have been found to eat fish is remarkable: 8 out of 13. Because of this large number of piscivores even though piscivory is relatively rare among cyprinids (Matthes 1963, Sibbing 1991*a*) the distinction between piscivorous types ('acute', 'bighead', 'bigmouth mini-eye' 'small-eye' and 'big-eye', 'dark', 'troutlike' and 'white hunch') and the non-piscivores will be maintained in the next section.

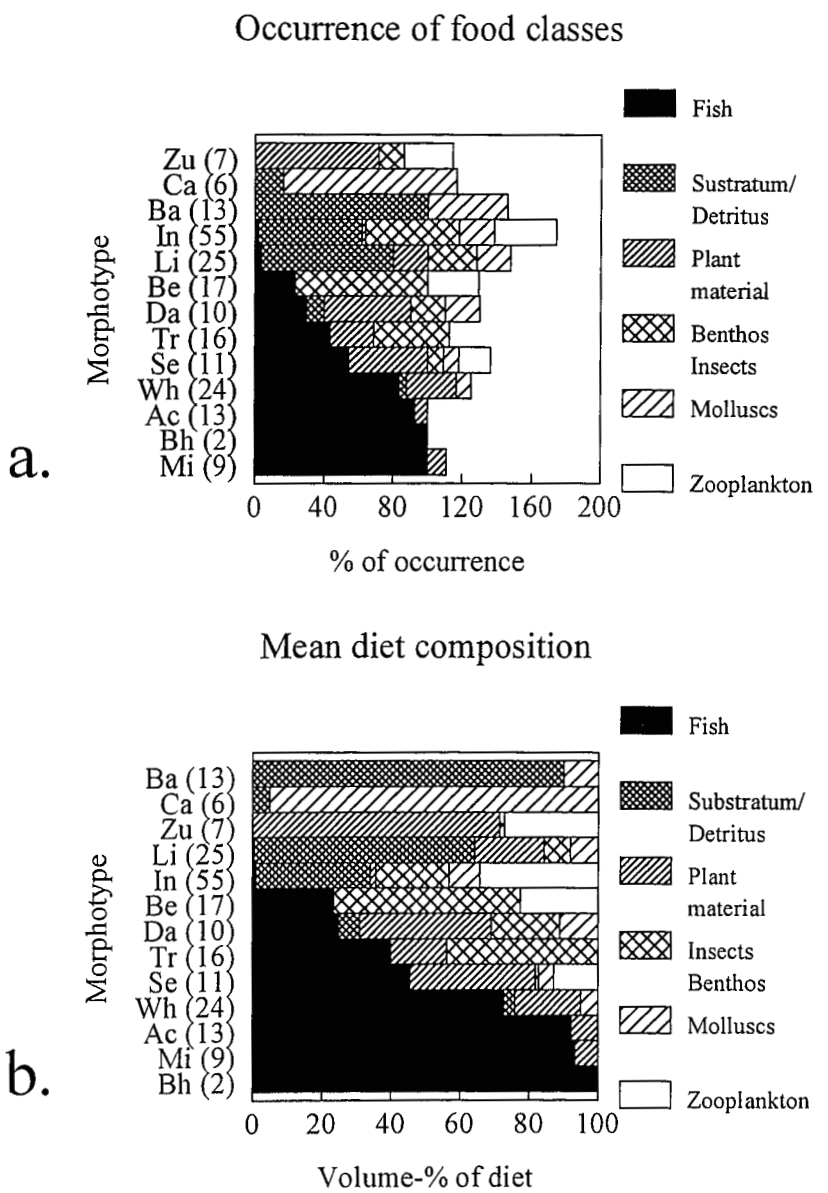


Fig. 2.9. Intestine contents analysis. The percentage of specimens with a certain food-category in its intestine is indicated, regardless of the volume-percentage each food-category contributes **(a)**, as well as a 'mean diet', reconstructed from the volume-percentage **(b)**. The number of specimens per morphotype is indicated between brackets.

Some morphological parameters in relation to piscivory

The results of comparing several morphological parameters directly involved with feeding are shown for each single morphotype in Table 2.4, and for piscivores and non-piscivores as a group in Fig. 2.10.

Piscivores show significantly (Student's t-test, $p<0.0001$) shorter intestines and anterior barbels and smaller protrusion lengths, while their gapes, premaxillary angles and protrusion angles are significantly larger, resulting in a relatively large terminal mouth. There are two major exceptions: 'barbel', although not piscivorous, has a gape area and premaxillary angle that fall in the range of piscivores. 'Bighead' has a protrusion length and angle, and a premaxillary angle that are more typical for non-piscivores. This is also apparent from Figure 2.5 in which the morphotypes are divided in two large groups, one of them being piscivorous, the other non-piscivorous. 'barbel' and 'bighead' are found in the group they do not belong to considering their diet.

DISCUSSION

Barbus morphotypes

The preliminary results that have been analyzed so far, show that it is very unlikely that all large *Barbus* from Lake Tana belong to one (polymorphic) subspecies. Although the exact taxonomic status of the different morphotypes is a matter of further research and synthesis, the circumstantial evidence for the existence of different populations is abundant. First of all the diversity in general appearance, but especially in the structures related to feeding, is striking, as is evident from Figure 2.2. From about 18 cm fork length, all different morphotypes were readily identifiable. Moreover, these initial distinctions are supported by our performed canonical discriminant analysis. Secondly, intermediates that could represent hybrids of the different morphotypes, constituted far less than 10% of the catch. Thirdly, there seems to be ecological differentiation in feeding habits and distribution in the lake.

The encountered morphological diversity parallels that found in European cyprinids (ranging from the deep-bodied, benthivorous and planktivorous bream, *Abramis brama*, to the spindle-shaped, piscivorous asp, *Aspius aspius*). The European cyprinids however, do differ in meristic counts and are separated not only in distinct species, but even in different genera, although (partly) fertile hybrids are not uncommon.

The differentiation we made in the field on general appearance is supported by our canonical discriminant analysis. The separation is not yet perfect, but so far only 17 external, more or less, 'traditional characters' (Schaefer 1991) were used, that do not reflect conspicuous features, such as colour, head shape or the prominence of the nuchal hump (Douglas et al., 1989). However, these latter characters were very important for the initial distinction of the morphotypes, based on general appearance. The fortunate aspect of this fact is that the qualitative (general appearance) and

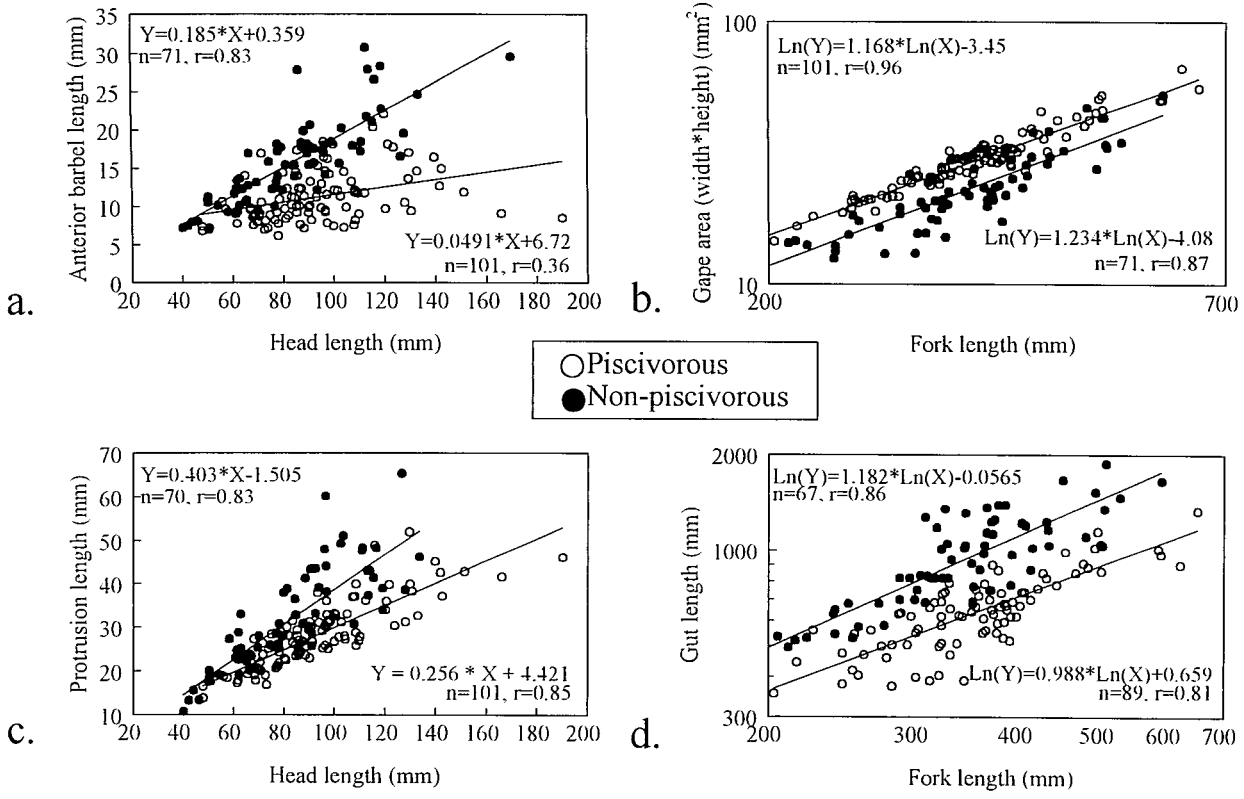


Fig. 2.10. Relation of some morphological parameters with piscivory. Anterior barbel length (ABL, **[a]**) and protrusion length (PrL, **[c]**) are expressed as linear functions of the head length. Gape area (GWxGH), **[b]**) and gutlength (Fig. **[d]**) are expressed as exponential functions of the fork length. Note the logarithmic scales in 10b and 10d. N= number of specimens, R= correlation coefficient.

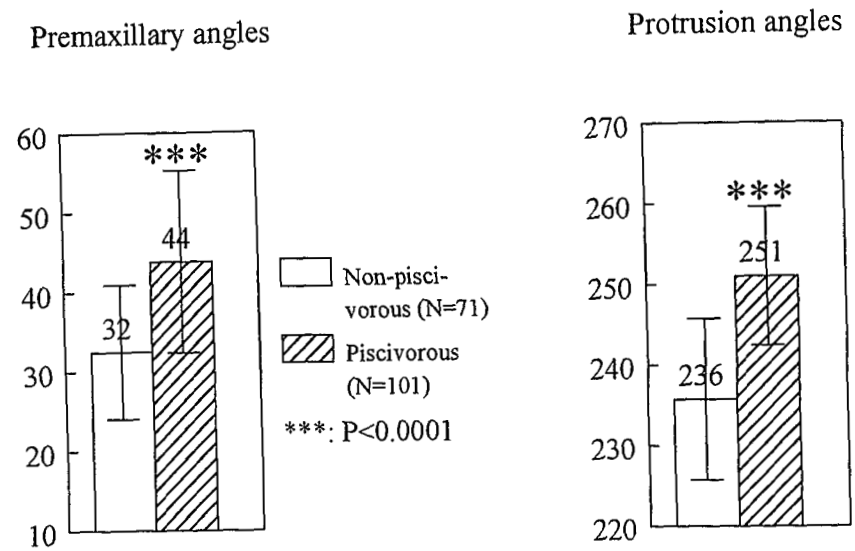


Fig. 2.11. Mean premaxillary and protrusion angles (PmA and PrA) with standard deviations. All differences between piscivores and non-piscivores are highly significant ($p<0.0001$, Student's t-test).

the quantitative (measurements) character-sets both support the same morphotype distinction. Some other characters, such as gut length did not provide a complete data set yet and could not be included in the analysis. Detailed truss measurements (Strauss & Bookstein 1982) are in progress. Still, most morphotypes can readily be separated from others, mostly by feeding-related characters.

Banister (1973) concluded that all *Barbus* species, described for Lake Tana should be considered as belonging to one subspecies of *Barbus intermedius*. In his analysis he used morphometric characters, that often resembled our measurements, as well as meristic counts (these varied extremely little in the fishes we measured). He looked at the distribution among all barbs, of each character separately. If it did not differ significantly from a normal distribution, he concluded that, based on this character, no species distinction could be made. In our opinion, essential information gets lost in this procedure, as the correlation of different characters within the individual is very important. A multivariate analysis of Banister's measurements might lead to other conclusions.

Another reason to suspect that Banister's analysis of the *Barbus* taxonomy is insuffucient, is that he looked at all specimens from all different East-African localities together. This pooled sample probably formed a continuous range of morphs, but does not appreciate local populations of discrete morphotypes. For example, it is quite possible that a discrete morphotype from Lake Tana (where intermediate morphs are rare) resembles a barb from a continuum of morphs from another locality. This idea was confirmed by looking at collections of *Barbus* from other parts of Ethiopia, that were made by a team of Russian ichthyologists (Mina personal communication) This neither proves that they therefore all belong to the same species, nor that the different morphotypes of Lake

Tana also form a continuum. Looking only at morphology, without taking into account what the distribution of the different morphs is at a certain locality, and without knowing whether a continuum of intermediate morphs, or discrete morphotypes are present, will prove insufficient for taxonomy, it is very important to study the total (morphological) population structure.

The series of barb morphotypes is parallelled by a differentiation into ecotypes. In particular the structural characters related to feeding are parallelled by a spectrum of intestine contents data. This is to be expected, as morphological adaptations of feeding structures will accurately reflect their ecological meaning (Schoener 1982).

'Piscivorous' fishes are morphologically distinct from 'non piscivorous' fishes, as is apparent from Figures 2.5 and 2.10. This is in accordance with earlier findings (Sibbing 1991*a*). Piscivorous cyprinids have a relatively large gape. A large protrusion would be unfavourable, because it would form a narrowed oral tube, thus decreasing the gape area (Sibbing 1991*a*). Small premaxillary and protrusion angles increase the downward direction of the mouth and therefore are unfavourable for piscivores, but advantageous for benthivores. Large barbels similarly are expected and found in benthivores, they probably have a sensory function, when sampling the substratum.

The number of 'piscivorous' morphotypes: 8 out of a total of 13, is remarkable, especially since cyprinids do not have oral teeth, probably a complicating factor for a piscivore. Because of these morphological restrictions, there are not many piscivorous species among cyprinids (Matthes 1963, Sibbing 1991*a*) and they only seem to occur where other piscivores are rare or absent, as is the case in Lake Tana, where *Clarias* sometimes feeds on other fishes, but is not a specialized piscivore. The external morphological differences between 'non-piscivores' and 'piscivores' is supported further by the intestine length data, that were not included in the multivariate analysis (Fig. 2.10). In the 'piscivorous' types the gut is significantly shorter, which agrees with previous findings in tropical cyprinids (Hofer 1988).

Diets of the different *Barbus* morphotypes do overlap to some extent. This was expected as cyprinids are known to be opportunistic feeders (Matthes 1963, Sibbing 1991*a*, 1991*b*, Lammens & Hoogenboezem 1991). The actual diet of the fish will likely depend heavily on the availability of food types in the environment. However, the morphology of both the external and internal feeding apparatus puts limitations on the abilities of a fish to utilize certain resources and is specialized towards some others (Sibbing 1989, 1991*a*). Bottom-feeding fish show a relatively large and downward protrusion and a small gape; 'piscivores' have a short protrusion and their large gape is directed anteriorly, in much the same fashion as in the European bream and asp and in African cyprinids (Matthes 1963). Also internal characters, especially concerning the branchial sieve (Zander 1906, Lammens et al. 1987, Hoogenboezem et al. 1991, Van den Berg et al. 1992), the palatal organ (Sibbing & Uribe 1985), the pharyngeal jaws (Sibbing 1991*b*) and the intestine (Hofer 1988) should be taken into account. Piscivores are also expected to contrast, e.g., benthivores in these aspects. By studying the morphological limitations and specializations, hypotheses on narrowed food-niches and trophical segregation among barbs can be developed, which should be

Table 2.4. Gut length, square root of the gape area, anterior barbel length and protrusion length expressed as a fraction of head length or fork length (mean, minimum, maximum and standard deviation). Mean, range and standard deviation are also shown for protrusion and premaxillary angles. Data are presented per morphotype and also for the complete piscivorous and non-piscivorous group. Note that the number of specimens is different for the gut length-measurements.

Morphotype	Gutlength / Fork length					√(Gape height*width) / Fork length (%)				Anterior Barbel Length/ Head length (%)				N
	Mean	s.d.	Min	Max	n (gut)	Mean	s.d.	Min	Max	Mean	s.d.	Min	Max	
Acute	1.69	0.25	1.25	2.28	16	8.28	1.02	6.66	10.75	11.93	2.81	7.01	18.28	20
Barbel	2.63	0.26	2.19	3.02	10	8.67	0.94	6.42	10.91	21.05	3.10	17.13	27.28	10
Bighead	1.89	0.44	1.33	2.40	3	8.67	0.42	8.00	10.86	13.63	2.25	10.58	17.60	6
Bigmouth big-eye	1.73	0.31	1.14	2.26	10	8.26	0.61	6.81	9.70	11.64	1.51	9.73	14.53	10
Bigmouth small-eye	1.70	0.22	1.34	2.07	9	8.55	0.48	7.40	9.70	8.53	1.61	5.54	11.25	10
Bigmouth mini-eye	1.85	0.24	1.45	2.29	10	9.11	1.17	6.32	11.90	10.14	2.73	4.53	15.17	10
Carplike	2.91	0.52	2.08	3.72	9	6.68	0.77	4.88	8.47	21.58	4.51	15.32	32.21	11
Dark	2.03	0.21	1.67	2.48	13	8.01	0.50	7.16	8.82	15.22	2.82	11.82	21.63	14
Intermedius	2.68	0.50	2.10	3.81	10	6.69	0.46	5.59	7.79	18.99	2.56	13.15	22.39	10
Lip	2.59	0.42	1.97	3.74	27	6.62	1.29	4.42	9.09	17.50	2.54	13.02	22.83	29
Troutlike	1.92	0.26	1.39	2.43	18	8.34	0.47	7.62	10.86	12.10	2.33	7.93	15.48	21
White hunch	1.81	0.25	1.27	2.14	10	8.58	0.46	7.49	9.67	17.83	2.90	12.41	23.71	10
Zurki	3.24	0.63	2.31	4.15	11	5.81	0.52	4.60	7.01	17.75	1.87	15.17	21.75	11
Non-piscivorous	2.76	0.53	1.97	4.15	67	6.77	1.29	4.42	9.92	18.88	3.37	13.02	32.21	71
Piscivorous	1.83	0.28	1.14	2.48	89	8.50	0.74	6.77	10.86	12.56	3.51	4.53	23.71	101

Table 2.4 (continued)

Morphotype	Protrusion length/Head length (%)				Protrusion angle (°)				Premaxillary angle (°)				N
	Mean	s.d.	Min	Max	Mean	s.d.	Min	Max	Mean	s.d.	Min	Max	
Acute	27.25	2.40	23.85	32.79	250.0	2.7	245	255	38.9	6.1	50	70	20
Barbel	40.43	5.62	31.57	50.00	237.5	8.1	220	245	39.5	5.7	40	60	10
Bighead	37.89	3.33	32.74	42.19	232.5	3.8	225	235	25.8	4.5	30	50	6
Bigmouth big-eye	33.00	3.34	27.96	37.87	253.5	3.2	250	260	51.0	7.3	35	50	10
Bigmouth small-eye	28.55	3.79	24.45	37.29	255.5	5.2	250	265	48.0	9.5	20	45	10
Bigmouth mini-eye	31.08	3.78	24.26	36.87	264.5	8.5	255	280	59.5	5.7	25	55	10
Carplike	32.06	2.79	28.35	35.84	238.6	6.1	230	245	32.7	5.8	35	60	11
Dark	32.78	3.26	26.90	40.77	250.0	5.7	240	260	48.2	6.2	20	60	14
Intermedius	36.38	2.15	32.60	39.96	237.5	8.7	225	250	30.0	7.7	20	30	10
Lip	42.40	7.09	31.64	62.45	231.6	11.9	205	245	28.3	6.5	30	50	29
Troutlike	29.70	3.01	23.10	36.87	247.6	6.8	240	260	37.9	12.5	35	65	21
White hunch	31.47	2.31	27.59	34.51	251.8	4.8	240	260	43.3	3.9	20	45	10
Zurki	33.06	4.44	27.00	40.46	240.5	5.0	230	250	39.1	9.7	25	45	11
Non-piscivorous	38.16	6.92	27.00	62.45	235.7	10.0	205	250	32.5	8.5	20	55	71
Piscivorous	30.65	4.11	23.10	42.19	251.0	8.6	225	280	43.8	11.4	20	70	101

tested in the field. Such studies, predicting diets from feeding structures and behaviour are now in progress.

Not only do the well distinguishable morphotypes utilize different trophic niches, there is also at least some spatial segregation among them as can be concluded from their depth and substratum distribution. These data are abundant, but not very detailed yet and investigations focused on this aspect are necessary.

To draw conclusions about the taxonomic status of the different *Barbus* morphotypes in Lake Tana it is essential to know whether reproductive isolation is present. As polymorphism and phenotypic plasticity can account for a significant amount of morphological differentiation (Meyer 1987,1989, Witte et al. 1990), only reproductive isolation can exclude polymorphism as the single explanation of this diversity. A spatial segregation in spawning grounds, or a temporal segregation in spawning periods, would be a strong indication for the existence of reproductive isolation. There are some observations of the temporal segregation of spawning (Wudneh personal communication), but further investigations are urgently required. The existence of several, reproductively isolated species would be very important for fisheries, as these species would represent different exploited fish stocks, which are the units to be managed to establish sustainable fisheries. Genetic evidence on the existence of different *Barbus* populations in Lake Tana is not available yet, but investigations of such kind are planned in our further research.

In conclusion, it seems unlikely that all the morphotypes, apparently representing different ecotypes, belong to one and the same subspecies of *Barbus intermedius*. Their evolution and exact taxonomic status is still unclear, but it is to be expected that eventually, several 'good' species will be found to exist.

A forgotten species flock ?

Compared with other African lakes with species 'flocks', Lake Tana is quite small and shallow, but also reasonably old. It is estimated that it was formed approximately 2 million years ago at the Pliocene-Pleistocene transition, by the blocking of the Blue Nile through volcanic eruptions (Mohr 1962, Baker et al. 1972). The river filled a shallow basin, which once was about three times as large as it is at the present. Nowadays the Blue Nile flows out of the lake only to make a sheer 40 m drop at about 30 km from its outflow. Except for the small tributaries flowing into it, Lake Tana seems to represent an isolated system. For a lake of this age, it is extremely poor in species, with one cichlid and one clariid species (Greenwood 1976). The cyprinids are the dominant taxon and of these only the large *Barbus* seem to show a wide variety in exploitation of resources, varying from detritus and macrophytes, to zooplankton and fish. Utilization of so many different trophical niches, including one that usually is not available to cyprinids - piscivory - indicates that resource partitioning acts as a competitive force, resulting in adaptive radiation, as it does in Lake Victoria haplochromines (Mayr 1984, Greenwood 1984, Witte et al. 1990). In Lake Tana, however, the number of species is much less than in Lake Victoria, making it easier to reconstruct the food web , to understand the ecosystem and to manage its fisheries.

Ancestral cyprinids are thought to have adapted to a bottom-dwelling life, developing jaw protrusion and losing oral teeth (Gosline 1973). This latter restriction probably is why piscivorous cyprinids are rare and can only develop if other specialized piscivores are absent. The presence of a whole range of unique piscivorous morphotypes could mean that they originated in the lake itself, isolated from other piscivores. This is an indication that the diversity of morphological and ecological parameters in the large *Barbus* of Lake Tana may be the result of intralacustrine specialization and even speciation. Epigenetic processes could have played an important role in this as the barbs were exposed to new (lacustrine) environmental circumstances in which several life history strategies could be successful (Balon 1988, 1992).

It can be hypothesized that the common riverine *Barbus* species, present in the Blue Nile when it was blocked by volcanic activity, have radiated into the new lacustrine niches that became available. Because of the lack of specialized piscivores, several *Barbus* morphs could develop piscivorous habits. It is possible that only *Barbus intermedius* was present when the lake was formed, as this is a common, riverine species in the rest of Ethiopia. If this is the case, we may be dealing with a species flock, still virtually undisturbed by human influences, which is unique in the world, since the only other known cyprinid species flock of Lake Lanao (Kornfield & Carpenter 1984) has virtually disappeared as a result of human influences. More research is urgently needed, especially on the question of whether the different types represent different species or only one polymorphic species. This is extremely important not only with regards to the management of developing fisheries, but also for evolutionary biology. But, first of all, the lake and its biodiversity have to be protected, unhappy introductions and a new Lake Victoria disaster (Witte et al., 1992) should be avoided at all costs.

ACKNOWLEDGEMENTS

We are grateful to the Development branch of the Ethiopian Orthodox Church (EOC/DICAD), and especially to His Grace Archbishop Timotheos and his staff, for all logistic support in Ethiopia, without which this study could not have started. The Fisheries Resources Development Department of the Ministry of Agriculture of Ethiopia is acknowledged, especially Mebrat Alem, Solomon Tibebu and Endale Lemma, for their considerable support and their permission to use the laboratory in Bahar Dar; Tesfaye Wudneh has been of valuable scientific and personal help. Wim Valen contributed illustrations to this paper. M.V. Mina contributed through stimulating discussions and comments on the manuscript. D.J. Siebert kindly made available and discussed the *Barbus* specimens of the British Museum (Natural History). The office for external relations of the Agricultural University provided the financial aid for this pilot study, later funded by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W 88-176, the Interchurch Foundation Ethiopia (ISE, Urk) and the Interchurch Coordination Commission of Development Projects (ICCO, Zeist).

Chapter 3

Morphological divergence during growth in the large barbs (*Barbus* spp.) of Lake Tana, Ethiopia.

Leo A.J. Nagelkerke[1], Ferdinand A. Sibbing[1] & Jan W.M. Osse[1]

[1] *Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

Published in: *The Netherlands Journal of Zoology* (1995) **45**: 431-454.

ABSTRACT

Recently the large Lake Tana barbs (genus *Barbus*) were categorized into at least 13 distinct morphotypes based on large differences in general morphology, distribution and feeding habits. They are probably different populations and may even constitute a unique cyprinid species flock. This study demonstrates that 11 of the 14 morphotypes (as an additional morphotype 'Shorthead' is identified in this paper) can already be distinguished by their general external features at fork lengths of less than 12 cm. These distinctions were verified by statistical analysis of morphometric data. The distinction of the morphotypes in small specimens supports the hypothesis that several distinct *Barbus* species exist in Lake Tana. Knowledge of the population structure and species composition is very important for the reconstruction of the evolutionary history and mechanisms of this unique fish community. Moreover, in order to protect the biodiversity of the lake, it is important that the fisheries in the lake only increase on a sustainable basis and a detailed knowledge of the fish community structure is vital to achieve this goal.

INTRODUCTION

History and current state

The number of species of large barbs (*Barbus spp.*) in Lake Tana, Ethiopia varies depending on the author describing them. Rüppell (1836) mentioned 5 *Barbus* and 1 *Labeobarbus* species, Boulenger (1902, 1911) distinguished 10 *Barbus* species and Bini (1940) discerned 10 species, with a total of 23 subspecies. Since the latest revision (Banister 1973) all large barbs from Lake Tana are considered as belonging to one subspecies: *Barbus intermedius intermedius* Rüppell, 1836.

Recent studies (Nagelkerke et al. 1994, Osse et al. 1993) have shown that at least 13 distinct morphotypes exist. The initial distinction, based on general appearance (Table 3.1), was supported by canonical discriminant analysis of 17 morphometric characters. One additional morphotype, 'Shorthead', previously considered to belong to the 'Intermedius' morphotype is presented in this study. The 14 morphotypes differ conspicuously in diet, some are polyphagous which is typical for cyprinid fishes (Lammens & Hoogenboezem 1991), while others specialize in fewer classes or only a single class of food organisms. Moreover, the morphotypes not only differ in general shape and feeding habits, but also show differences in distribution over depth and substratum.

Table 3.1. Morphotypes of the large Lake Tana barbs with qualitative and semi-quantitative descriptions, used to distinguish morphotypes in the field (adjusted from Nagelkerke et al. 1994). Internal characters are not included.

Trivial name	Name code	Qualitative description, based on general appearance
Acute	Ac	Head longer than body depth, tapering and narrow (interorbital width equal to eye diameter); terminal mouth; shallow body; silvery white
Barbel	Ba	Irregular, slightly concave dorsal head profile; both pairs of barbels longer than eye diameter, very thick and dark-coloured; lower jaw directed obliquely upward; large, downward protrusion
Bigmouth big-eye	Be	Very large eye (diameter equal to snout length) lower jaw directed obliquely upward, often extending beyond the upper jaw; terminal mouth; nuchal hump
Bighead	Bh	Head longer than body depth, with convex dorsal profile; large, downward protrusion with a very large inferior gape; lips well developed, without lobes; small eye
Carplike	Ca	Head short (length 5 times in fork length) and wide (eye diameter 2 times in interorbital width); head shorter than body depth; usually a large anal opening; eye diameter at least two times in snout length; barbels longer than eye diameter; small, inferior gape; golden-yellowish
Dark	Da	Conspicuous nuchal hump; large terminal gape; lower jaw directed obliquely upward, not extending beyond the upper jaw; straight dorsal head profile; very dark brown-reddish to black
Shorthead	Sh	Short head (head length 5 times in body length); gape larger than in Zu; body spindle-shaped and not especially deep (body depth same or smaller than head length); small barbels, length c. two-thirds of eye diameter; yellowish green; usually under 25 cm fork length; large eye
Intermedius	In	No extreme characters; downward protrusion; medium-sized inferior gape; medium-sized to long barbels (equal or longer than eye diameter); head length 4 to 4½ times in fork length
Lip	Li	Well-developed lips, usually with large lobes on lower or upper jaw or on both; barbels thick and longer than eye diameter; large, downward protrusion
Bigmouth mini-eye	Mi	Head longer than body depth; terminal, wide gape; small eye (three eye diameters in snout length); spindle-shaped, slender body; greenish / yellowish
Bigmouth small-eye	Se	Long lower jaw directed upward, extending beyond the upper jaw; very large terminal mouth; two eye diameters in snout; slightly concave dorsal head profile; nuchal hump
Troutlike	Tr	Spindle-shaped, but relatively deep body (head shorter than body depth), straight dorsal profile; terminal mouth; silvery-yellowish
White hunch	Wh	Nuchal hump (variable in size), body very wide in the pectoral area; wide head with slightly concave dorsal profile; lower jaw directed obliquely upward; jaws equal in length; gape (sub)terminal
Zurki	Zu	Deep-bodied (head shorter than body depth); shortest head (head length 5 times in fork length); small barbels; small, inferior gape; dark green

Problem

It is hypothesized that some of these morphotypes constitute biological species, because of the remarkable morphological and ecological differences. The aim of this study is to test this hypothesis by examining whether the morphotypes diverge at an early stage of development, or whether all morphotypes show similar development until they reach a standard length of approximately 20-25 cm and only then start diverging, as is suggested by Mina et al. (1993). There are no indications for large ecological differences (such as in diet or habitat) between the juvenile barbs. Therefore, early morphological divergence, if consistent with adult morphology, would strongly suggest a genetic basis for these differences, instead of being caused exclusively by phenotypic plasticity. Such a genetic basis would support the existence of real biological species. Evidence from temporal and spatial segregation in spawning of some morphotypes would support this.

The present study demonstrates that, in contrast to Mina et al. (1993), for at least 11 morphotypes small specimens (fork length less than 12 cm) can be identified, mostly by the same characters as larger fishes.

Identification of the separate fish stocks and reconstruction of their ecological role is of major importance for monitoring the intensifying fisheries, in order to combine sustainable fisheries with protection of biodiversity in Lake Tana (Sibbing et al. 1994). The existence of several populations or even species of barbs within different ecological niches (ecotypes) would complicate the reconstruction of a food web as well as fisheries management in comparison to a situation with only one panmictic population of *B. intermedius*.

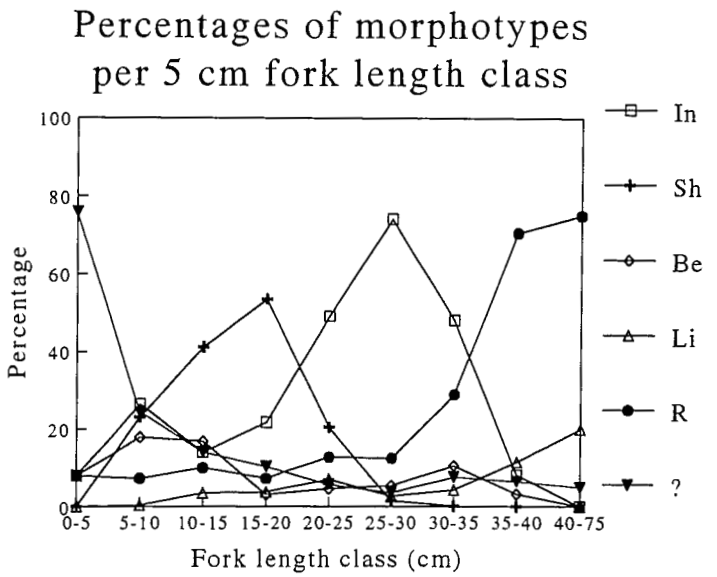
MATERIALS AND METHODS

Fishes

From November 1992 to October 1993 a large size range of barbs of many morphotypes - distinguished by their habitus - were collected using both bottom and surface gill nets (stretched mesh size from 16 to 100 mm) and also bottom trawling (cod-end stretched mesh size of 20 mm) (Fig. 3.1*a*). These fishes were collected as part of a large ecological monitoring programme. A sample of 464 fishes was collected and measured (Table 3.2).

Eleven of the 14 morphotypes are considered in this study (Table 3.2). The numbers caught of small 'Carplike' (Ca), 'Bigmouth mini-eye' (Mi) and 'Troutlike' (Tr) were too small for a proper analysis.

a



b

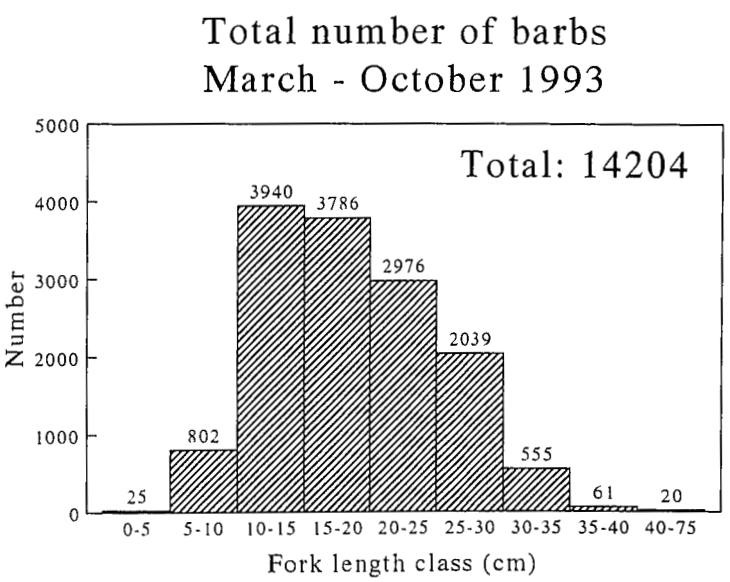


Fig. 3.1. (a) The percentage of four of the most abundant *Barbus* morphotypes in the catch per 5 cm fork length classes. Name codes as in Table 3.1. 'R'= sum of the other morphotypes, '?'= barbs that could not be included in any of the morphotypes. Note that already in the 10-15 cm fork length class more than 80% of the barbs can be identified as belonging to a specific morphotype. **(b)** The total number of barbs caught in the period March-October 1993, per 5 cm length class.

Table 3.2. The material used in this study: minimum and maximum FL (cm), numbers in the different length classes and total numbers.

Morphotype	Minimum FL (cm)	Maximum FL (cm)	Numbers FL ≤ 20 cm	Numbers FL > 20 cm	Numbers 10 ≤ FL ≤ 15 cm	Numbers 25≤FL≤ 35 cm	Total
Acute (Ac)	5.4	37.5	28	31	20	16	59
Barbel (Ba	11.0	31.6	7	5	3	3	12
Bigmouth big-eye (Be)	8.7	33.9	23	15	15	9	38
Bighead (Bh)	11.9	42.8	5	21	4	11	26
Dark (Da)	11.1	36.5	8	9	5	4	17
Shorthead (Sh)	8.9	30.8	24	11	11	4	35
Intermedius (In)	5.2	39.4	42	26	15	12	68
Lip (Li)	9.7	54.4	23	36	11	12	59
Bigmouth small-eye (Se)	9.2	82.4	24	30	14	2	54
White hunch (Wh)	8.0	63.5	28	28	14	11	56
Zurki (Zu)	10.7	35.8	13	27	6	19	40
Total			225	239	118	103	464

Measurements

To verify whether the small fishes belonged to one of the known morphotypes, the following 12 parameters were measured on fresh specimens and analyzed (Fig. 3.2):

- Anterior barbel length (ABL)
- Body depth (BD)
- Fork length (FL)
- Gape height (GH)
- Gut length (GL)
- Gape width (GW)
- Head length (HL)
- Lower jaw length (LJL)
- Orbit diameter (OD)
- Protrusion angle (PrA)
- Length of protrusion chain with closed mouth (PrC)
- Protrusion length (PrL)

This set of parameters was selected because (1) it gave good resolution between morphotypes and (2) they are related to feeding behaviour. Differences in feeding ecology among the Lake Tana barbs are conspicuous (Nagelkerke et al. 1994). All the aforementioned characters were measured in the same way as described in Nagelkerke et al. (1994), except for: (1) LJL, which was defined as the distance between the caudal tip of the retro-articular bone and the rostral edge of the symphysis

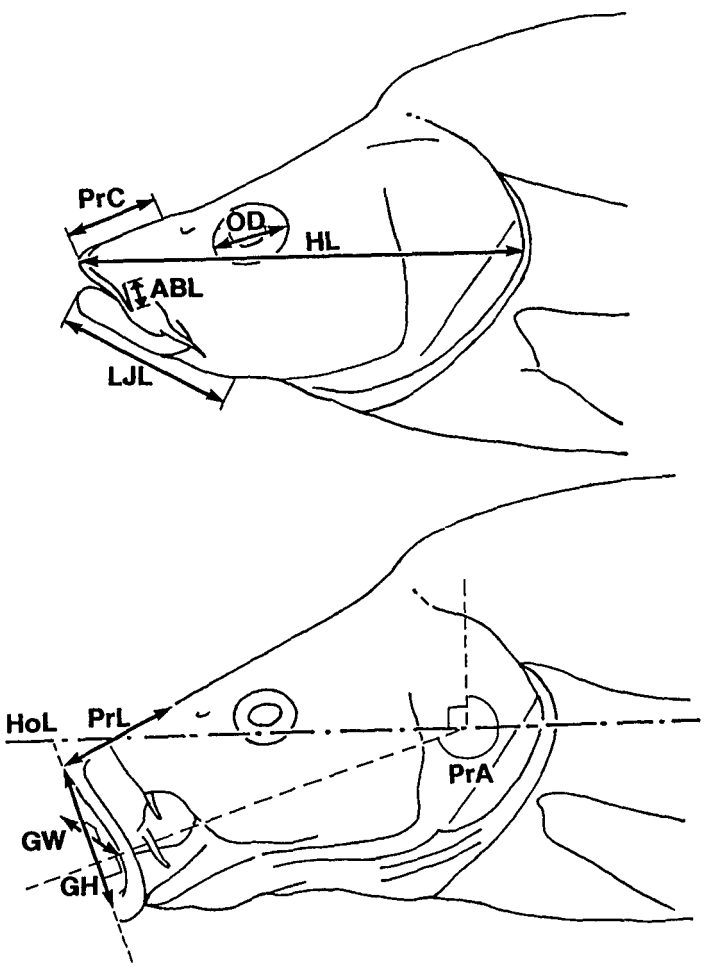


Fig. 3.2. Nine of the eleven measuring parameters. Abbreviations are explained in the text. BD and GL are not shown. HoL is the horizontal line through the straight caudal part of the lateral line (adapted from Nagelkerke et al. 1994).

of the dental bones, (2) PrC, which is the length between the rostral tip of the symphysis of the premaxillae and the rostral edge of the supra-ethmoid in the medial plane, measured with closed mouth (PrL is measured between the same points, but with the mouth completely opened), and (3) GL, which is the length of the complete, dissected gut. Note that a larger PrA means that the mouth opens more terminally.

We assume that these characters differ among morphotypes in a qualitatively similar fashion in small and large fishes. Due to allometric growth, however, morphometric differences in small fishes are expected to be quantitatively smaller (Osse 1990). This is also related to the diets of juvenile fishes, which tend to be more similar than those of adults.

Data processing

Regression analysis was performed for each of the metric characters. Linear regressions were performed over the whole range of FLs. To analyze the differences among morphotypes for the values of a certain character, analysis of covariance (ancova) was performed for the metric parameters, and analysis of variance (anova) in the case of PrA, as this angle was considered to be a shape parameter independent of FL. The specimens of each morphotype were split into two groups (smaller and larger than 20 cm FL respectively) and analyzed independently. The least square means of the character (adjusted for the covariate, either being FL or HL) were tested for their differences using Gabriel's statistic for multiple unplanned comparisons (Sokal & Rohlf 1981). The level for statistical significance was set at $p < 0.01$. Anova and ancova were performed using Statistical Analysis System (SAS) software.

An additional shape analysis was performed by means of principal components analysis (PCA) of the metric parameters for small and large specimens separately. To decrease the influence of size on the analysis, the FL ranges were narrowed (10 - 15 cm FL and 25 - 35 cm FL) and parameters were standardized by subtracting the mean value and dividing by the standard deviation (Povel 1986). Moreover, by narrowing the size groups of small and large fishes there is a FL difference of at least 10 cm between individuals of the two groups. Therefore, similar PCA results for small and large fishes cannot be due to the fact that the largest individuals of the small size group are of approximately the same FL (i.e. 20 cm) as the smallest specimens of the large size group.

Eigenvectors were calculated from the correlation matrix, as this is insensitive to constant differences, such as size (Povel 1986). The PCA was performed using the NTSYS-pc package, version 1.80 (Exeter Software, Setauket, New York).

RESULTS

A new morphotype: 'Shorthead'

An additional morphotype is presented in this study. It was previously considered to belong to the 'Intermedius' (In) morphotype, but it can be distinguished by morphological and ecological parameters. 'Shorthead' (Sh) as it is called, is a small morphotype (seldom larger than 25 cm FL) and looks intermediate between In and 'Zurki' (Zu) (Fig. 3.3, Table 3.1). It has, like Zu, a shorter head (HL c. 5 times in FL) and smaller barbels (ABL is c. two-thirds of the eye diameter) than In, but the body is not very deep (BD smaller or as large as HL) and spindle-shaped, unlike Zu. Sh has a larger gape than Zu, similar to In. Its colour is yellowish-green.

Sh was found to be equally abundant as In (Fig. 3.1*a*). However, it is usually found in shallower water, near the surface. Gut contents analysis showed that its diet is quite different from In or Zu, with zooplankton and adult insects constituting a major part of its food (results not shown). In contrast, In shows a more benthivorous diet, while Zu feeds mainly on macrophytes.

Identification of morphotypes

The percentage of fishes in trawl and gill net catches (total of 14,204 fishes, Fig. 3.1*b*) that could be allocated to a particular morphotype sharply increased with the length of the fish (Fig. 3.1*a*). According to Mina et al. (1993) morphotypes can only be distinguished reliably after they reach 25-30 cm standard length. In contrast, we found that more than 80% of fishes from the fork length class of 10 to 15 cm (of a total of almost 4,000 fishes) could already be allocated to a particular morphotype. The percentage of unidentifiable barbs does not exceed 8% in fork length classes larger than 20 cm FL. These unidentifiable large specimens are usually caught near the shore and will be discussed later. Sh and In dominate the catch in the size classes between 10 and 35 cm FL and reach maximum lengths of c. 30 and 40 cm FL respectively (Table 3.2). At larger FLs morphotypes that attain a larger maximum size become more abundant.

Specimens of Ac, Ba, Be, Bh, Da, Sh, In, Li, Se, Wh and Zu can be distinguished at FLs less than 12 cm FL (procedure in 'materials and methods'). Small specimens of Mi, Ca and Tr were never identified with certainty and are therefore not included in this study. Small specimens were initially (during sorting of the catches) assigned to a certain morphotype if their general habitus (Table 3.1, Fig. 3.3) was similar to that of larger specimens of that morphotype, taking into account that certain measures, such as eye diameter, are relatively large in young fishes (cf. Fig. 3.5*d*).

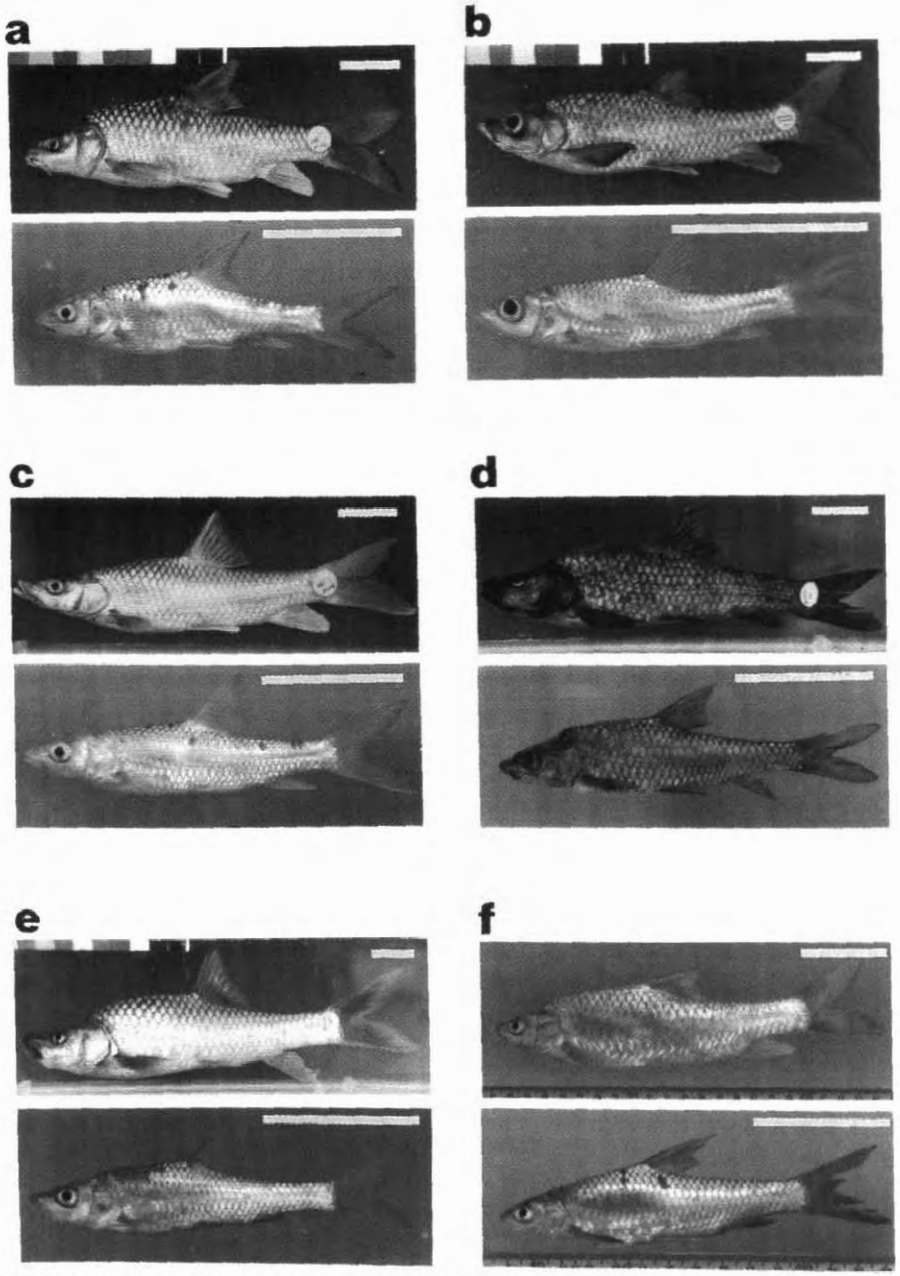


Fig. 3.3. Large (FL > 20 cm, top) and small (FL ≤ 20 cm, bottom) specimens of 6 *Barbus* morphotypes, showing the similarities in general habitus between small and large specimens of the same morphotype. **(a)** Intermedius **(b)** Bigmouth big-eye **(c)** Acute **(d)** Dark **(e)** Bigmouth small-eye **(f)** Shorthead. Scale bar is 5 cm.

Verification of morphotype assignment in small fishes

To verify the morphotype distinction among small fishes it was examined whether the differences in morphometric characters among morphotypes were qualitatively similar in small and large specimens (e.g. if morphotype 'X' has a larger HL than morphotype 'Y' in large specimens, it was examined whether small specimens of morphotype 'X' also have a larger HL than small 'Y' specimens).

To compare size and direction of differences of the morphological parameters among the morphotypes an analysis of covariance (ancova) was performed, thereby adjusting for the covarying parameter on the abscissa (FL or HL). The regressions of head length (HL), lower jaw length (LJL), gape height (GH), gape width (GW), anterior barbel length (ABL), body depth (BD), and gut length (GL) versus fork length (FL), were analyzed as well as length of the protrusion chain with closed mouth (PrC), protrusion length (PrL), and orbit diameter (OD) versus HL. Size and direction of differences (adjusted for the covariate) between morphotypes were tested for small (FLs $\leq$ 20 cm) and large fishes (FLs > 20 cm) separately (examples of such regression lines in fig. 3.4). The regression lines of the different morphotypes are arranged in the same order for both small and large specimens (for HL: Zu has the smallest, Ac the largest for both size groups; for LJL: Zu has the smallest, Ac the largest for both size groups). It should also be noted that the regression lines fit well for the whole size range of data, indicating that there are no important deviations from linear growth for these parameters in the measured size group. The results for other parameters and morphotypes are similar.

To examine whether the morphological differences among morphotypes are consistent in both the small and large size groups, all parameters were tested for significant differences between morphotypes. This was done separately for the small and large fishes (Table 3.3). When parameters differ significantly between morphotypes in both size groups it is generally in the same direction (e.g. the PrA in Se is larger than the PrA of all other morphotypes, in both the small and the large specimens). Sometimes parameters differ significantly between morphotypes in one of the size groups and not in the other. These parameters can be used to distinguish morphotypes in only one of the size groups; they are not consistent over the whole size range, but they are not contradictory either. Examples of this are (1) LJL of small Li, which is significantly smaller than in small In, while there is no significant difference in LJL between large Li and In, and (2) OD, which in large Ac is significantly larger than in large Bh, while there is no significant difference in OD in small Ac and Bh. Of 339 significant differences in the small and 313 in the large size group only 3 are in a different direction and therefore contradictory between small and large fishes. LJL in Ac and Ba is larger than LJL of Se in the small size group, but smaller in the large size group, and PrC of Li is smaller than that of Bh in the small size group and the other way around in the large size group. The number of differences between morphotypes that occur consistently in both small and large fishes are shown in Table 3.4. In conclusion it can be said that, with one exception (Da and Wh), there are often many significant differences between morphotypes that hold over the whole range of

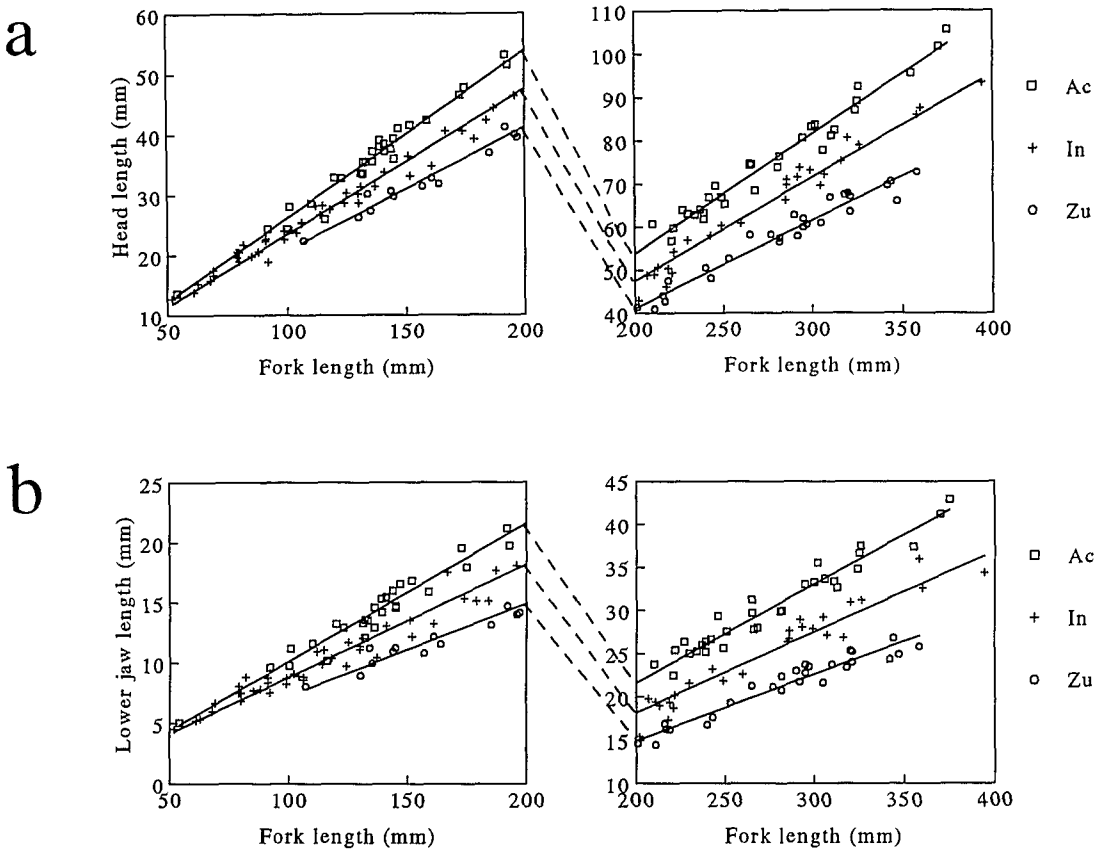


Fig. 3.4. (a) Head length versus fork length for the In, Ac and Zu morphotypes, separated for FL smaller and larger than 20 cm to improve the resolution in the small size group. The regression line, calculated for the whole range of fork lengths for each morphotype, fits well to both size groups. **(b)** Lower jaw length versus fork length for the In, Ac and Zu morphotypes, separate for FL smaller and larger than 20 cm. The regression line, calculated for the whole range of fork lengths fits well to both size groups. Name codes as in Table 3.1.

Fls. Table 3.4 can be used as a dissimilarity matrix and clustered using the UPGMA (unweighted pair-group method, arithmetic average). The resulting tree shows two main groups, corroborating the distinction between 'piscivorous' and 'non-piscivorous' groups as defined by Nagelkerke et al., 1994.

To examine which parameters are most important for morphotype distinction, the number and percentages of significant differences in each morphometric parameter was counted for both size-groups separately and for all fishes together (Table 3.5). All parameters account for an important number of significant differences in both size groups of fishes (minimum of 44, 33, and

27%, maximum of 67, 65, and 58% for small, large and all fishes respectively). Most and least important parameters may differ between small and large fishes. In small fishes HL, LJL and PrL account for the largest number of significant differences, while GL, PrC and BD are least important. In large fishes ABL, GL, LJL, and PrA are most important, while BD, PrC, and PrL account for the smallest number of significant differences. When considering the whole size range, ABL, HL, LJL, and PrL account for most significant differences, BD, GL, and PrC for the least.

A graphic representation of the differences among morphotypes for 5 parameters is shown in fig. 3.5. These ratios confirm that differences in small and large specimens are generally in the same direction, although the ascending order of the large size group is not always reflected in the small size group (cf. Table 3.3). Zu and Sh have the smallest HL and LJL (in both size groups), while Ac and Bh have the largest HL (both size groups) and Se the largest LJL (only in the large size group). PrL is smallest in Ac and largest in Bh, Ba and Li (in both size groups). Bh and Se have the smallest OD (in both size groups, although small Ba also show a small eye), Be and Sh the largest (in both size groups, although Be has by far the largest OD in the small size group). Note that the relative eye size in small fishes (Fig. 3.5*d*) is much larger than in large specimens of the same morphotype. This is a generally observed fact, resulting from negative allometric growth. Ba, Bh and Li have the smallest PrA (in both size groups), Se the largest and thus the most terminal opening mouth (in both size groups). In general, PrA is smaller in the small size group, which means that irrespective of morphotype, the mouth becomes more terminal during growth.

The facts that (1) there is always at least one parameter which, over the whole range, accounts for a significant difference between two morphotypes that holds over the whole size range (except for the combination Da - Wh), (2) the number of statistically significant differences between morphotypes in the groups of small and large fishes (339 v. 313 respectively) is approximately the same, and (3) there are several parameters that contribute to a large number of significant differences in both small and large size groups (HL, LJL, ABL, and PrA) suggest that fishes from both size groups can be classified consistently.

However, parameters accounting for a large number of statistically significant differences are not necessarily convenient field characters and vice versa. Significant differences could be caused by small within-group variances, while the mean values of two groups for this parameter differ only slightly. Only parameters with differences between groups large enough to be noticed in field conditions are useful as key characters in these conditions. A smaller share in the number of significant differences can still mean that the character is especially useful for distinguishing a specific morphotype from the others in the field. An example of this is OD which does not account for a very large number of statistically significant differences, but which is very useful as a field character, since the differences in OD are large enough to be easily observed. This is especially clear in large specimens, e.g. when comparing the Be morphotype with others.

Table 3.3. Comparisons of the measuring parameters between different morphotypes. The lower left part of the table (left of the 'X' signs) shows the comparisons between fishes ≤ 20 cm FL, the upper right part the comparison between fishes > 20 cm FL. Only parameters that are significantly ($p<0.01$) different are indicated. A '-' sign indicates that the parameter has a smaller value for morphotype 'i' (columns) than for morphotype 'j' (rows). E.g. when looking at the comparison of Ac and Ba in large fishes (top row, column 2), 'ABL' is indicated, meaning that Ba (i) has a significantly larger ABL than Ac (j). When this comparison is made in small fishes (row 2, column 1) '-ABL' is indicated, meaning that Ac (i) has a significantly smaller ABL than Ba. Therefore the difference between Ac and Ba is consistent over the whole size range when considering ABL. Significant differences that are of opposite sign in small and large fishes (and are therefore contradictory) are underlined.

		i																							
		Ac		Ba		Be		Bh		Da		Sh		In		Li		Se		Wh		Zu	
j	Ac		X	ABL PrL GL	-HL -PrA	GH OD	-HL	GH ABL PrC PrL	-OD -GL -PrA	GH ABL PrL		ABL OD BD GL	-HL -LJL -GW -PrA	ABL PrC PrL BD GL	-HL -LJL -GW -PrA	ABL PrC PrL GL	-HL -LJL -GW -PrA	LJL GH GL PrA	-HL	ABL	-HL -LJL	ABL OD BD GL	-HL -LJL -GH -GW
	Ba	HL GH PrA	-ABL -PrL -BD	X		OD PrA	-ABL -PrL	HL PrC	-ABL -OD -GL	PrA	-ABL -GL	OD	-HL -LJL -GW -ABL -PrL		-LJL	PrC	-LJL -GW	LJL GH PrA	-ABL -PrL -BD	PrA	-ABL -PrL	BD GL PrA	-HL -LJL -GH -GW -ABL -PrL
	Be	HL LJL GW PrC GL	-OD -BD	LJL GW ABL PrL GL	-GH -OD -PrA	X		HL ABL PrC PrL	-OD -GL -PrA		-OD	ABL GL	-HL -LJL -GH -GW -OD -PrA	ABL PrC PrL BD GL	-LJL -GH -OD -PrA	ABL PrC PrL GL	-LJL -GW -OD -PrA	LJL GH PrA	-OD -BD	GW ABL	-LJL -GH -OD	ABL BD GL	-HL -LJL -GH -GW -OD
	Bh	PrA	-GH -ABL -PrC -PrL	ABL	-HL -GH -PrC -PrL	OD PrA	-HL -GH -ABL -PrC -PrL	X		OD PrA	-PrC -PrL	OD GL	-HL -LJL -GH -GW -PrC -PrL	ABL OD BD GL	-HL -LJL -GH -GW -PrC -PrL	ABL PrC OD GL	-HL -LJL -GH -GW	LJL OD GL PrA	-HL -ABL -PrC -PrL	ABL OD GL PrA	-HL -LJL -GH -PrC -PrL	OD BD GL PrA	-HL -LJL -GH -GW -PrC -PrL
	Da	HL LJL	-PrL -BD	LJL ABL PrL		OD	-PrL	HL GH ABL PrC PrL	-OD -PrA	X		OD GL	-HL -LJL -GH -GW	ABL BD GL	-HL -GH -GW	ABL PrC PrL GL	-HL -LJL -GH -GW -PrA	LJL GL PrA	-ABL	ABL	-GH	OD BD GL	-HL -LJL -GH -GW

		i																					
		Ac		Ba		Be		Bh		Da		Sh		In		Li		Se		Wh		Zu	
j	Sh	HL LJL GH GW PrA	-ABL -PrL -OD -BD	HL LJL GH GW ABL PrL	-OD	HL LJL GH GW OD PrA	-ABL -PrC -PrL -BD -GL	HL LJL GH GW PrC PrL	-OD -BD -PrA	HL LJL GH GW		X		HL ABL PrC PrL	-OD	HL ABL PrC PrL	-OD	HL LJL GH GW PrA	-ABL -OD -BD -GL	HL GW PrA	-OD -GL	BD GL	-HL -GH -GW
	In	HL LJL GH GW PrA	-ABL -PrL -BD -GL	LJL GW ABL PrL		LJL GH OD PrA	-ABL -PrC -PrL -BD -GL	HL LJL GH PrC PrL	-BD -GL -PrA	LJL GH	-ABL -BD -GL	OD	-HL -LJL -GH -GW -ABL -PrC -PrL -GL	X		PrC PrL	-GW	HL LJL GH GW PrA	-ABL -PrC -PrL -BD -GL	GW PrA	-PrL -GL	OD GL PrA	-HL -LJL -GH -GW -ABL -PrC -PrL
	Li	HL LJL GH GW PrA	-ABL -PrC -PrL -OD -BD -GL	HL LJL GW ABL	-PrC -BD	HL LJL GH GW OD PrA	-ABL -PrC -PrL -BD -GL	HL LJL GH GW PrC PrL	-OD -BD -GL	HL LJL GH GW PrA	-ABL -PrC -PrL -BD -GL	PrA	-HL -ABL -PrC -PrL -BD -GL	HL LJL GH GW PrA	-ABL -PrC -PrL -OD	X		HL LJL GH GW PrA	-ABL -PrC -PrL -BD -GL	LJL GW PrA	-ABL -PrC -PrL -GL	OD BD GL PrA	-HL -LJL -GH -ABL -PrC -PrL
	Se	HL LJL GW	-PrL -PrA	LJL ABL PrL BD	-PrA	HL GW OD BD	-PrC -GL	HL GH ABL PrC PrL	-PrA	HL OD BD	-PrA	ABL OD BD	-HL -LJL -GH -GW -PrC -PrA	ABL PrL BD GL	-LJL -GH -PrA	ABL PrC PrL OD BD GL	-LJL -GH -GW -PrA	X		ABL BD	-LJL -GH -PrA	ABL OD BD GL	-HL -LJL -GH -GW -PrA
	Wh	HL LJL	-ABL -PrL -BD	LJL ABL PrL	-PrA	OD	-ABL -PrC -PrL -GL	HL GH PrC PrL	-PrA	OD	-GL	OD	-HL -LJL -GH -GW -PrA	PrL OD GL	-HL -LJL -GH -GW -PrA	ABL PrC PrL OD BD GL	-HL -LJL -GH -GW -PrA	PrA	-HL -GW -ABL -BD	X		OD BD GL	-HL -LJL -GH -GW -ABL
	Zu	HL LJL GW	-ABL -PrL -OD -BD -GL	HL LJL GH GW ABL PrL	-OD	HL LJL GH GW OD	-ABL -PrL -BD -GL	HL LJL GH GW PrC PrL	-OD -BD -GL -PrA	HL LJL GH GW	-GL	GW	-GL	HL LJL GH GW PrC	-OD	HL LJL GH ABL PrC PrL	-PrA	HL LJL GH GW PrA	-ABL -OD -BD -GL	HL LJL GH GW	-OD -GL	X	

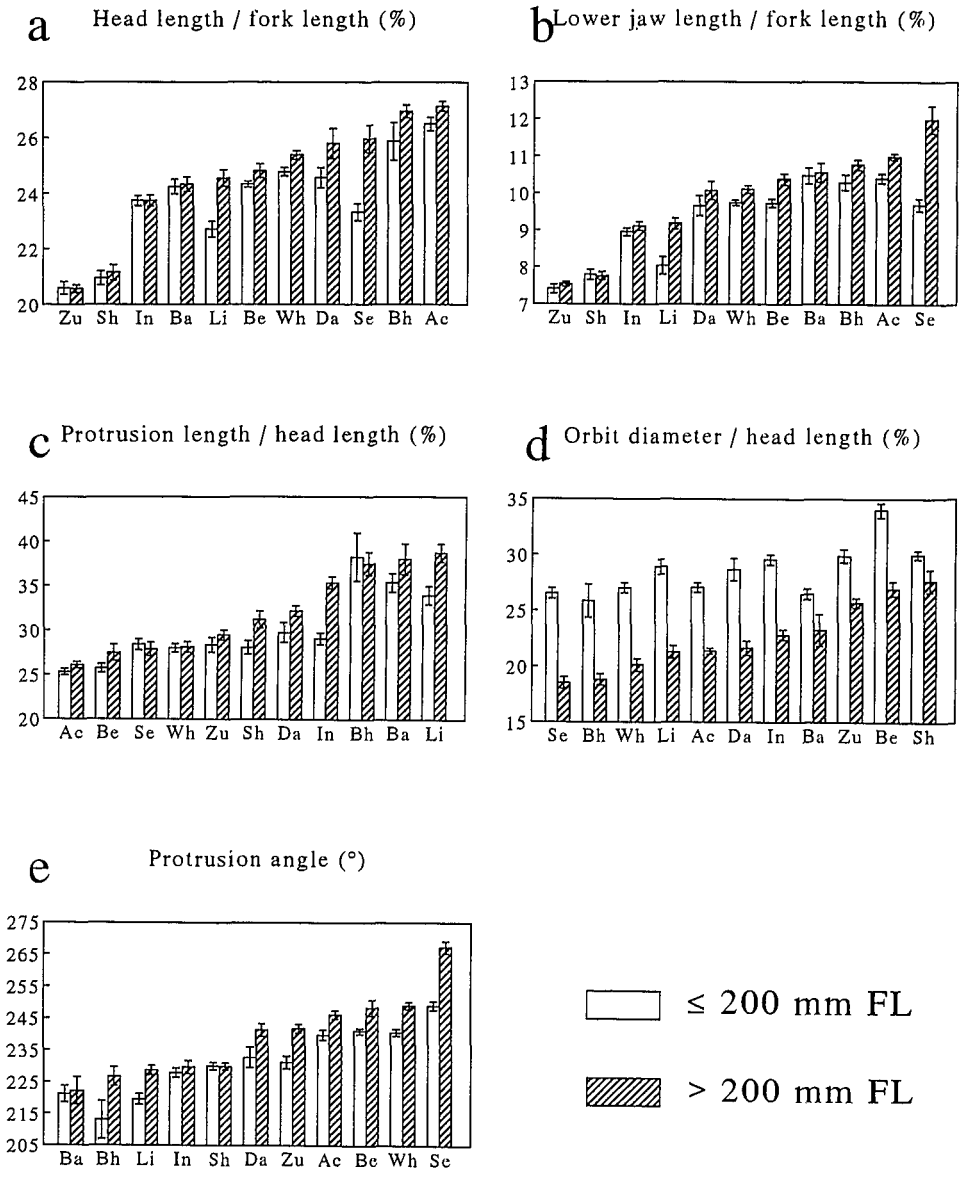


Fig. 3.5. Ratios (in %) of **(a)** head length, and **(b)** lower jaw length versus fork length, and **(c)** protrusion length and **(d)** of orbit diameter versus head length. **(e)** Protrusion angles. Open bars = FL ≤ 20 cm; hatched bars = FL > 20 cm. Name codes as in Table 3.1. Ratios are shown only as a graphical representation of the results. They were not statistically tested, but parameters were analyzed by means of ancova. Morphotypes are arranged according to increasing ratio or angle of the large size group. Standard errors of the means are indicated.

Table 3.4. Number of significant differences between the morphotypes that hold over the full size range of FLs (extracted from Table 3.3). Eight or more significant differences, as well as the case with 0 significant differences are bold-printed. An UPGMA-tree, using this table as a dissimilarity matrix is also shown.

		i										
		Ac	Ba	Be	Bh	Da	Sh	In	Li	Se	Wh	Zu
j	Ac	X										
	Ba	4	X									
	Be	2	4	X								
	Bh	5	3	6	X							
	Da	1	1	1	4	X						
	Sh	7	6	**8**	7	4	X					
	In	**8**	1	**9**	7	4	5	X				
	Li	**8**	3	**8**	6	**9**	4	3	X			
	Se	2	4	2	5	1	**8**	7	**9**	X		
	Wh	3	3	2	5	**0**	4	4	7	3	X	
	Zu	**8**	6	**8**	**10**	5	2	6	7	**9**	6	X

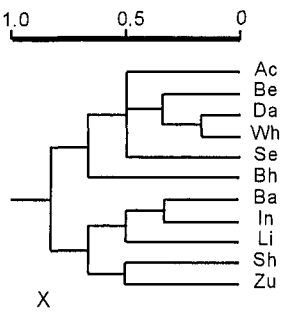


Table 3.5. Number of significant differences (and percentages of the maximum of 55 pairwise comparisons) between the morphotypes per morphometric parameter, for small, large and all fishes. The parameters that account for most frequent significant differences are bold-printed for each group. Note that parameters that are most important in small fishes (especially HL and LJL) also account for a large number of significant differences in large fishes, but other parameters have become even more prominent (especially ABL and GL).

Morphometric parameter:	Fishes ≤ 20 cm FL:		Fishes > 20 cm FL:		All fishes:	
	n:	%	n:	%	n:	%
HL	**37**	**67**	31	56	**31**	**56**
LJL	**36**	**65**	**32**	**58**	**28**	**51**
GH	34	62	28	51	22	40
GW	30	55	27	49	26	47
ABL	32	58	**36**	**65**	**32**	**58**
PrC	24	44	21	38	21	38
PrL	**36**	**65**	26	47	**28**	**51**
OD	28	51	29	53	23	42
BD	26	47	18	33	15	27
GL	24	44	**33**	**60**	20	36
PrA	32	58	**32**	**58**	27	49
Total:	339	56	313	52	273	45

Multivariate analysis of shape differences between morphotypes

To get an overall picture of shape differences among morphotypes a principal component analysis (PCA) of all metric characters was performed. The results of the PCA (Table 3.6, Fig. 3.6) are similar for both size groups. The first 3 PCs account for more than 80% of the variance. PC1 is not taken into account in the rest of the analysis, as it is mainly considered to represent size and not shape. PC2 accounts for 20.2 and 21.6% of variance for the small and large size group respectively and PC3 for 8.5 and 15.7%. PC3 is more important in the large size group. For both size groups ABL, GL and BD have the highest factor loadings (correlation between principal component and character) for the second principal component (PC2) and PrL, OD and BD for PC3. It is striking that HL and LJL have low factor loadings in PC2 and PC3, although they are responsible for a high proportion of significant differences between morphotypes. This may be caused by the fact that 15 - 20% of variance has not been accounted for in PC1-PC3, or that the differences in HL and LJL are not very large, but have low within-group variances. On the other hand, OD, and especially BD, are parameters that do not contribute to many significant differences between morphotypes are important in the PCA.

The position of the centroids of the morphotypes in the small and large size groups is similar, but mirrored in the PC3 axis. This is reflected in the high factor loadings for PC2 that have opposite signs in the small and large size groups. Exceptions are, on the one hand the centroids of Ba and In and of Sh and Wh on the other: they are very close in the large size group, while they are well separated in the small group. The centroids of Da and Se, however, are separated in the large size group, while they are very close in the small group.

The overlap (shown by the polygons in Figure 3.6) of the morphotypes is considerable in both size groups, but larger in the small size group. This can be explained by the fact that small fishes of different morphotypes are more alike than large fishes, but also by the fact that the absolute measuring values are smaller in small fishes, which increases the relative measuring error.

The PCA supports the results of the ancova and anova that the morphotypes differ from each other in a similar way in small and large specimens, in both the factor loadings of the PC2 and PC3 and the position of the centroids of the morphotypes.

DISCUSSION

The most important question to be answered at the moment for management of fish stocks, conservation of biodiversity and evolutionary studies is whether we are dealing with one panmictic population of barbs or with different populations or species. Nagelkerke et al. (1994) showed that not only distinct morphotypes are present, but that they also occupy different ecological niches which is reflected by diet and by distribution differences related to depth and substratum. Diet analysis shows that some morphotypes are typically polyphagous (In, Li) using a large variety of

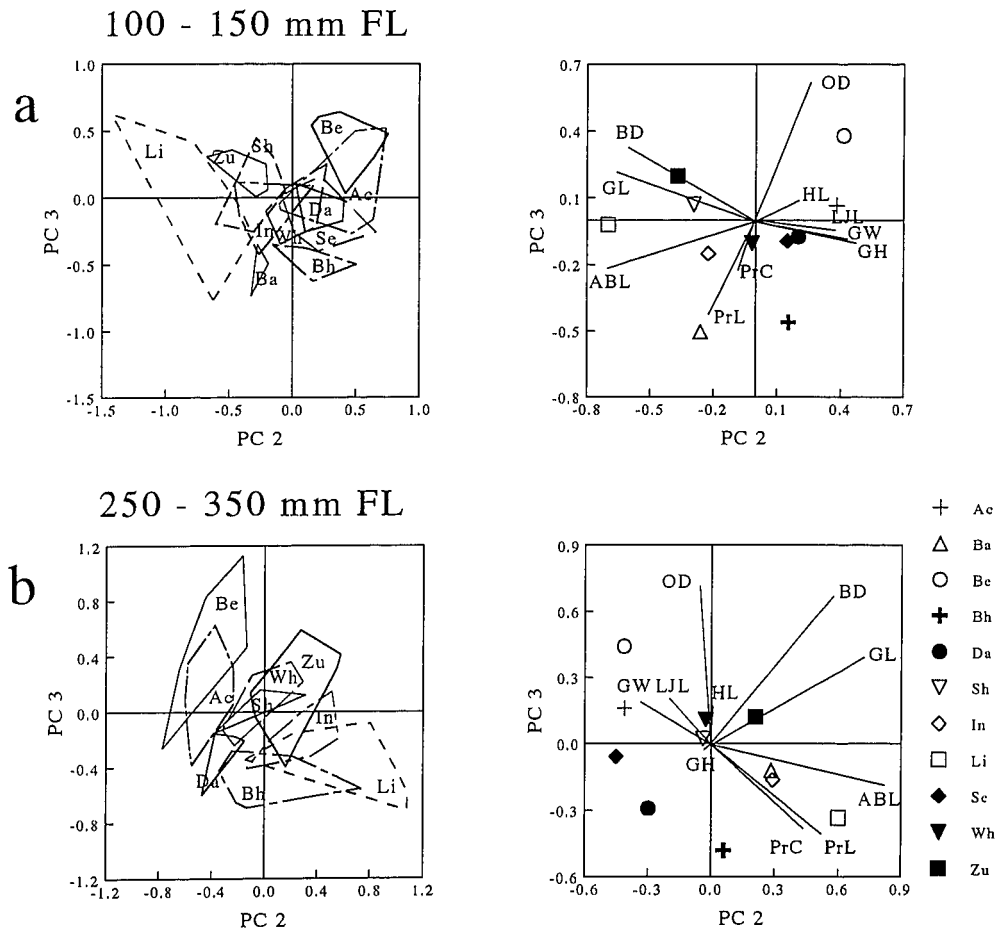


Fig. 3.6. Principal components analysis of **(a)** fishes between 10 and 15 cm FL and **(b)** fishes between 25 and 35 cm FL. At the left polygons surrounding the scores on PC2 and PC3 of all specimens of a morphotype are shown; to the right biplots are shown with (1) centroids of the scores on PC2 and PC3 of the morphotypes and (2) the factor loadings of the original characters on PC2 and PC3. In (b) polygons of Ba and Se are not shown, because there are only two data-points for each and they fall within the range of In and Ac respectively.

food items, while others are more or less specialized in e.g. macrophytes (Zu), molluscs (Ca) or fish (Ac). They also showed that this ecological differentiation is reflected by morphological parameters: measures such as gut length, protrusion length, gape size and barbel length are important for food capture and processing (in)abilities. This morphological, trophic and spatial differentiation supports the idea that at least some morphs represent different *Barbus* species.

Table 3.6. Eigenvalues (%) and factor loadings of the second and third principal component for a small and a large size group of fishes. The three parameters with the highest absolute factor loadings are bold-printed for each principal component.

	Fishes 10-15 cm FL		Fishes 25-35 cm FL	
	PC2	PC3	PC2	PC3
Eigenvalue (%):	20.2	8.5	21.6	15.7
Cumulative:	77.4	85.9	65.8	81.5
HL	0.206	0.091	0.010	0.170
LJL	0.375	-0.044	-0.197	0.206
GH	0.477	-0.099	-0.030	-0.026
GW	0.435	-0.082	-0.337	0.195
ABL	**-0.706**	-0.216	**0.822**	-0.188
PrC	-0.083	-0.223	0.438	-0.380
PrL	-0.218	**-0.421**	0.523	**-0.406**
OD	0.262	**0.624**	-0.052	**0.717**
GL	**-0.660**	0.220	**0.728**	0.397
BD	**-0.603**	**0.333**	**0.575**	**0.671**

The divergence of juvenile barbs

Mina et al. (1993, 1996) confirm the existence of discrete morphotypes, but suggest that the morphological divergence of the barbs starts most frequently in the standard length interval between 20-25 cm. According to their studies only fishes larger than 25 cm standard length can be assigned to specific morphotypes in 90 % or more of the cases. Standard lengths of 20-25 cm correspond to fishes in their 3th to 5th year of life, according to their age estimates. However, the present study shows that 11 morphotypes can already be distinguished at FLs of about 10 cm (Figs 3.1, 3.5, 3.6, Table 3.2) and that their shape differences are similar in both small and large specimens. Using the age estimation of Mina et al. (1993) this would mean that morphotypes diverge and attain morphologies very similar to the adult fishes in their first year. The discrepancy between this study and the one of Mina et al., might be due to the fact that in the latter no small fishes were examined. The standard length of the onset of divergence was calculated by extrapolating data of the large fishes (the authors themselves were very much aware of the risk of doing this). Adding small fishes to their study probably would have changed the slopes of the regression lines, thereby changing (and most probably decreasing) the standard length at which divergence starts. The parameters which are not consistent over the whole size range indicate that the linear growth curves for these parameters are, in fact, not parallel in these morphotypes, which results in smaller or larger differences between morphotypes in either the small or the large size

groups. The few cases in which the differences between morphotypes are significant, but have an opposite sign in small and large specimens is caused by a similar effect, but here the linear growth curves of these morphotypes cross. However, for each pair of morphotypes (except the Da and Wh) there is a number of parameters that consistently contribute to significant differences over the whole size range, which indicates the early divergence of morphotypes. This early divergence is additional support for the existence of different species of *Barbus* in Lake Tana.

Even the existence of discrete morphotypes over the entire size range is no absolute proof that the diversity in morphotypes is not due to phenotypic plasticity. Discrete phenotypic variation (polyphenism) has been described (Dgebuadze 1995, Stearns 1989, Witte et al. 1990), and is even considered as a contributing factor to speciation (West-Eberhard 1989). Polyphenism however, is usually described as the existence of two or three alternative phenotypes, triggered by some clear environmental factor (Dgebuadze 1995, Witte et al. 1990). There are no indications for such a factor: juvenile Lake Tana barbs do not occupy clearly different habitats or trophic niches. Moreover, the high number of discrete morphotypes (14, of which 11 can be distinguished as juveniles, instead of the usual two or three) also suggests that there is at least some genetic base to this diversity.

In addition to the application of morphometric methods for qualifying and quantifying population differences between the *Barbus* morphotypes, additional data from the analysis of allozymes, and nuclear and mitochondrial DNA are in progress (Dixon et al. 1994; Berrebi & Valiushok in prep.). The first results indicate a moderate genetic divergence between morphotypes. In our opinion, however, gathering data on segregation in spawning (temporal, spatial, behaviourial) is another essential way to find conclusive answers to the species question. Preliminary data indicate spatial and/or temporal segregation of Be and Ac on the spawning grounds. In contrast with e.g. the haplochromine cichlids of Lake Victoria all the barbs appear to spawn in the rivers or river mouths, and they do not show distinct colouration patterns. These are regarded as major clues for species distinction of cichlids, because of their important role in the recognition of specific mates (van Oijen et al. 1981). Such apparent pre-mating isolation mechanisms seem to be absent among the *Barbus* morphotypes. Further research is urgently needed to establish the status and options for protection of this unique species flock.

A hypothesized evolutionary history of the Lake Tana barbs

The *Barbus* morphotypes of Lake Tana can be divided in three groups. The first consists of the 11 examined morphotypes that can already be distinguished from a FL of 10 cm. The second group consists of three morphotypes (Ca, Mi and Tr) of which specimens smaller than 20 cm FL were never found with certainty. It is possible that they were never caught because they are spatially segregated from other juvenile *Barbus* morphotypes, but it may well be that they arise from the pool of small fishes that cannot be recognized yet as any of the described morphotypes (Fig. 3.1*b*, Mina et al. 1996). It must be made explicit here that unidentifiable fishes have not been included in the In morphotype, since this can be distinguished by specific characters, such as the downward protrusion in combination with orbit diameter and head length. The third group

(maximum of 8% of all fork length classes, Fig. 3.1*b*) consists of fishes some of which (especially larger specimens) resemble, but are not the same as any of the described morphotypes. Some of these may well be distinct, as yet undescribed morphotypes, but the majority (especially those found near the shore close to the vegetation) forms a morphologically continuous range, mostly being somewhat similar to In and Da.

Brunelli (1940), Nagelkerke et al. (1994) and Mina et al. (1996) suggest that a combination of several distinct biological species next to a group of interbreeding, variable barbs might be present. The 11, early diverging, distinct morphotypes suggest the existence of separate populations or species. The other 3 morphotypes, of which no small specimens have been found until now (Ca, Mi and Tr) still could form different populations or a single polymorphic population. However, preliminary investigations in September 1994 suggest there is reproductive segregation of Tr. The third group of fishes forming a continuous morphological range most probably constitutes an interbreeding group of fishes.

The variability of the latter group resembles that of the riverine *Barbus intermedius* population of the Ethiopian highlands (Mina pers. comm., pers. obs.). Therefore it is hypothesized that this third group resembles the barbs of the Blue Nile that were present in the river, when it was blocked by volcanic activity in the early Pleistocene (Mohr 1962) and Lake Tana was formed. When the lake was formed a range of new lacustrine environments became available to the barbs. Adaptive radiation has led to the great morphological and ecological diversity of the barbs as is seen today. The barbs that radiated into the new open water environment are the most distinct and the most likely to be true biological species (Ac, Ba, Be, Sh, In, Se). The barbs that live near the shore, in circumstances more similar to riverine conditions (vegetation, shallow water, occurrence of terrestrial insects *etc.*) still exhibit the 'typical' (variable) morphology and ecology of riverine *Barbus intermedius*.

The large Lake Tana barbs offer an opportunity to study the evolution of a unique cyprinid species flock. In contrast to the cyprinid species flock of Lake Lanao on the Philippines (Kornfield & Carpenter 1984), and to the haplochromine cichlids of Lake Victoria (Witte et al. 1992) it is still intact. As it only consists of a limited number of species, it is feasible to actually resolve its phylogeny and to understand the process of its evolution into different ecological niches.

ACKNOWLEDGEMENTS

We would like to thank M.V. Mina for stimulating discussions and interesting ideas and G.D.E. Povel for advices on multivariate statistics. C.D.N. Barel is acknowledged for his valuable comments improving the manuscript. The Fisheries Resources Development Department of the Ministry of Agriculture of Ethiopia is thanked, especially Mebrat Alem, Solomon Tibebu and Endale Lemma for their warm support and their kind permission to use the laboratory in Bahar Dar. We are grateful to the Ethiopian Orthodox Church (DICAD), especially His Grace Archbishop Timotheos and his staff, for supporting us in logistics. Asfaw Berhe, Girma Mengistu, Geert van Snik, Michiel Helmes and Suzanne van Gaans are acknowledged for help in fishing, administration and social aspects during the field work. Brian Dixon helped with the improving of the English text.

This research was funded by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W 88-176, the Interchurch Foundation Ethiopia (ISE, Urk) and the Interchurch Coordination Commission of Development Projects (ICCO, Zeist).

Chapter 4

Reproductive segregation among the large barbs (*Barbus intermedius* complex) of Lake Tana, Ethiopia. An example of intralacustrine speciation?

Leo A.J. Nagelkerke[1] & Ferdinand A. Sibbing[1]

[1]*Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

Published in: *The Journal of Fish Biology* (1996) **49**: 1244-1266.

ABSTRACT

Reproductive segregation among the large barbs, *Barbus intermedius* complex, *Cyprinidae*, of Lake Tana, Ethiopia, was investigated in the mouths and upstream reaches of rivers tributary to the lake, during the spawning seasons of 1993 and 1994. The percentage of running fish of four *Barbus* morphotypes (Acute [Ac], Bigmouth big-eye [Be], Intermedius [In], and Shorthead [Sh]) peaks with the highest water level of the lake. Large differences are apparent in the minimum fork length of running fish among morphotypes (c. 12 cm for male Sh and 28 cm for male Bigmouth small-eye [Se]). Significant differences occur in temporal, but especially in spatial patterns of the relative abundance of running morphotypes, when we compare the lake itself with the four major river mouths and their upstream reaches. These different relative abundances are clearest among Ac, Be, In, Sh and Troutlike (Tr). Also, the absence from the rivers of some morphotypes that are usually abundant in the lake itself (Barbel [Ba], Dark [Da], Lip [Li], and Zurki [Zu]), and the abundant presence in the rivers of Tr, rare in the lake, strengthen the hypothesis that spatial and/or temporal spawning segregation is present among the morphotypes. There are indications that Bighead (Bh) and Zu spawn in the lake itself, while other morphotypes were only found running in or near rivers. Combined with the morphological, ecological, and genetic differences, these data suggest the existence of several *Barbus* species, forming a unique species flock, which probably evolved within the lake. The presence of several, instead of one *Barbus* species complicates management of sustainable fisheries and protection of the lake's biodiversity. Present results show the importance of the rivers for *Barbus* reproduction and stress the urgent need for careful management of fishing activities in spawning times and areas.

INTRODUCTION

Lake Tana (northern Ethiopia) appears to be a natural laboratory for evolutionary studies (Nagelkerke et al. 1994, 1995*a*, Sibbing et al. 1994). The large barbs of the lake, previously described as *Barbus intermedius* Rüppell 1836, Cyprinidae, can be divided into at least 14 distinct morphotypes (Nagelkerke et al. 1994, 1995*b*, Osse et al. 1993, cf. Table 4.1 for names and abbreviations). The hypotheses about the taxonomic status of the morphotypes are: (1) they all belong to one, phenotypically plastic species: *Barbus intermedius* (Banister 1973); (2) they all constitute different species; (3) there is a combination of a number of morphologically distinct species and one or several phenotypically plastic species, the latter showing late ontogenetic divergence into different morphotypes (Brunelli 1940, Mina et al. 1993, 1996, Nagelkerke et al. 1995*b*).

Based on the large (distinct) morphological and ecological differentiation between morphotypes it is increasingly likely that the morphotypes are distinct species, forming a unique cyprinid species flock (Nagelkerke et al. 1994, 1995*b*, Sibbing et al. 1994). This is supported by the first results of genetic analyses (Dixon et al. 1994, 1996). Knowledge of the nature of the diversity

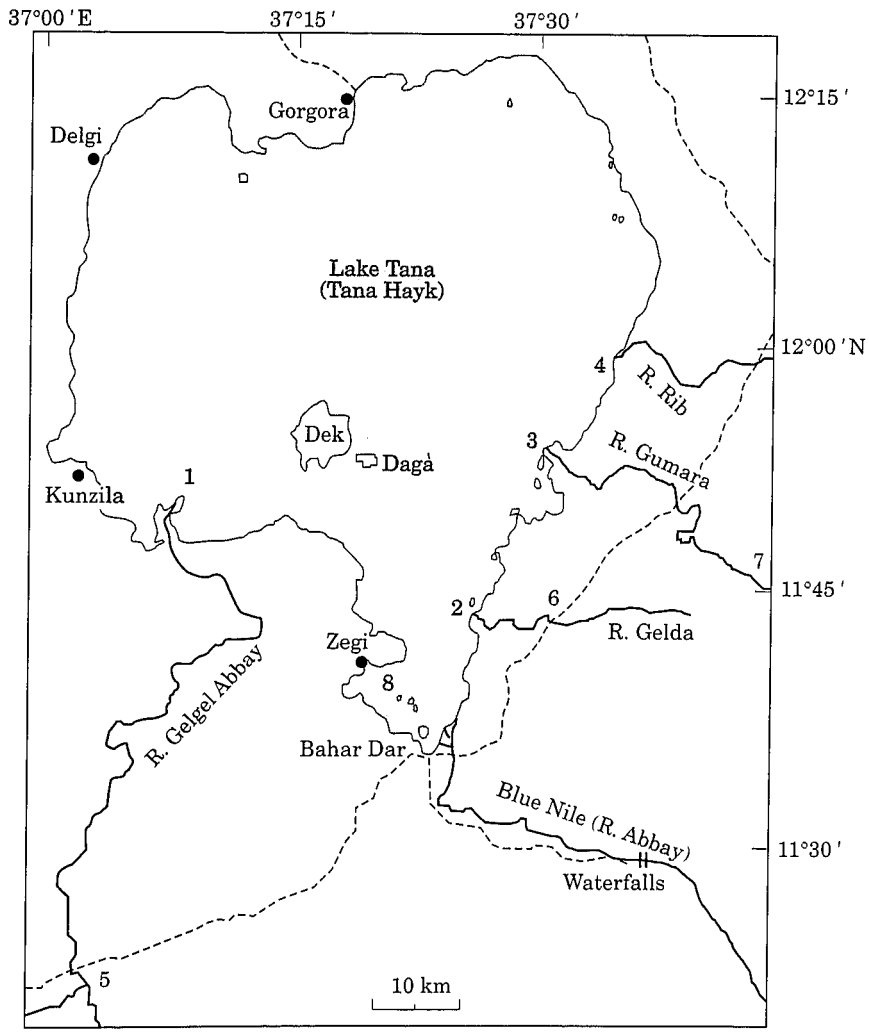


Fig. 4.1. Map of Lake Tana with all sampling points: (1) Gelgel Abbay mouth, (2) Gelda mouth, (3) Gumara mouth, (4) Rib mouth, (5) Gelgel Abbay upstream, (6) Gelda upstream, (7) Gumara upstream [Wanzaie], (8) Zegi Bay.

Table 4.1. The 14 morphotypes composing the Lake Tana *Barbus intermedius* complex. Names and abbreviations follow Nagelkerke et al. (1994, 1995*b*).

Trivial name:	Name code:
Acute	Ac
Barbel	Ba
Bigmouth big-eye	Be
Bighead	Bh
Carplike	Ca
Dark	Da
Intermedius	In
Lip	Li
Bigmouth mini-eye	Mi
Bigmouth small-eye	Se
Shorthead	Sh
Troutlike	Tr
White hunch	Wh
Zurki	Zu

among the *Barbus* species is required for proper management of sustainable fisheries (Sibbing et al. 1994). Insight into the population structure of the *Barbus* complex is of the greatest importance not only for fisheries development, but also for conservation purposes.

Morphological, ecological and genetic evidence all contribute to solving the question whether different good *Barbus* species are present in Lake Tana, but data on segregated spawning provide more direct evidence for the existence of different biological species. Hence the aim of this study was a quantitative investigation of sizes, sites and times of spawning of the Lake Tana *Barbus* morphotypes.

The addressed questions are:

1. Is there spatial segregation among the morphotypes; where do the different morphotypes spawn?
2. Is there temporal segregation among the morphotypes; when do the different morphotypes spawn?
3. Is there a differentiation in size of spawning among the morphotypes?

The answers to these questions will also give guidelines as to what areas should be protected in what season to assure the recruitment of the future fish stocks (Nagelkerke et al. 1995*a*).

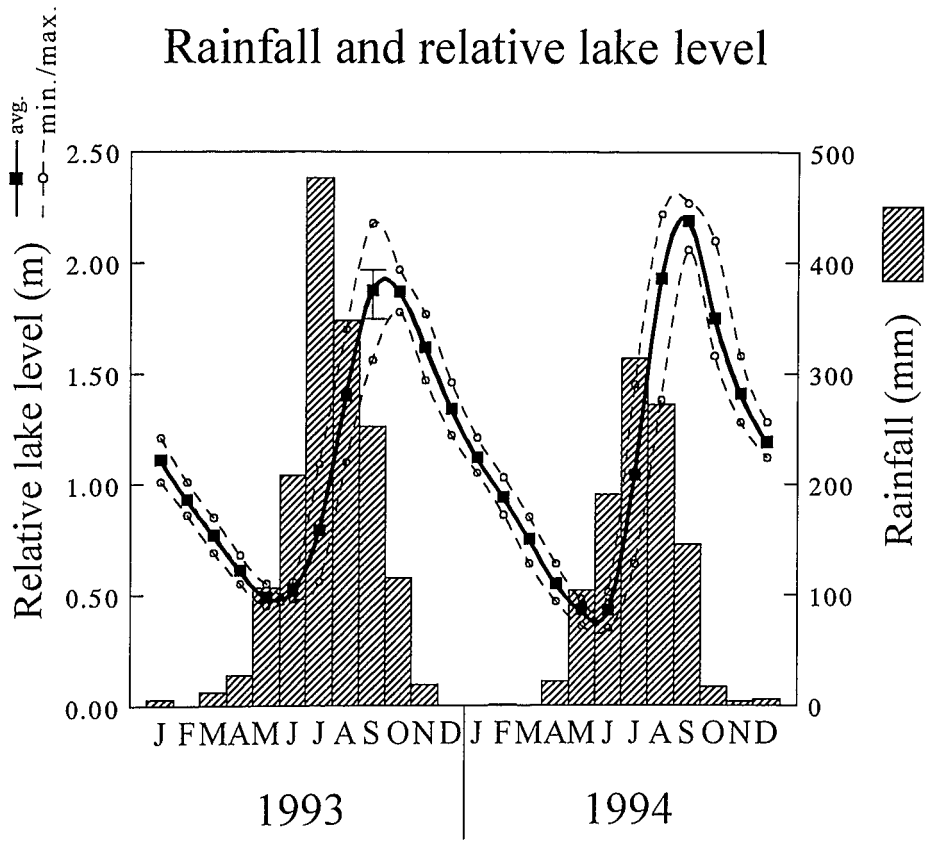


Fig. 4.2. Rainfall (bars) and relative lake level (filled squares and solid line are average values, open circles and dotted lines are minimum and maximum values per month) in 1993 and 1994. The lake level of September 1993 is missing, but was estimated using data of the period 1984 to 1990. The error bar indicates the approximate reliability of the estimated value. Note the strong seasonality of the rainfall (peak in July and August) and lake level (peak in September-October). (Sources: National Meteorology Office, National Water Resources Department, Addis Ababa, Ethiopia).

MATERIALS AND METHODS

Study Area

Lake Tana is situated at an altitude of c. 1800 m, in the northern highlands of Ethiopia. It has a mean depth of 8 m (maximum depth is 14 m), an area of c. 3150 km^2 and is characterized as oligotrophic (Rzóska 1976).

Data from earlier expeditions suggested that before spawning the barbs migrate towards the river mouths (Nagelkerke et al. 1995*a*). It was not known whether they migrate upstream for spawning, or stay in the river mouths where extensive flooded areas develop during the rainy season. Therefore attention was focused on the mouths and upstream reaches of the four largest rivers tributary to Lake Tana.

Samples were taken in Lake Tana and in the mouths of the following rivers (Fig. 4.1):

1. Gelgel Abbay (11°,51' N; 37°,08' E)
2. Gelda (11°,44' N; 37°,26' E)
3. Gumara (11°,53' N; 37°,29' E)
4. Rib (11°,59' N; 37°,34' E).

All these rivers are permanent, although there is a strong seasonality in rainfall and lake level (Fig. 4.2). The rivers are much swollen at the peak of the rainy season (July and August) and the lake level reaches its maximum c. two months later.

All rivers have extensive papyrus, *Cyperus papyrus*, swamps in their mouths. Gelda is the smallest river of the four, both in width and in length (approximately 30 km), being relatively shallow (0.5 to 2 m) and containing gravel beds and relatively clear water during the sampling period (September-October 1993 and 1994). Gelgel Abbay is the largest river with a length of more than 100 km. The mouth of this river extends into the lake by an elongated papyrus peninsula. Gumara and Rib are both c. 80 km long. The latter three rivers flow through a plain for a considerable part of their length (at least 30 km), and can attain depths up to *c.* 10 m during the sampling period. Only farther upstream do rapids and cataracts occur. Small rivers tributing to these rivers contain clear water and gravel beds during this time of the year, while the main streams are heavily silt-laden.

In addition to the samples from the river mouths, samples were obtained from the upstream reaches of:

5. Gelgel Abbay, where the road from Bahar Dar to Addis Ababa crosses the river, approximately 70 km upstream (11°,23' N; 37°,02' E).
6. Gelda, where the road from Bahar Dar to Gondar crosses the river, approximately 10 km upstream (11°,43' N; 37°,30' E).
7. Gumara, at Wanzaie (hot springs), approximately 30 km upstream (11°,46' N; 37°,43' E).

To compare the composition of catches in the rivers and river mouths with the catch from Lake Tana itself the last sampling area was chosen in the lake:

8. Zegi Bay, (11°,40' N; 37°, 19' E).

Table 4.2. All experimental fishing efforts during 1993 and 1994.

River/location in lake:	Position:	Date:	Method:
Gelgel Abbay	upstream	26-Sep-94	cast net
	mouth	26-Sep-94	gill net
Gelda	upstream	20-Sep-94	gill net
		22-Sep-94	gill net
	mouth	09-Sep-93	gill net
		21-Sep-94	gill net
Gumara	upstream	15-Sep-94	scoop net
	mouth	15-Sep-93	gill net
		12-Oct-93	gill net
		16-Sep-94	gill net
		29-Sep-94	gill net
		06-Oct-94	gill net
		13-Oct-94	gill net
		20-Oct-94	gill net
Rib	mouth	23-Sep-94	gill net
Zegi Bay	open water	22-Sep-94	trawl net

Data collection

During the periods of 9 September until 12 October 1993 and of 15 September until 20 October 1994 data have been collected by:

1: interviews with local fishermen (only in 1994) to obtain information on migrations and concentrations of fishes and on the occurrence of young fish; five fishermen from the Gumara and Rib region, and three from the Gelgel Abbay area were interviewed with help of an official of the local Ministry of Agricultural, who interpreted for us (for details see Results);

2: experimental fishing in three different ways (cf. Table 4.2):

a. Hiring local fishermen to fish upstream in the rivers, using artisanal methods. This included cast netting in Gelgel Abbay and scoop netting in Gumara.

b. Gill net fishing in the mouths of all mentioned rivers and upstream in Gelda. Different combinations of polyfilament gill nets (60, 80, and 100 mm stretched mesh size), and monofilament gill nets (25, 32, and 44 mm stretched mesh size) were used, during 8-14 h in the river mouths. In the upstream reaches of Gelda only these monofilament nets were used during 4 h. The inclusion of the small, monofilament gill nets assured that the smallest barbs

caught were juveniles, so that a reliable estimate of the minimum size of maturity could be made.

c. Trawl fishing in Zegi Bay. The trawl net had a cod end cover of 40 mm stretched mesh size. Each haul lasted 30 min.

Table 4.3. Gonad maturation stages for cyprinids, according to and Pet et al. (1996), modified from De Silva et al. (1985) .

Maturation stage:	Male:	Female:
1	Immature, impossible to distinguish females from males. Gonads are a pair of transparent strings running along body cavity wall	Immature, impossible to distinguish females from males. Gonads are a pair of transparent strings running along body cavity wall
2	Unambiguously male, very small testes, white-reddish, not lobed, tube-shaped strings	Unambiguously female, very small ovaries, tube shaped and reddish, eggs not visible
3	Larger testes, white-reddish, somewhat lobed, starting to flatten sideways	Ovary somewhat larger and starting to flatten sideways, eggs visible, but very small
4	Large testes, white-reddish, lobed, flattened sideways	Larger ovary, flattened sideways and almost covering body cavity wall, eggs yellowish
5	Large, white testes, some sperm runs out when testis is cut	Large and full ovary, completely covering body cavity wall, yellowish eggs run out when ovary is cut
6	Large white testes, running, large amount of sperm runs out when testis is cut	Running, yellow eggs can be extruded by putting pressure on the abdomen
7	Spent, empty testes, reddish and wrinkled	Spent, wrinkled ovary, reddish, containing a few yellow eggs

The fork length (FL) of each fish was measured to the nearest 0.5 cm and the gonad maturation stage was determined (Table 4.3). Of each morphotype, finally the minimum FL of running fish (gonad maturation stage 6) was determined separately for females and males. Fishes of at least that size (FL_{min}) were considered potentially running, *i.e.* of mature size. The percentage of running barbs was calculated from the number of fish of mature size only.

We concentrated exclusively on running fish, because (1) we wanted to be absolutely certain that we would only consider fish that would spawn in the current season, and (2) these fish were most likely to spawn very close to the place where they were caught: fish with maturation stages 4 and 5 might still be able to migrate a considerable distance prior to the actual spawning. During the sampling periods, however, we hardly found any fish of stages 4 and 5 (less than 1% of

the total number). In almost all cases fish were either running or still immature (gonad stages 3 or less), therefore we chose the most conservative estimate and only used running fish for our calculations.

The frequencies of occurrence of the morphotypes at certain sites and times were analysed with a G-test for independence (Sokal & Rohlf 1981) using BIOMstat, version 3.01 software (Exeter software, Setauket, New York). With this test the frequencies of occurrence (as listed in tables 4.5, 4.6, and 4.7) were compared among columns (differences between places and times) and especially among rows (differences between morphotypes). Statistically significant differences indicate temporal and/or spatial segregation of morphotypes and form the main body of evidence for reproductive isolation.

The G-test requires frequencies of at least three: therefore, sometimes frequencies of morphotypes had to be pooled when the frequencies of individual morphotypes were less than three. This pooling was done in such a way that the resolving power of the test was optimized.

A significance level of $p<0.05$ was used, unless otherwise stated. In the case of multiple pairwise comparisons between morphotypes, or between places and times, the level of significance was taken as $p< [0.05/n]$(in which n is the total number of comparisons), in order not to overestimate the number of significant differences (Cooper 1968).

RESULTS

Spawning migration

Local fishermen were interviewed with the help of an official from the local Ministry of Agriculture. The primary source of income of these fishermen is agriculture and they only fish during the season when fish is abundant in the rivers. Therefore we expected them to be able to give valuable information on migration patterns in the rivers. Moreover, fishermen from the Lake Tana area recognize different 'morphs' of the *Barbus intermedius* complex, indicating them with local names, as was already observed by Rüppell (1836). Most of these local names are consistent with one of our morphotypes (or with a combination of two similar morphotypes).

Five fishermen from the Gumara/Rib region (the upstream reaches of these rivers are quite near to each other and fishermen often fish in both rivers) and three from the Gelgel Abbay region were interviewed. The questions were as follows: (1) when do they fish (season and time of day)?; (2) why only then?; (3) how often do they fish?; (4) which fishes do they catch?; (5) do they notice any migration of the fish?; (6) do all barbs occur together or do they group according to morphotype?; (7) do they notice the occurrence of young fish in the rivers? Questions and answers were interpreted by the local official. The answers were written down, evaluated with the official and consequently processed in a qualitative way. Although the interviews differed from each other in detail, a (more or less) consistent, qualitative, picture of the migration of *Barbus* in the rivers emerged (Fig. 4.3):

June (*May* in Gelgel Abbay): The fishes (barbs of many types and *Varicorhinus beso* Rüppell) start migrating up the rivers when the rainy season starts and the rivers increase in size.
July: The migration up the rivers continues. There is no fishing, because of the strong currents. From the end of this month fish from the Gumara R., start their return to the lake and the fishery gradually starts.
August: Both migration up and down the rivers is reported. Fishing continues in Gumara.
September: Intensive fishing activities in Gumara, especially on returning barbs, although still some migration upstream is reported. According to some fishermen large groups of young fish can be seen in Rib in this month. In Rib fishing only starts in this month. In Gelgel Abbay fish return to the lake when the "water becomes clear" i.e. at the end of the rainy season. Only then fishing starts in this river.

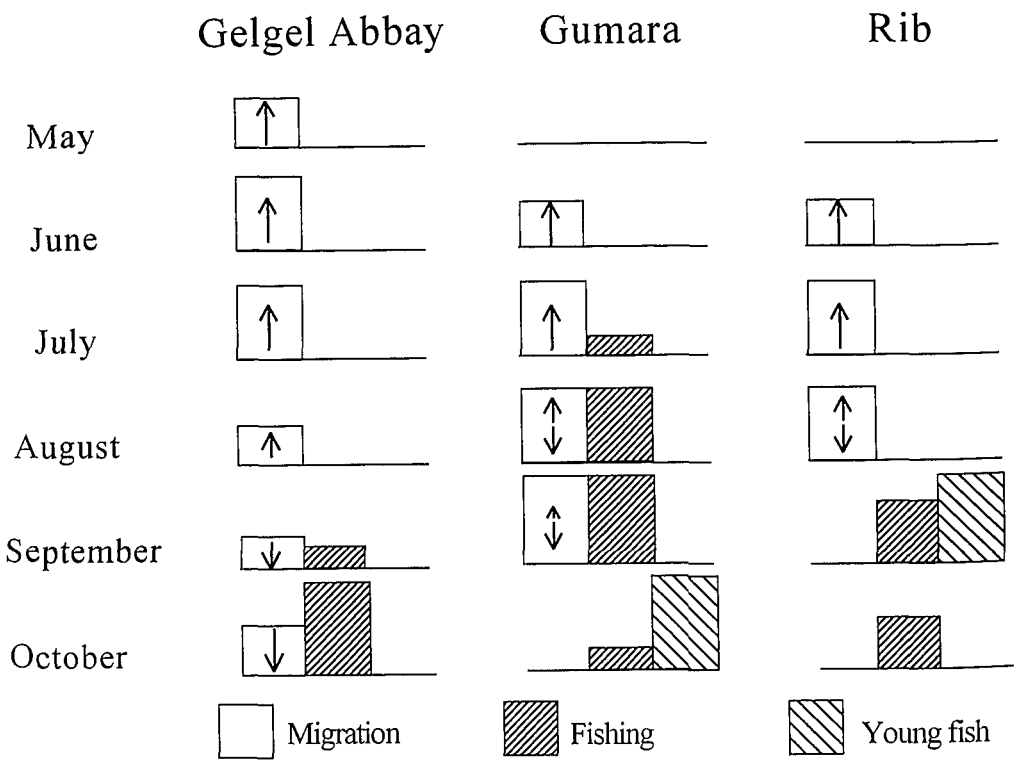


Fig. 4.3. A qualitative, graphic representation of the interviews with local fishermen about spawning of barbs in the Gelgel Abbay, Gumara and Rib rivers. Migration (arrows pointing upwards indicate migration upstream, those pointing downward, migration downstream), intensity of fishing activity and the occurrence of young fish are indicated. The height of the bars gives a strictly qualitative impression of the intensity of these three phenomena as was apparent from the interviews.

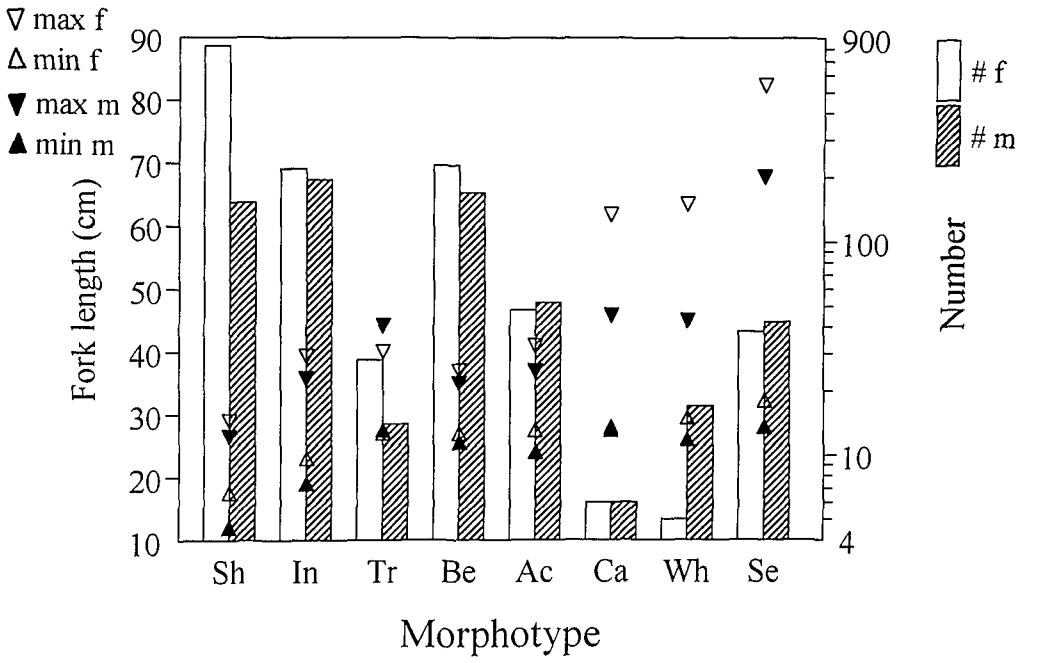


Fig. 4.4. Minimum and maximum fork lengths (FL_{min} and Fl_{max}, left Y-axis, open triangles are females, solid triangles are males) of running barbs. The bars (right Y-axis, note the log-scale) indicate the total number per morphotype (separately for females [f, open bars] and males [m, stippled bars]). Morphotypes are sorted according to increasing FL_{min}. Note that there are large differences in the FL_{min} for both males and females. Fishes with small FL_{min} also have a lower FL_{max} value. The morphotypes Ba, Bh, Mi and Zu were not found running at all; Da and Li in very small numbers (less than 5) and are not included in this graph.

October: Young fish reported in Gumara. Fishing stops in Gumara during this month. In Gelgel Abbay most catch is made from October to March, but most likely this concerns riverine fishes.

The overall impression from the interviews is that the upstream migrations occur only during increase of the lake level, i.e. over three to four months (from June until September, cf. Fig. 4.2). Such a prolonged period of migration invites the investigation of temporal segregation of the different morphotypes during spawning.

We do not know whether the spawning barbs tend to group according to morphotype in the rivers, or that they all mix. One fisherman at Gumara and one at Gelgel Abbay said that there is a grouping according to morphotype; another said that all types of *Barbus* were found together.

Table 4.4. Size of running barbs. Coefficients (a,b) of statistically significant ($p<0.05$) sigmoid curves ($Y = 100/[1+\exp^{(a-bX)}]$) describing the maturation of different *Barbus* morphotypes with fork length (FL). X = FL class (2 cm); Y = percentage of running barbs; Total = number of fish per morphotype and per sex; R^2 = correlation coefficient; n = the number of data points (FL classes); $FL_{50\%}$ = FL at which 50 % of the individuals is running, according to the sigmoid ($FL_{50\%} = a/b$); FL_{min} = smallest FL at which a running specimen of a morphotype was found.

Morphotype:	Sex:	Total number of fish:	a:	b:	R^2:	n (number of FL classes):	$FL_{50\%}$ (=a/b) (cm):	FL_{min} (cm):
Ac	♀	54	54.06	1.91	0.88	11	28.3	27.5
	♂	57	87.03	3.27	0.58	8	26.6	24 .0
Be	♀	227	94.54	3.27	0.88	7	28.9	27.0
	♂	169	-	-	-	-	-	25.5
In	♀	237	41.16	1.71	0.47	9	24.0	23.0
	♂	204	65.72	2.97	0.87	9	22.1	19.0
Se	♀	42	-	-	-	-	-	32.2
	♂	43	-	-	-	-	-	28.0
Sh	♀	829	65.76	2.92	0.62	7	22.5	17.5
	♂	159	-	-	-	-	-	12.0

Size of running *Barbus* morphotypes

The minimum FL of running fish (FL_{min}) differs among morphotypes (Fig. 4.4, Table 4.4), with Sh having the smallest FL_{min} for both females and males (17.5 and 12 cm respectively). Se has the largest FL_{min} for both females and males (32.2 and 28 cm respectively). Usually the FL_{min} for males is smaller than for females. In Tr and Ca there is no difference between females and males in this respect.

FL_{min} is based on the smallest running specimen, which may be an exceptional fish. Therefore the relation between FL and the percentage of running barbs has been described as a sigmoid curve (Fig. 4.5). Only in this case this percentage was calculated from all barbs (of the same morphotype) caught in the sampling events (Table 4.2), not only from the barbs of mature size. The sigmoid curve is described by:

$$Y = \frac{100}{1 + e^{(a-bX)}}$$

in which X is a 2 cm FL class, Y the percentage of running barbs, and a and b are constants. This formula can also be written as:

$$\ln(\frac{100}{Y}-1)=a-bX$$

To estimate the best values for a and b, linear regression has been performed in which the left term of the equation was taken as the dependent variable and X as the independent variable. If the regression was statistically significant ($p<0.05$) the values for a and b are listed in Table 4.4, as well as the FL at which 50% of the fish are running, according to the sigmoid curve ($FL_{50\%}$):

$$FL_{50\%}=\frac{a}{b}$$

The values of $FL_{50\%}$ are larger than those of FL_{min} in all cases and show the same pattern as the latter, i.e. Sh has the smallest FL_{min} and $FL_{50\%}$, for In these values are larger, and for Be and Ac the largest (for Se no significant $FL_{50\%}$ values could be calculated).The steepness of the curves shows that the barbs attain mature size with only a few centimeters growth (an average of 1.8 cm from 10 to 90% running; an average of 3.7 cm from 1 to 99% running). Together with the differences in FL_{min} and $FL_{50\%}$ this suggests differences in reproductive strategies during the life histories of the morphotypes.

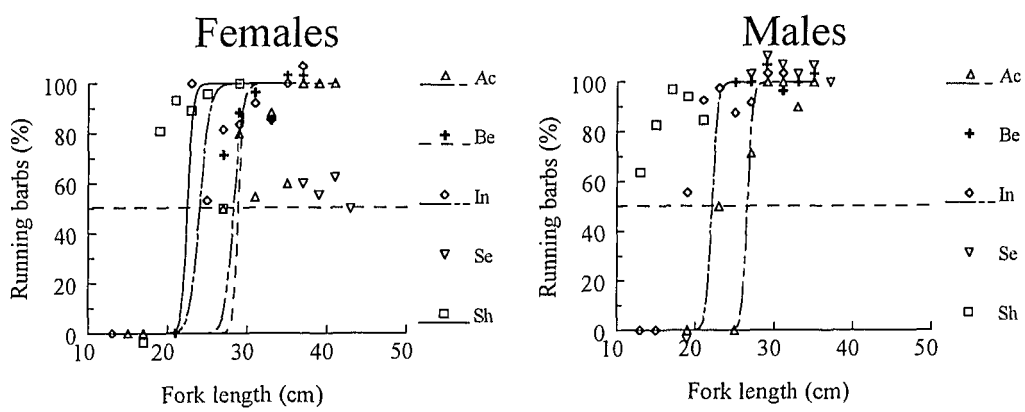


Fig. 4.5. The percentage of running fish as a function of fork length class for females and males of the morphotypes Ac (upward pointing triangles), Be (crosses), In (diamonds), Se (downward pointing triangles) and Sh (squares) (cf. Table 4.4). Symbols are printed on top of each other on the 0 and 100% axes if they overlap. Sigmoid curves through the points are shown, if they are statistically significant. Note the steep lines and the differences among morphotypes in fork length at which 50% of the individuals are running ($FL_{50\%}$), both suggesting real differences in spawning.

Temporal patterns in running morphotype composition

The percentage of running barbs is shown for the Gumara River mouth (Fig. 4.6), because for this station the longest time series exists, and most fish have been caught here (c. 1500). It is clear from this figure that the peak for running barbs occurs between 10 and 30 September, for all four morphotypes shown. This period corresponds with the highest lake level (Fig. 4.2).

In view of the general question whether segregation during spawning occurs among the morphotypes, it was investigated whether the relative abundance of the running morphotypes changed with time (Fig. 4.7*a*). Additionally, pairwise comparisons between all periods were made and it was analysed whether relative morphotype abundances differed over the whole time period (pairwise differences between morphotypes). A G-test was performed on the data from Table 4.5*a*, which resulted in a statistically very significant overall time effect ($p<0.001$). This means that the overall morphotype composition is associated with the date.

All periods differ significantly from each other in morphotype compositions when compared pairwise (Fig. 4.7*a*). This means that during the whole investigated period changes occur

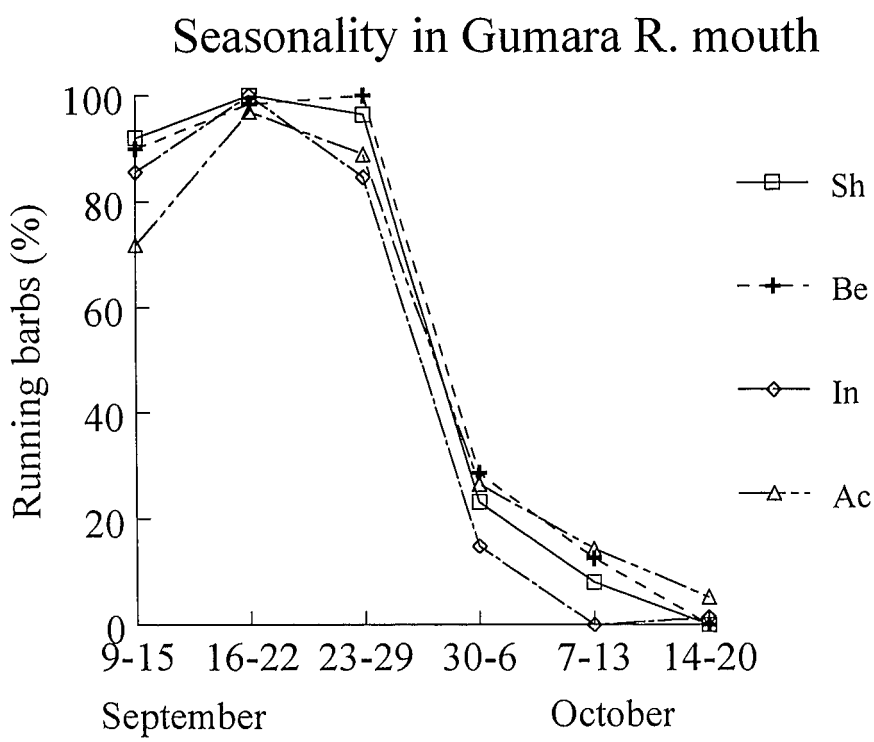


Fig. 4.6. Percentage of running barbs (of the morphotypes Sh [squares], Be [crosses], In [diamonds] and Ac [triangles]) in the Gumara River mouth, derived from the total number of barbs of mature size, per morphotype, as a function of time. The number of running barbs peaks between 10 and 30 September. Other morphotypes were not abundant enough to be included in this graph.

in the relative abundances of running morphotypes. During the fourth period (i.e. the fourth until the sixth week) the number of barbs had decreased considerably (hence the pooling of the last three weeks) and the morphotype composition did not change much. This corresponds with a decrease in the percentage of spawning barbs during this period (Fig. 4.6).

The pairwise differences in relative abundances of morphotypes over the whole time period are summarized in Table 4.5*b*. The most important conclusion from this analysis is that of the six pairwise comparisons between the four most abundant morphotypes (Ac, Be, In, and Sh), five comparisons show significant differences. Only Be does not differ significantly from In.

Geographical patterns in running morphotype composition

Another way of investigating segregation during spawning was to analyse the relative abundances of the running morphotypes in relation to the different rivers (geographical differences in morphotype composition; Fig. 4.7*b*). In this case only the river mouths were taken into account and not the upstream reaches, because only from the mouths were sufficient numbers of barbs caught.

Table 4.5*a*. Temporal composition of running barbs in the Gumara River mouth. Data represent absolute numbers of running specimens. Note that the first three periods have a length of seven days, while the last period is three weeks long.

Morphotype:	9-15 Sep:	16-22 Sep:	23-29 Sep:	30 Sep. -20 Oct:
Ac	23	32	16	14
Be	135	189	27	3
In	95	137	33	10
Sh	278	155	215	52
Wh	6	6	3	4
Others	52	33	9	3

Table 4.5*b*. Statistically significant ($p<0.05$, indicated by asterisks) differences between running morphotypes in their relative abundances over the investigated time period.

	Ac	Be	In	Sh	Wh	Others
Ac	x					
Be	*	x				
In	*	-	x			
Sh	*	*	*	x		
Wh	-	*	-	-	x	
Others	*	-	-	*	-	x

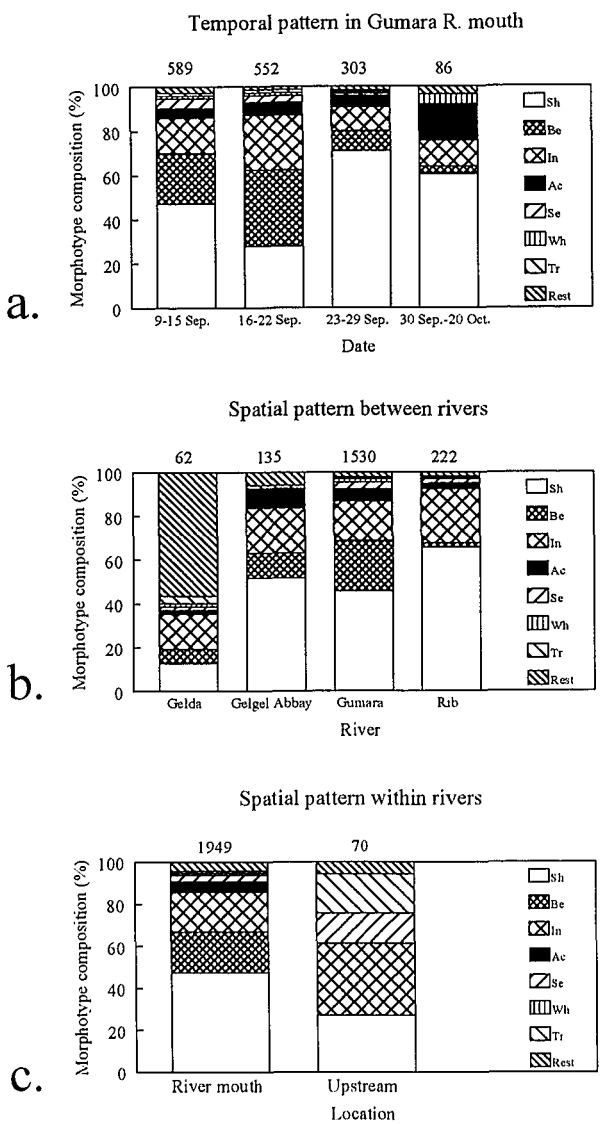


Fig. 4.7. Morphotype composition of running barbs. Percentages are taken from the total number of running barbs, which is indicated on top of each bar. **(a)** Morphotype composition in the Gumara R. mouth as a function of time. These data have been analysed with a G-test (cf. Table 4.5). Note the decrease in the total number of barbs after 30 September, indicating the end of spawning activity at this site. **(b)** Morphotype composition as a function of geographic location (i.e. in four different river mouths). These data have been analysed with a G-test (cf. Table 4.6). Note that Gelda is the most aberrant river. **(c)** Morphotype composition as a function of the position within the rivers (river mouth or upstream). All fishing efforts listed in Table 4.2 are included, except for the one at Zegi Bay. These data have been analysed with a G-test (cf. Table 4.7). Note the complete absence of Ac and Be from the upstream reaches and the abundance of Tr here.

The overall geographical effect on the morphotype composition was analysed, as well as the pairwise differences between the rivers, and finally, the pairwise differences in relative abundance between the running morphotypes over all rivers. A G-test was performed on the data from Table 4.6*a*. Because the G-test requires frequencies to be at least 3, Ac and Da have been pooled, as well as Wh, Tr and Se (cf. Materials and methods).

There is a statistically very significant overall geographical effect ($p<0.001$) and all river mouths differ significantly from each other (cf. Fig. 4.7*b*). Gelgel Abbay and Gumara are most similar, with Sh and In together making up 65-75 % of the running barbs. Be, and (to a lesser extent) Ac also contribute to the catch considerably. Rib resembles this pattern, but here Be is much less abundant. Gelda is the most aberrant river, when considering the morphotype composition. Sh contributes more than 40% of all running fish in Gelgel Abbay, Gumara and Rib, but less than 15% in Gelda. Moreover, more than 55% of the barbs caught in the Gelda mouth do not belong to any clear morphotype. These fish probably belong to the variable group of barbs that are abundant in the shore area of Lake Tana (Nagelkerke et al. 1995*b*).

The pairwise differences in relative abundance among morphotypes, for all river mouths are summarized in Table 4.6*b*. Among the four most abundant morphotypes (Ac, Be, In and Sh) four of the six possible comparisons show significant differences. Only the relative abundances of In do not differ significantly from those of Sh and Ac-Da.

Table 4.6*a*. Spatial composition of running barbs among the different river mouths. Data represent absolute numbers of running specimens.

Morphotype:	Gelda R.	Gelgel Abbay R.	Gumara R.	Rib R.
Ac-Da	5	11	90	6
Be	4	15	354	4
In	10	28	275	55
Sh	8	70	700	146
Wh-Tr-Se	4	4	83	7
Others	31	7	28	4

Table 4.6*b*. Statistically significant ($p<0.05$, indicated by asterisks) differences between running morphotypes in their relative abundances over all river mouths.

	Ac-Da	Be	In	Sh	Wh-Tr-Se	Others
Ac-Da	x					
Be	*	x				
In	-	*	x			
Sh	*	*	-	x		
Wh-Tr-Se	-	-	-	-	x	
Others	*	*	*	*	*	x

Spatial patterns within rivers in running morphotype composition

Segregation in spawning can also occur because of differences in morphotype composition within the rivers. Therefore it was investigated whether there are differences between the river mouths and the upstream reaches in the relative abundances of the running morphotypes (Fig. 4.7*c*). Also, pairwise comparisons of the relative abundances per morphotype were made over the whole river (i.e. mouth and upstream reaches together). A G-test was performed on the data from Table 4.7*a*. Except for In, Sh and Tr, morphotypes had to be pooled in several groups to make frequencies at least three and allow the test.

We observe a statistically very significant overall effect ($p<0.001$)(Fig. 4.7*c*). One of the most remarkable observations is that Tr, a very rare morphotype (less than 1% of the total lake catch during 1990-1995) was relatively abundant upstream (approximately 20% of all running barbs), while it only contributed around 1% to the running specimens in the river mouths. The opposite can be said for Ac and Be, that together contribute more than 20% of the catch in the river mouths, but are completely missing upstream.

Table 4.7*a*. Spatial composition of running barbs between river mouths and upstream reaches. Data represent absolute numbers of running specimens.

Morphotype:	River mouth:	Upstream:
Ba-Da-Se-?	131	11
Be-Ac-Wh-Ca	504	3
In	368	24
Sh	924	19
Tr	22	13

Table 4.7*b*. Statistically significant ($p<0.05$, indicated by asterisks) differences between the running morphotypes in their relative abundances over the position in the river (mouth or upstream reaches).

	Ba-Da-Se-?	Be-Ac-Wh-Ca	In	Sh	Tr
Ba-Da-Se-?	x				
Be-Ac-Wh-Ca	*	x			
In	-	*	x		
Sh	*	-	*	x	
Tr	*	*	*	*	x

The pairwise differences in relative abundance among morphotypes for the whole river are summarized in Table 4.7*b*. The most remarkable conclusion from this table is that Tr differs in relative abundance from all other morphotypes. Also In and Sh show a difference in relative abundance. The other morphotypes could not be analysed separately, especially because of the complete absence of Ac and Be from the upstream reaches, and therefore had to be pooled with

other morphotypes. However, this absence in itself also indicates the large differences between river mouths and upstream reaches.

Barbus in the lake during the spawning season

During the 1994 spawning season a 30 min trawling haul at Zegi Bay yielded a catch of c. 150 fishes, consisting predominantly of Sh and In. No running fishes were present. In a subsample all fishes were either not ripe (gonad maturation stage 3 or less) or spent (stage 7). This strongly suggests that fish that are present in the lake during this time are either juveniles that did not participate in spawning, or adults that returned from the rivers to recover from spawning. It should also be noted that during the spawning season catches in the open lake area decreased sharply.

Missing morphotypes

The frequent occurrence in the upstream reaches of the rivers of a morphotype rare in the lake (Tr) is striking, but it is also unusual that some morphotypes that are quite abundant in the lake, such as Ba, Da, Li, and Zu were now almost, or completely absent from the catches (both in the river mouths and upstream). Bh and Mi were not found running at all in the 1993 and 1994 catches, but these morphotypes are always rare. On 11 October 1995, however, one male and one female Bh were found running in the littoral zone on the west side of the Bahar Dar Gulf, very close to the town and far from any of the known spawning grounds in or near the rivers.

DISCUSSION

The temporal and/or spatial segregation in spawning between the different *Barbus* morphotypes is the central problem of this study. Such segregation proves the existence of separately reproducing populations, i.e. separate biological species, and would allow a final choice between the hypotheses about the taxonomic identity of the different morphotypes (Nagelkerke et al. 1994, 1995*a*, 1995*b*).

Where do the large barbs spawn?

The rivers appear to play a crucial role in the reproduction of most *Barbus* morphotypes. Spawning takes place upstream in the rivers, or in the river mouths. This corroborates with *e.g.* Skelton et al., (1991), stating that all lacustrine *Barbus* species migrate towards rivers for reproduction. None of the *Barbus* specimens caught in Zegi Bay (a part of the lake itself) at the time of the spawning peak, were reproducing there. Most probably the spent fish migrated here to recover.

Some data suggest, however, that not all morphotypes depend on the rivers for reproduction. In November 1992 a trawl catch near the Gelda River mouth (but in the lake itself) consisted mainly of running Zu (Tesfaye Wudneh pers. comm.) and on 11 October 1995 running Bh were found in the littoral zone of the lake, far from any river. These observations suggest that these morphotypes (and perhaps also others that were completely missing in the rivers) spawn in the lake itself, possibly in another period.

No direct observations of segregated spawning in the river mouths are available: the water is turbid and spawning might take place at night, or between the vegetation. Conspicuous male colouration (as e.g. in haplochromine cichlids) is absent. Therefore, we focused our study on data of maturation size and spatial and temporal patterns of relative abundances of the running morphotypes.

When do the large barbs spawn?

The interviews with the fishermen (Fig. 4.3) indicated that spawning migrations occur from June until the end of September, a period of four months. Spawning has been recorded until November in the upstream reaches of Gelda R. (M. Mina, pers. comm.). Such an extended spawning season suggests that there is enough opportunity for temporal segregation, although our data show a clear peak for four running morphotypes (Ac, Be, In, Sh) in the Gumara River mouth between 10 and 30 September (Fig. 4.6), exactly coinciding with the peak lake level (Fig. 4.2). The early migration of barbs, as reported by the local fishermen (Fig. 4.3), might concern the morphotypes we called missing as we did not find them in any numbers, although they are relatively abundant in the lake. Especially the absence of running Ba, Bh, Li and Zu, both in river mouths and upstream, was conspicuous.

The timing of spawning and spawning migration is correlated with rainfall for some Sri Lankan *Barbus* species (De Silva et al. 1985), with water temperature and level for *Barbus barbus* (L.)(Baras & Cherry 1990) and with water temperature for the Mediterranean *Barbus sclateri* Günther (Rodriguez-Ruiz & Granado-Lorencio 1992). Also in Lake Tana, spawning activity is highly correlated with the rainy season. The exact timing of reproduction however, might differ among the Lake Tana *Barbus* morphotypes: those that spawn in the river mouths could be dependent on the flood plains (that vastly increase with the lake level) for shelter and food for larvae and juveniles, while morphotypes that migrate far upstream to spawn might have other demands, such as clear, well oxygenated water.

Size of maturation of the *Barbus* morphotypes; different life histories?

The minimum FL of running fish (FL_{min}) and the FL at which 50% of the individuals are running ($FL_{50\%}$) show that there are large and consistent differences between some of the morphotypes for these parameters (e.g. Sh has a FL_{min} for males and females of 12 and 17.5 cm respectively, Se of 28 and 32.2 cm; $FL_{50\%}$ shows similar differences among morphotypes). The

steepness of the sigmoid curves (Fig. 4.5, Table 4.4) shows that the barbs attain mature size with only very little growth (on average 1.8 cm from 10 to 90% ripe fish). This suggests the differentiation in life-history traits among morphotypes, possibly including age of first spawning, life span and growth rate. According to Crawford & Balon (1994), such differences could even be instrumental in speciation events.

Segregation in spawning among *Barbus* morphotypes

The overall and pairwise differences in relative abundances among morphotypes give evidence for significant temporal or spatial spawning segregation or a combination of both. The differences in temporal patterns in relative abundances in the Gumara River mouth, especially during lake level increase (Fig. 4.7*a*, Table 4.5) suggest temporal segregation among Ac, In, and Sh, and between Be and Ac, Sh and Wh, but it might also be spatial, if at a certain time one morphotype migrates upstream and another does not. Something similar may apply to conspicuous differences in spatial patterns of relative abundances within rivers (Fig. 4.7*c*, Table 4.7). At first glance this suggests spatial segregation between Tr, which was found primarily upstream, and the four most abundant morphotypes (Ac, Be, In, and Sh), which were found in the river mouths, but it could also be a temporal effect if the latter four morphotypes would migrate upstream at a later stage than Tr.

However, the almost complete absence of very abundant, river mouth morphotypes (Fig. 4.7*c*) such as Ac and Be from the upper reaches of the rivers (in three separate fishing events from 15-26 September 1994), and the relatively high proportion of a rare morphotype (Tr) upstream compared to the river mouth, make it likely that there is a real spatial pattern in which Ac and Be never reach the upstream reaches, while others do.

Geographical differences in morphotype compositions play a lesser role in spawning segregation (Fig. 4.7*b*, Table 4.6), although Be differs from In and Sh in its relative abundances. Differences between Gelgel Abbay, Gumara and Rib rivers are not large, which may be caused by the fact that they have similar characteristics. Gelda has the most aberrant fish composition and it also is the shortest, narrowest and shallowest of the four rivers investigated.

The presence of hybrids between *Barbus* morphotypes

Reproductive isolation is a decisive character in the distinction of biological species, and minimizes hybridization between them. However, in the catch of large Lake Tana barbs there is always a low percentage (*c.* 5-10%) of (nearly) adult fish (FL > 20 cm) that cannot be allocated to any particular morphotype. We hypothesized that these specimens either belong to (1) new, until now, undescribed morphotypes, and/or to (2) individuals of a phenotypically plastic population (Nagelkerke et al. 1995*b*). It is also likely that a number of these fish are hybrids between morphotypes, especially when they show intermediate morphologies. We even positively identified four specimens as hybrids between a *Barbus* morphotype and *Varicorhinus beso* (which is an

evolutionary hexaploid, like the 'large' African barbs, cf. Golubtsov & Krysanov 1993, Guégan et al. 1995) on a morphological basis (the presence of a horny-edged, shovel-shaped lower jaw, unknown in Lake Tana *Barbus*, in combination with the presence of well developed barbels, unknown in *Varicorhinus*). The occurrence of hybrids does not weaken the presence of real species, since hybridization, even intergeneric hybridization, is common among cyprinids in general (Buth et al. 1991, Howes 1991, Meagher & Dowling 1991), and among *Barbus* species in particular (Machordom et al. 1990, Poncin et al. 1994). Persistent hybridization at low levels does not necessarily threaten the genetic integrity of two parent groups (as shown for sticklebacks by McPhail 1993, and for cyprinids by Dowling & Moore 1984).

A scenario of intralacustrine speciation of the Lake Tana *Barbus* species flock

How did the present Lake Tana *Barbus* species evolve? One hypothesis is that Lake Tana was invaded from affluent rivers by several riverine *Barbus* species that were already present in the rivers before the formation of the lake. This is highly unlikely, because even now the (highly variable) riverine large *Barbus* population of the whole of the Ethiopian high plateau is considered as one species, and the ancestral Lake Tana *Barbus* probably resembled it, as it occurred in similar conditions. Since the whole Lake Tana basin is very shallow and saucer-shaped, with a very regular bottom profile (Mohr 1962) it is also not likely that Lake Tana was subdivided previously into several isolated lakes or pools that could have supported vicariant speciation events. Therefore it seems most likely that the *Barbus* speciation has occurred within (an undivided) Lake Tana itself.

Previously (Nagelkerke et al. 1995*b*), we hypothesized that intralacustrine speciation has occurred among the barbs of Lake Tana and possibly is still going on. Intralacustrine speciation of fishes has been described especially for cichlids (Meyer et al. 1990, Schliewen et al. 1994). There are several hypothesized mechanisms, ranging from sympatric speciation (Schliewen et al. 1994) to complete (micro)allopatric speciation in the several basins and fragmented habitats within a lake (Fryer 1996).

The controversy over which speciation mechanisms occur is mirrored by the debate over the relationship between morphological differentiation and speciation. Fryer (1996) states that such differentiation occurs after speciation in cichlid fishes (which is in accordance with the allopatric speciation mode), while others claim that disruptive selection can take place in a situation when there is no complete segregation between populations (Rosenzweig 1978, Schliewen 1994, Schluter 1994), i.e. morphological and ecological divergence precede speciation. The initial tendency to diverge is thought to be related to the increased frequency of behavioural patterns associated with some consistent change in the environment (e.g. the availability of a new food source).

In Lake Tana, the different *Barbus* morphotypes prefer different habitats (as characterized by water depths and substratum types, cf. Nagelkerke et al. 1994), which are not randomly distributed over the lake. However, during the reproductive period, most of them were found to migrate towards the rivers, where the chances of encountering other morphotypes is high. Nevertheless, the present results show that reproductive segregation has evolved. Synthesizing this

and previous results leads us to the following hypothetical evolutionary scenario:

After Lake Tana was formed, through volcanic blocking of the Blue Nile, a population of riverine barbs was present from the same river, probably resembling the riverine *Barbus intermedius*, which is still found all over the Ethiopian high plateau. This population was (and still is) isolated from others through the 40 m high waterfalls that isolate Lake Tana from the lower Blue Nile (Fig. 4.1). The riverine *Barbus intermedius* populations from Ethiopia are known to be highly variable in morphology (M. Mina pers. comm., pers. observations). As a number of new lacustrine environments (e.g. lake bottom in deep, open water; pelagic in deep, open water) with their specific resources became available, incipient morphotypes might have radiated into different niches. This probably started from the shore-areas, which resemble the riverine habitat more closely than the open water of the lake, because of stronger terrestrial influences. Most barbs not belonging to any specific morphotype occur near the shore and they are most like riverine barbs (and probably like the ancestral barbs that invaded the lake) (Nagelkerke et al. 1995*b*).

However, the only way that (genetically based) morphological differentiation could have become fixed is by (at least partially) assortative mating. The question therefore is how assortative mating can develop when all barbs migrate towards the rivers for reproduction. Spawning is associated with the rainy season and the rise of the lake level. Which factors actually trigger spawning is not clear, but whatever they are (e.g. changes in water temperature, water level, pH, conductivity, silt load) the triggers are bound to be strongest in the rivers (which drain water from a large area into the lake), and will occur there prior to noticeable effects in the open water of the lake; changes in water quality will diffuse gradually from the rivers into the whole of the lacustrine environment. If an incipient morphotype has its feeding grounds in the open water of the lake, the spawning triggers might well reach it later than they reach fish feeding near the river mouths. The larger the distance, the longer the lag period will be, especially because the fish still have to migrate towards the rivers after the spawning trigger has reached them. This temporal shift will increase the chance of an incipient morphotype to encounter specimens of the same (incipient) morphotype and (partially) assortative mating will take place. It is more difficult to explain spatial differences in spawning, but if the barbs follow a gradient of the spawning trigger, and all barbs need a similar difference along this gradient to start spawning (e.g. a concentration or temperature difference), it can be expected that barbs that migrate from the open water spawn closer to the river mouths than barbs that live near the rivers throughout the year. The latter is corroborated by the fact that spawning barbs in the river mouths are mostly open-water feeders, such as Ac, Be, In and Sh, while a shore-dweller such as Tr is found far upstream (cf. Nagelkerke et al. 1994).

So, an extensive new lake area, providing a new variety of habitats as well as temporal and/or spatial shifts in the triggering of spawning, might be basic for promoting speciation in a group of fishes. Specific intrinsic features of the fishes are apparently also requested, since neither *Oreochromis* nor *Clarias* have radiated extensively. The limited variability of the morphologies of these two species in comparison with *Barbus* could be part of the explanation.

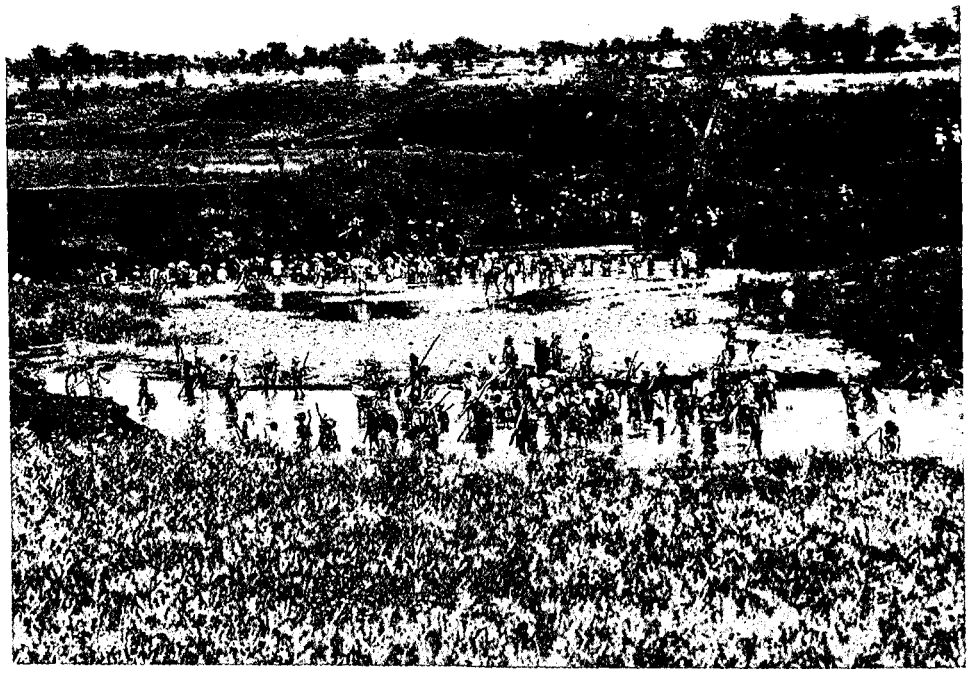


Fig. 4.8. An impression of the traditional fishing by poisoning in the Gelda River. Upstream the dried and crushed seeds of the leguminous *berberra* tree (*Milletia ferruginea*) are thrown in the river. The poisoned fish float downstream, where they are caught by scoop nets. In September this type of fishing is sometimes performed every other day, by up to two hundred fishermen (photograph by F.A. Sibbing).

CONCLUSIONS

Apparently there exists a significant segregation in spawning among the four most abundant morphotypes: Ac, Be, In and Sh and the relatively rare Tr. Tr is segregated from the rest by its preference for the upper river reaches. Ac is only segregated from Be temporally (Ac's spawning peak being somewhat later). Be, In and Sh are segregated both temporally and spatially (between different rivers). In and Be have their spawning peaks in the week of 16-22 September, Sh one week later (Fig. 4.7*a*). Be has its main spawning ground at Gumara; Sh is rare at Gelda and abundant in the other river mouths; In is distributed evenly over the different river mouths (Fig. 4.7*b*).

The differences between the upstream reaches and the river mouths however, appear to be the most important in spawning segregation (Fig. 4.7*c*), because they are more extreme, with the total absence upstream of morphotypes that are abundant in the river mouths (Ac and Be). The observations of running Bh and Zu in the lake itself complete the picture of some morphotypes spawning in the lake itself (Bh and Zu), some in the river mouths (Ac and Be) and some upstream (Se and Tr). In and Sh occur in the whole river, with Sh preferring the river mouth.

These morphotype composition patterns do not present final proof for the occurrence of spawning segregation among all different *Barbus* morphotypes, but together with the data on size of maturity, they provide considerable evidence for the existence of spawning segregation and the existence of a unique cyprinid species flock.

Implications for fisheries

Management for sustainable fisheries will be more complex when several species are present instead of just a single stock of *Barbus*. More detailed knowledge of the community structure and resource partitioning is required.

The importance of the rivers for the reproduction of *Barbus* makes the fish stock vulnerable for overfishing during the spawning migration (Craig 1992, Nagelkerke et al. 1995*a*). We observed high fishing pressure in the river mouths during the spawning season (Nagelkerke et al. 1995*a*) as well as intensive fishing by poisoning with the dried and crushed seeds of the *berberra* tree (*Milletia ferruginea*, Leguminosae) in the upstream reaches of Gelda (Fig. 4.8). This traditional method was already reported by Rüppell (1836), but probably has increased substantially with the growth of the human population. Upstream in Gumara scoop netting was performed. The impact of all types of fishing pressure is still unclear, but protection of the future stocks by closing certain sites for some period seems required.

Both the vulnerability of spawning stocks, and the presence of several *Barbus* species in the lake should be taken into account when evaluating management schemes aiming at sustainable exploitation and protection of the lake's biodiversity, affecting the stability and resilience of the ecosystem (Lévêque 1995).

ACKNOWLEDGEMENTS

We thank Ato Sintayehu GebreMariam and Ato Tarekegn Mengistu of the Ministry of Agriculture in Addis Ababa for their cooperation, which greatly increased the feasibility of our programme; the Region 3 Ministry of Agriculture Bureau in Bahar Dar for cooperation in the local implementation of our programme; Dr Belay Demisse, Ato Feleke Belay, Dr Shiferaw WoldeTsadik and Dr Gualu Wunegnaw for discussions. Ato Wereta for helping us contact local fishermen, and for interpreting the interviews; Ato Asfaw Berhe, Ato Girma Mengistu and Ato Tewodros Nega, for cooperation throughout 1994; Ato Wandosen Shiferaw for driving, translating and teaching Amharic; and Prof. Jan Osse for valuable comments on the manuscript.

This study was funded by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W88-176, the Interchurch foundation Ethiopia/Eritrea (Urk, The Netherlands) and the Interchurch Coordination Commission for Development Projects (ICCO, Zeist, The Netherlands).

Chapter 5

A revision of the large barbs (*Barbus* spp., Cyprinidae, Teleostei) of Lake Tana, Ethiopia, with a description of seven new species.

Leo A.J. Nagelkerke[1] & Ferdinand A. Sibbing[1]

[1]*Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

Accepted: *Zoölogische Verhandelingen Leiden*

ABSTRACT

The large barbs (genus *Barbus*) of Lake Tana, Ethiopia, have been divided into a maximum of 10 species and 23 subspecies (Rüppell 1836, Boulenger 1902, 1907, 1911, Bini 1940), but have been considered as belonging to one species since the latest revision by Banister (1973): *Barbus intermedius* Rüppell, 1836. Recently these barbs were categorized in at least 14 distinct morphotypes (Nagelkerke et al. 1994, 1995*a*, 1995*b*), which differ widely in general morphology, distribution, feeding habits, spawning characters and genetic traits, probably forming a unique cyprinid species flock.

This study shows the relations between the previous species and subspecies descriptions and the 14 morphotypes and describes 7 new species: *Barbus crassibarbis* for the Barbel morphotype, *B. megastoma* for Bigmouth small-eye, *B. longissimus* for Bigmouth mini-eye, *B. tsanensis* for Intermedius, *B. brevicephalus* for Shorthead, *B. truttiformis* for Troutlike, and *B. platydorsus* for White hunch. An explanation for describing these new species, while some previously described (sub)species were not found, is suggested. An identification key for barbs larger than 15 cm standard length is provided.

This species-distinction is not only scientifically important, but also enables the identification of fish-stock units, needed for the development of sustainable fisheries and the protection of biodiversity.

INTRODUCTION

The genus *Barbus*

The cyprinid genus *Barbus* Cuvier & Cloquet, 1816, at present includes c. 800 species in Eurasia and Africa. It is generally accepted that the genus is a paraphyletic assemblage within the subfamily Cyprininae (Howes 1987), but a proper revision of the phylogenetic relations among the different species of the genus *Barbus* has not been performed until now. This is reflected in the confusing situation described in the next paragraphs (for example, it is unclear whether the genus *Varicorhinus* can be considered as a taxon of true generic rank, or that phylogenetically it is part of the genus *Barbus*).

The type species of the genus: *Barbus barbus* (L.) 1758, the widespread European barb, belongs to, what is called, *Barbus 'sensu stricto'*. This is a monophyletic group of European and some north-African species (Lévêque & Daget 1984). This group of evolutionary tetraploids is now considered to form the subgenus *Barbus* (*Barbus*) (Berrebi 1995).

The 'large' African barbs, which have more or less parallel striae on the exposed part of the scales, are generally larger than 150 mm standard length as adults and lack noticeable body markings (such as dots or stripes; Howes 1987). These barbs are included in *Barbus 'sensu lato'*,

which is probably composed of several phylogenetic lineages. According to Howes (1987) the *Barbus intermedius* complex of Lake Tana belongs to one of these (possibly monophyletic) lineages: the barbins, which also includes the genus *Varicorhinus* Rüppell, 1836. The 'large' Lake Tana barbs could therefore be more related to *Varicorhinus*, than they are to *Barbus 'sensu stricto'*. This is corroborated by studies of Oellerman and Skelton (1990) and by Golubtsov and Krysanov (1993), who found that 'large' *Barbus* from South-Africa and Ethiopia (among which *B. intermedius*) as well as *Varicorhinus beso* from Ethiopia are all evolutionary hexaploids, while 'small' African barbs are evolutionary diploids. Moreover, hybrids of 'large' *Barbus* and *Varicorhinus* have been found several times in Lake Tana (Nagelkerke and Sibbing 1996).

The status of the genus *Barbus* is all the more confusing, because (1) vague terms (e.g. 'large' or '*sensu stricto*') are used, (2) taxonomic categories do not reflect phylogenetic findings (as in the case of *Varicorhinus*), or (3) phylogenetic lineages do not have a formal taxonomic rank at all (e.g. barbins). In an attempt to at least clear part of this problem, Berrebi recently (1995) proposed that all hexaploid,'large' African barbs belong to the subgenus *Barbus* (*Labeobarbus*) (Rüppell 1836).

The *Barbus intermedius* complex of Lake Tana

Banister (1973) lumped 50 nominal species and subspecies of East-African barbs into one species: *Barbus intermedius* Rüppell, 1836, including all 'large' barbs from Lake Tana. The latter were even considered as belonging to a single subspecies: *B. intermedius intermedius*. Recently it was shown that at least 14 distinct morphotypes exist (Osse et al. 1993, Nagelkerke et al. 1994, 1995*b*) and that 11 of them can already be distinguished at fork lengths of less than 100 mm (Nagelkerke et al. 1995*b*). They also differ considerably in their ecology (Nagelkerke et al. 1994, Sibbing et al., 1994). It is probable that these *Barbus* morphotypes constitute the world's only known intact cyprinid species flock (Nagelkerke et al. 1994, 1995*a*, 1995*b*). Additional evidence that the *Barbus* morphotypes constitute real species comes from (1) their segregation in spawning (Nagelkerke & Sibbing 1996), and (2) studies by Dixon et al. (1994, 1996) on the major histocompatibility complex. These show that there is no sharing of class II β chain alleles among at least four of the *Barbus* morphotypes (Acute, Intermedius, Lip, and Troutlike) suggesting that they belong to separate gene pools.

The cumulating evidence that the different Lake Tana *Barbus* morphotypes are real biological species is so convincing that we decided to assign species names to the 14 morphotypes. For this purpose it was necessary to establish which morphotypes are synonymous with which previous species and subspecies descriptions. Therefore, the morphotypes were compared with the descriptions and illustrations of (1) Rüppell (1836), who mentioned 5 *Barbus* and 1 *Labeobarbus* species, (2) Boulenger (1902, 1907, 1911), who distinguished 10 *Barbus* species and (3) Bini (1940), who even discriminated 10 species with 23 subspecies. All type material was investigated, except Bini's, since this was lost (P.G. Bianco, personal communication).

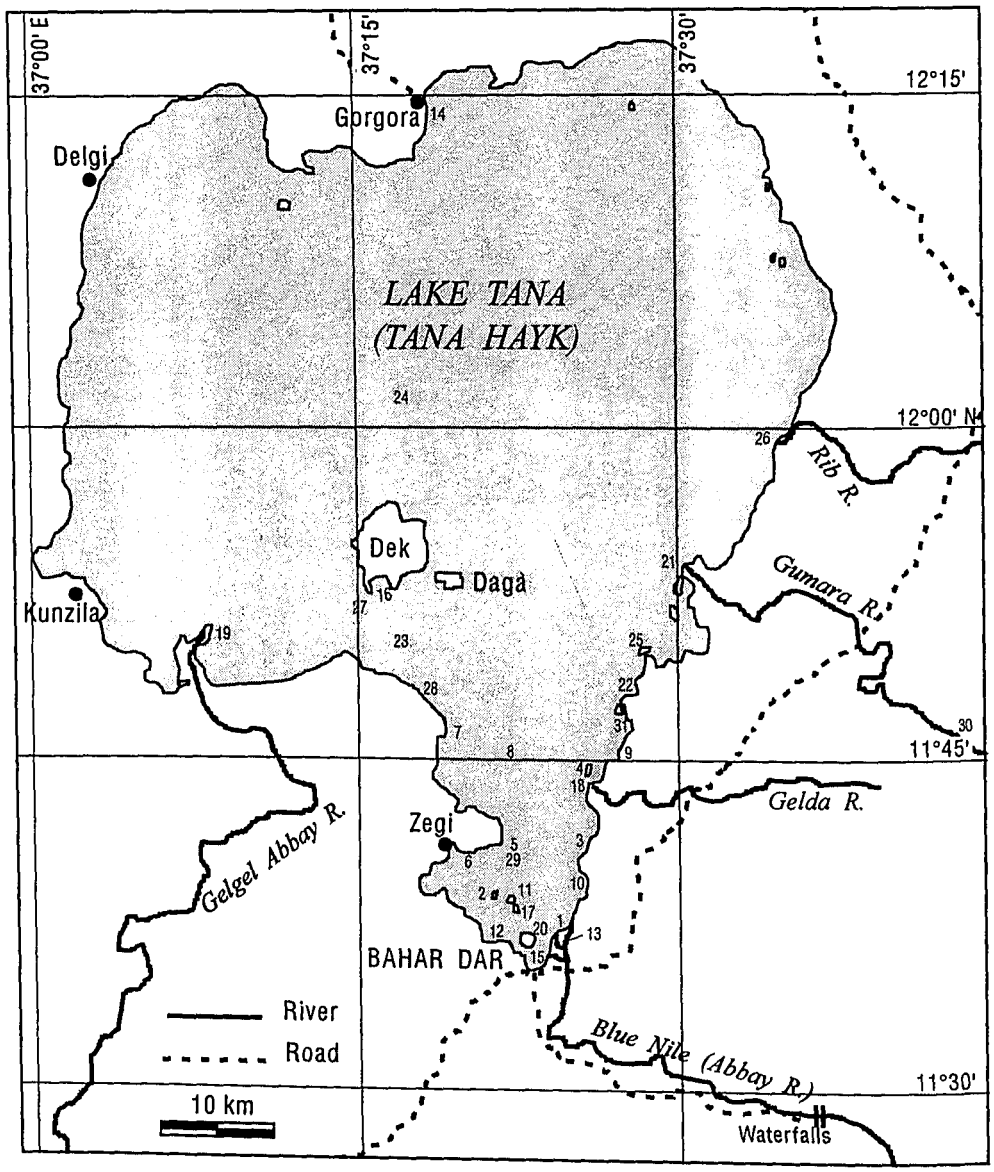


Fig. 5.1. Localities in Lake Tana, where the material used in this study was caught (see also Table 5.1). Catches were also made at additional sites all over the lake during 1990-1995.

Table 5.1. Collection localities, their numbers (cf. Fig. 5.1), depth, substrate (m: mud; r: rock; s: sand), and coordinates. Locality 9, Korata, is most probably the place where Rüppell (1836) purchased the fishes he described (he calls it 'Goraza').

Locality number:	Locality name:	Depth:		Substrate:	Coordinates:	
		min:	max:		latitude (N):	longitude (E):
1	Debre Mariam	1.5	4.5	m/s	11°, 38'	37°, 24'
2	Kibran	6	8.2	m	11°, 39'	37°, 21'
3	Mebra	1.5	6	m/s	11°, 41'	37°, 25'
4	Bet menzo	6.5	12	m/s	11°, 45'	37°, 25'
5	Mehal Zegi	10.5	12.5	m	11°, 42'	37°, 22'
6	Zegi town	2	5	m	11°, 40'	37°, 19'
7	Ambo Bahir	2	2	m	11°, 46'	37°, 19'
8	North mid-gulf	11	14	m/s	11°, 45'	37°, 22'
9	Korata (=Goraza, cf. Rüppell, 1836)				11°, 45'	37°, 27'
10	Yigashu	4	4	m/s	11°, 40'	37°, 25'
11	Kentefami	5	8.5	m/s	11°, 40'	37°, 23'
12	Airport	5.2	5.2	m	11°, 37'	37°, 21'
13	Blue Nile	1.7	4.5	m/s	11°, 37'	37°, 24'
14	Angara	9	9	m	12°, 13'	37°, 18'
15	Bahar Dar				11°, 36'	37°, 23'
16	Dek port	3	8	s	11°, 53'	37°, 16'
17	Entos	2.5	5	r	11°, 39'	37°, 22'
18	Gelda mouth	1.75	7.5	m/s	11°, 44'	37°, 26'
19	Gelgel Abbay mouth	1.5	9	m	11°, 51'	37°, 08'
20	Gerimah	2	3	m/r/s	11°, 37'	37°, 23'
21	Gumara mouth	2	3	m	11°, 53'	37°, 29'
22	Gunjapa	5	5	r	11°, 48'	37°, 28'
23	Halfway Dek and mainland	6.2	8.2	m/s	11°, 51'	37°, 17'
24	NNE Dek	10.5	10.5	m/s	12°, 01'	37°, 17'
25	Rema	5	10.5	m/r	11°, 51'	37°, 28'
26	Rib mouth	4	4	m	11°, 59'	37°, 34'
27	South-Dek	3	7	r/s	11°, 52'	37°, 14'
28	Tekoddo	2	2	r	11°, 48'	37°, 18'
29	Ura	7	9	m/r	11°, 41'	37°, 22'
30	Wanzaie				11°, 46'	37°, 43'
31	Yzuri	1.5	1.5	m	11°, 47'	37°, 28'

MATERIALS AND METHODS

Material was caught by trawl and gill net fishing in Lake Tana (Fig. 5.1, Table 5.1) from October 1990 until November 1995 (stretched mesh sizes were 20-40 mm and 16-140 mm respectively).

Table 5.2. All large *Barbus* (sub)species that have been described for Lake Tana ('§'indicates that the (sub)species is only known from Lake Tana), the authors that first used the names as such, the years of publication, type locality, category of type (asterisks indicate that these specimens have been studied) and numbers, museum and registration numbers. BMNH = British Museum (Natural History), London, MNHN = Musée nationale d'Histoire Naturelle, Paris, SMF = Senckenberg Museum, Frankfurt a.M. Data from Daget et al. (1986). Figure numbers refer to the plates showing Rüppel's, Boulenger's and Bini's illustrations (see appendix).

(Sub)species:	Figure:	Author:	Year:	Type locality:	Type:	Museum:	Number:
B. affinis	4, 8	Rüppell	1836	Goraza, Zana-See	holotype *	SMF	6786
B. affinis affinis§	18	Bini	1940				
B. affinis brevibarbis§	19	Bini	1940				
B. affinis nedgia§	20,21	Bini	1940				
B. brevibarbis§	9	Boulenger	1902	Zegi, Bahardar, Lake Tsana	syntypes (4)*	BMNH	1902.12.13: 295-198
B. brunellii§	36	Bini	1940	Lago Tana	syntypes (8)		lost
B. brunellii acutirostris§	37	Bini	1940	Lago Tana	syntypes (8)		lost
B. dainellii§	38, 39	Bini	1940	Lago Tana	syntypes (6)		lost
B. dainellii macrocephalus§	40	Bini	1940	Lago Tana	holotype		lost
B. degeni§	11, 22	Boulenger	1902	Zegi and Bahardar, Lake Tsana	syntypes (2)*	BMNH	1902.12.13: 328-331
B. degeni leptorhinus§	23	Bini	1940	Lago Tana	syntypes (8)		lost
B. duchesnii	7, 24	Boulenger	1902	Bahardar and Mogre River	syntypes (2)*	BMNH	1902.12.13: 305-306
B. duchesnii ibridus§	26	Bini	1940	Lago Tana	syntypes (6)		lost
B. duchesnii maximus§	25	Bini	1940	Lago Tana	syntypes (5)		lost
B. elongatus§	5	Rüppell	1836	Goraza, Zana-See	holotype *	SMF	6779
B. gorguari§	3, 16, 41	Rüppell	1836	Goraza, Zana-See	holotype *	SMF	2586
B. gorguarii macrophtalmus§	42	Bini	1940	Lago Tana	holotype		lost
B. ilgi	31	Pellegrin	1905	Rivière Akaki, affluent de l'Aouache	holotype *	MNHN	1905-257
B. intermedius	1, 13	Rüppell	1836	Goraza, Zana-See	holotype *	SMF	6778
B. intermedius intermedius		Banister	1973				
B. intermedius gorgorensis§	29	Bini	1940	Lago Tana	syntypes (11)		lost
B. intermedius leptosoma§	27	Bini	1940	Lago Tana			
B. intermedius microstoma§	28	Bini	1940	Lago Tana	syntypes (12)		lost
B. leptosoma	10	Boulenger	1902	Zegi, Lake Tsana	syntypes (3)*	BMNH	1902.12.13: 300-302

Table 5.2. (continued)

(Sub)species:	Figure:	Author:	Year:	Type locality:	Type:	Museum:	Number:
Labeobarbus nedgia	6	Rüppell	1836	Goraza, Zana-See	holotype	SMF	2619
B. nedgia	12	Günther	1868				
B. platystomus§	15	Boulenger	1902	Bahardar, Lake Tsana	syntypes (2)	BMNH	1902.12.13: 274-275
B. platystomus dagâ§	33	Bini	1940	Lago Tana	syntypes (9)		lost
B. platystomus dekkensis§	34	Bini	1940	Lago Tana	syntypes (17)		lost
B. platystomus platystomus§	32	Bini	1940				
B. platystomus prognathus§	35	Bini	1940	Lago Tana	syntypes (2)		lost
B. surkis	2, 14, 30	Rüppell	1836	Goraza, Zana-See	holotype	SMF	untraceable

The initial distinction of 13 morphotypes was based on the general appearance of *c.* 14,000 kg of fresh fish that were examined in the field in 1990 (Nagelkerke et al. 1994). A fourteenth morphotype was distinguished later (Nagelkerke et al. 1995*b*).

From 1990 until 1995 all areas of the lake have been investigated, including the middle, western and northern parts, although the emphasis was on the southern parts, within a range of 30 km from Bahar Dar. Approximately 40,000 barbs have been caught, of which around 2,000 were preserved in a 4%, pH neutral formaldehyde solution. After at least one month the specimens were transferred to ethanol solutions of gradually increasing concentration (from 30-70%). For the formal species descriptions, 10 specimens of each morphotype were picked from the collection of preserved specimens.

The studied museum specimens belong to: British Museum (Natural History), London (BMNH); Musée Nationale d'Histoire Naturelle, Paris (MNHN); Senckenberg Museum, Frankfurt am Main (SMF) and are listed in Table 5.2. New type material, described in this study, is deposited in the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH).

Counts and measurements largely follow Hubbs and Lagler (1947) and Holčik et al. (1989) and are listed in Table 5.3. Some of the head measurements are shown in Fig. 5.2. Coded qualitative measurements are shown in Fig. 5.3.

RESULTS

Comparison of the large *Barbus* morphotypes with previous species descriptions

The inadequacy of the previous descriptions of the large *Barbus* species of North-eastern Africa is notorious. This was already stated by Worthington (1932) and was one of the main reasons for Banister (1973) to lump 50 nominal species and subspecies (including all those from Lake Tana) into one species: *Barbus intermedius*.

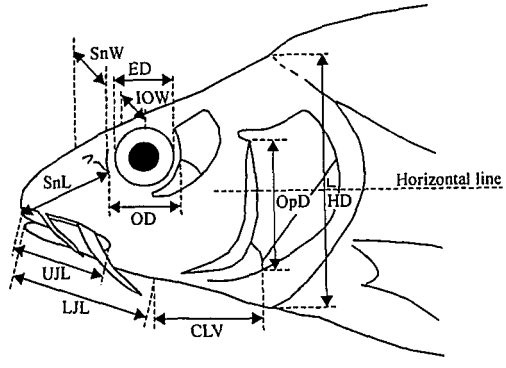


Fig. 5.2. Some of the metric head measurements (see also Table 5.3):ventral cheeck length (CLV), eye diameter (ED), head depth (HD), interorbital width (IOW), lower jaw length (LJL), orbit diameter (OD), operculum depth (OpD), snout length (SnL), snout width (SnW), and upper jaw length (UJL).

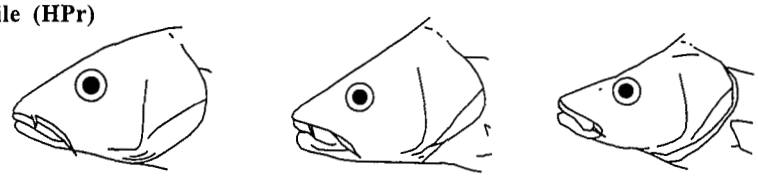
The previous descriptions are not sufficiently distinctive for two reasons:

1. The qualitative parameters are often vague (e.g. 'slightly larger than') or ill-defined (e.g. 'thick lip' or 'small mouth')
2. The 'traditional' quantitative parameters (both meristic and morphometric) are too limited in number. Moreover, they are often not distinctive and do not include conspicuous body shape differences (e.g. the presence of a nuchal hump).

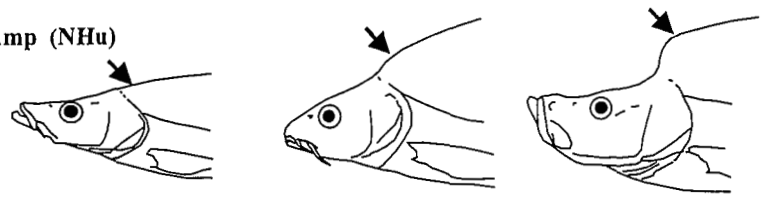
Rüppell (1836) only mentioned a few quantitative characters (such as head length - body length and head length - body depth ratios) in his description of the Lake Tana species, and not even the same set for every species. It is also difficult to compare his measurements with those of the other authors, because he used different characters (including gut length, which is a very informative measure, [cf. Nagelkerke et al., 1995*b*]). His qualitative descriptions, however, are clear. It was especially helpful that he included the local (i.e. around the southern shores of Lake Tana) Amharic names for the different species, because nowadays the local fishermen still use these names (Table 5.4). Rüppell's illustrations are not very accurate in body dimensions and shapes: they tend to be exaggerated (Appendix, plate 1).

Boulenger (1902, 1907, 1911) usually mentions the 'traditional' character set, which, unfortunately, is not distinctive enough for the Lake Tana barbs. In "The fishes of the Nile" (1907), some valuable background information on the Lake Tana specimens is given, including the local Amharic names that sometimes differ from the ones Rüppell recorded. Boulenger's illustrations are of excellent quality (Appendix, plate 2).

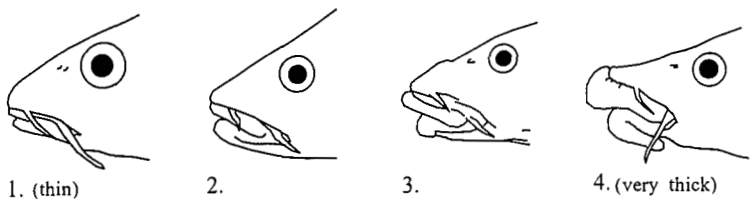
Head Profile (HPr)



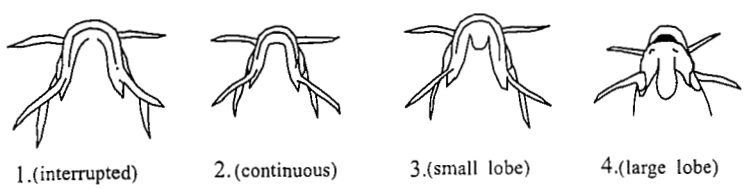
Nuchal Hump (NHu)



Upper Lip Development (ULD)



Lower Lip Development (LLD)



Anterior Extension of Lower Jaw (ExLJ)

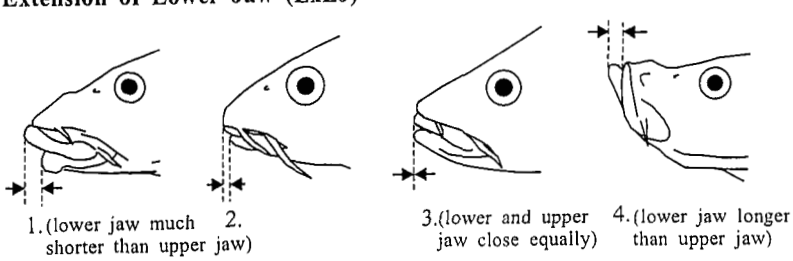


Fig. 5.3. Coded qualitative characters (see also Table 5.3).

Table 5.3. Counts, measurements and coded qualitative characters, their abbreviations and sources/descriptions; B,O,W & W-M: Barel et al. (1977); H&L: Hubbs & Lagler (1947); H,B & E: Holčik et al. (1989); N,S,B,L&O: Nagelkerke et al. (1994); N,S&O: Nagelkerke et al. (1995*b*) (see also Fig. 5.2). All measurements are taken directly between the given points, except when otherwise stated under source/description; e.g. horizontal, or vertical means that measurements are taken parallel, or perpendicular to the horizontal (as defined in Nagelkerke et al. 1994). The coded qualitative characters are adapted from Douglas et al. (1989)(see also Fig. 5.3).

Measurements and counts:	Abbreviation:	Source/description:
Meristics:		
Dorsal fin rays (simple)	DFSi	H&L
Dorsal fin rays (branched)	DFBr	H&L
Anal fin rays (simple)	AFSi	H&L
Anal fin rays (branched)	AFBr	H&L
Pectoral fin rays (total)	PFT	H&L
Ventral fin rays (total)	VFT	H&L
Scales on lateral line	ScLL	H&L
Predorsal scales	ScPrD	H&L
Scales from dorsal fin to lateral line (forward)	ScDL	H,B&E
Scales from anal fin to lateral line	ScAL	H&L
Scales from ventral fin to lateral line	ScVL	H,B&E
Circumpeduncular scales	ScCp	H&L
Circumference scales	ScCf	H&L
Morphometrics:		
Standard length (European)	SL	H,B&E; horizontal
Fork length	FL	H,B&E; horizontal
Total length	TL	H&L; horizontal
Head length	HL	H,B&E (excluding the opercular membrane)
Body depth	BD	H&L; vertical
Body width	BW	H,B&E
Caudal peduncle length	CPL	H,B&E; horizontal
Caudal peduncle depth (= minimum body depth *sensu* H,B&E)	CPD	H,B&E; vertical
Predorsal length	PDL	H&L
Preanal length	PAL	H&L
Preventral length	PVL	H,B&E
Prepectoral length	PPL	H,B&E
Pectoral-ventral length	PeVe	H,B&E
Ventral-anal length	VeAn	H,B&E
Dorsal spine length	DSpL	distance between the base of the first spine and the tip of the longest spine (without the soft extension of the spine)

Table 5.3 (continued).

Measurements and counts:	Abbreviation:	Source/description:
Dorsal fin base length	DBL	H&L
Anal fin length	AFL	H&L
Anal fin base length	AFB	H&L
Pectoral fin length	PeFL	H&L
Pectoral fin base length	PeBL	H,B&E
Ventral fin length	VFL	H&L
Ventral fin base length	VBL	H,B&E
Upper caudal fin lobe length	UCL	distance between the insertion of the most anterior ray and the most distant tip of the upper caudal lobe
Lower caudal fin lobe length	LCL	distance between the insertion of the most anterior ray and the most distant tip of the lower caudal lobe
Head depth at occiput	HD	H&L; vertical
Head width	HW	H&L
Snout length	SnL	distance between the rostral tip of the symphysis of the premaxillary bones and the ventral tip of the rostral processus of the lateral ethmoid (i.e. the anterior edge of the orbit)
Snout width	SnW	distance between the ventral tips of the rostral processus of the left and right lateral ethmoids
Eye diameter	ED	maximum diameter of the eye, measured within the ligamentous ring around it
Orbit diameter	OD	distance between the ventral tip of the rostral processus of the lateral ethmoid and the rostral tip of the symphysis of suborbitals 3 and 4
Postorbital length	POrL	H,B&E
Interorbital width	IOW	H,B&E
Operculum depth	OpD	distance between the dorsal tip of the pre-operculum, and the ventral tip of the symphysis of the interoperculum and the subopercullum
Ventral cheek length	CLV	distance between the caudal tip of the retro-articular, and the ventral tip of the symphysis of interoperculum and subopercullum
Anterior barbel length	ABL	N,S,B,L,O
Upper Jaw length	UJL	H&L
Lower jaw length	LJL	N,S&O
Protrusion length	PrL	N,S,B,L,O
Oral gape width	GW	N,S,B,L,O
Oral gape height	GH	N,S,B,L,O
Angular measurements:		
Protrusion angle	PrA	N,S&O
Dorsal head inclination	DHI	B,O,W&W-M
Gape inclination	GI	B,O,W&W-M
Coded qualitative characters:		
Head profile	HPr	Coded qualitative character (Fig. 5.3)
Nuchal hump	NHu	Coded qualitative character (Fig. 5.3)
Upper lip development	DLD	Coded qualitative character (Fig. 5.3)
Lower lip development	LLD	Coded qualitative character (Fig. 5.3)
Anterior extension of lower jaw	ExLJ	Coded qualitative character (Fig. 5.3)

Bini (1940) already mentioned that Boulenger's descriptions were very difficult to work with for some of the species. This reflects our experiences completely. As an example he showed that a series of measurements and meristic counts for *B. affinis* Rüppell, *B. brevibarbis* Boulenger and *B. nedgia* (Rüppell) overlap. The number of scales on the lateral line for these species were 31-37, 31-33 and 29-36 respectively, the number of unbranched (Roman numerals) and branched (Arabic numerals) rays in the dorsal fin IV 8-9, IV 9 and IV 8-9. This uniformity of meristic traits was also mentioned by Boulenger (1902) himself. In Bini's example also morphometric characters overlap, e.g. the ratio eye diameter / head length for the three species is given as 4-6$^2/_3$, 4-6$^1/_3$ and 4-8 respectively. Bini's own descriptions however, also suffer from the same problem: morphological differences between the barbs cannot be attributed to a ratio of one or a few characters. A large set of characters should be regarded simultaneously (Nagelkerke et al. 1994, 1995*b*). Bini's qualitative characters are often vague; his illustrations, however, are of good quality (Appendix, plate 3 and 4).

The general insufficiency and incomparability of the descriptions makes the illustrations, provided by the different authors, very important in comparing our morphotypes with previously described species, especially if the type material is lost, as is the case with all Bini's material (P.G. Bianco, personal communication) and with the holotype of *B. surkis* Rüppell (already mentioned by Banister [1973]). The illustrations are shown in the appendix.

All Lake Tana *Barbus* morphotypes as described in Nagelkerke et al. (1994, 1995*b*) will be treated successively and their affinity with the examined type material and the text and/or illustrations of Rüppell (1836), Boulenger (1902, 1907, 1911) and Bini (1940) will be discussed: discriminative characters will be emphasized, and a proper scientific name will be assigned.

If a morphotype is found to be synonymous with a specific subspecies, we elevate the subspecies name to the species level, as we do not see any reason to assume that sympatric subspecies (in our view a *contradictio in terminis*) could be present. Table 5.4 lists the morphotypes, the synonymous descriptions, local, Amharic names and the final species name that is assigned.

Acute (Ac)

Neither Rüppell nor Boulenger describe a fish which resembles Ac. Its long (HL 28-31% of SL), narrow head (HW 38-43% of HL), slender body (BD 23-26% of SL, BD<HL), terminal oral gape with a prominent lower jaw, and the silvery colour clearly resemble Bini's descriptions of *B. brunellii* and *B. brunellii acutirostris*. Bini states that both are very similar, but that *B. brunellii acutirostris* is distinguished by its more slender body and its more acute head. A conspicuous meristic character of Ac is the number of scales from the dorsal to the lateral line (ScDL), which (on average) is the highest of all morphotypes (median is 6.5; range is 5.5 to 7). Bini mentions this high number (range from 5.5 to 6.5) for *B. brunellii acutirostris*, but not for *B. brunellii* (ScDL=5.5). Moreover, the illustration of *B. brunellii* (Appendix: fig. 36) does not resemble Ac at all, while that of *B. brunellii acutirostris* (Appendix: fig. 37) does. Therefore it is concluded that

Ac is synonymous with the latter. As we did not find a fish resembling *B. brunellii* we assign Acute to the species *B. acutirostris* Bini.

Table 5.4. Morphotypes, their local names (according to Rüppell [R], Boulenger [B], or this study [N&S]), the most similar, previous descriptions (the interpretations of particular authors is indicated with *s.* [*sensu*]) , and the species to which they are assigned.

Morphotype:	Local, Amharic names:	Synonyms:	Species name:
Acute (Ac)	-	*B. brunellii acutirostris* Bini	*B. acutirostris* Bini
Barbel (Ba)	-	-	*B. crassibarbis* spec. nov.
Bigmouth big-eye (Be)	Fétaté (N&S)	*B. gorguari macrophtalmus* Bini	*B. macrophtalmus* Bini
Bighead (Bh)	-	*B. dainellii* Bini	*B. dainellii* Bini
Carplike (Ca)	Zurki (N&S)	*B. surkis* Rüppell (s. Boulenger) *B. intermedius gorgorensis* Bini	*B. gorgorensis* Bini
Dark (Da)	Gorguari (R) Assa Baria (B) Assabaria (N&S)	*B. gorguari* Rüppell	*B. gorguari* Rüppell
Intermedius (In)	-	*B. intermedius leptosoma* Boulenger (s. Bini)	*B. tsanensis* spec. nov.
Lip (Li)	Nedgia (R) Lento, Liento (B) Lunte (N&S)	*Labeobarbus nedgia* Rüppell *B. nedgia* (Rüppell) *B. affinis nedgia* (Rüppell)(s. Bini) *B. degeni* Boulenger *B. degeni leptorhinus* Bini	*B. nedgia* (Rüppell)
Bigmouth mini-eye (Mi)	Afedist (N&S)	-	*B. longissimus* spec. nov.
Bigmouth small-eye (Se)	Wuscabash, Wuscafash, Affacul (B) Afedist (N&S)	*B. gorguari* Rüppell (s. Boulenger, Bini)	*B. megastoma* spec. nov.
Shorthead (Sh)	-	-	*B. brevicephalus* spec. nov.
Troutlike (Tr)	-	-	*B. truttiformis* spec. nov
White hunch (Wh)	Gobit (N&S)	-	*B. platydorsus* spec. nov.
Zurki (Zu)	Surkis (R) Zurki (N&S)	*B. surkis* Rüppell (s. Rüppell, Bini)	*B. surkis* Rüppell

Barbel (Ba)

The only description which more or less fits Ba is that of *B. platystomus dekkensis* by Bini. The large downward mouth, with the lower jaw falling inside the upper jaw and the long barbels are similar to Ba, while also 5 other morphometric characters that were compared coincide well (however, the interorbital width is 25 to 30% of the head length in Ba, and 30 to 35% of HL in *B. platystomus dekkensis*) Also, the illustration (Appendix: fig. 34) is not too convincing, showing the slightly concave dorsal profile of the neurocranium, shared with Ba, but masking the general head shape because of the opened mouth. The thick, dark barbels, which are one of the most diagnostic characters in Ba, are not convincing either in this illustration. As the illustrations are generally of good quality, it can therefore be assumed that the barbels of *B. platystomus dekkensis* are not as

conspicuous as in Ba. Thus, there is no adequate description of Ba available. We therefore consider Barbel as a new species: *B. crassibarbis* spec. nov.

Bighead (Bh)

None of Rüppell's descriptions fits this morphotype. One of Boulenger's syntypes of *B. brevibarbis* (field n°352; which is also the one illustrated in his publications[1907, 1911: Appendix: fig. 9]), resembles Bh superficially in general appearance, lower lip development (a continuous lower lip without large lobes), a downwardly opening mouth, and some morphometric parameters (head length is 29% of SL for this syntype, 28-34% for Bh; eye diameter 16% for this syntype, 11-17% for Bh). Some other morphometric characters of this syntype do not fit Bh however. Body depth is larger (28% of SL) in this specimen than in Bh (21 to 26% of SL). The interorbital width is also larger in Boulenger's syntype (30% of HL, 20-26% in Bh).

A complicating factor is the observation that not all syntypes appear to belong to the same species. The specimen with field n°398 is similar to n°352 in general appearance, including lip development. The other two syntypes are different in these respects.

Both descriptions of *B. dainellii* and *B. dainellii macrocephalus* by Bini largely hold for Bh. Especially the long head (31-33% of SL for *B. dainellii*, 33% for *B. dainellii macrocephalus* , and 28-34% for Bh), slender body (BD 20-22% of SL for *B. dainellii*, 22% for *B. dainellii macrocephalus*, and 21-26% for Bh, BD<HL for all), large downward opening mouth and well-developed lips correspond well. The interorbital width of *B. dainellii macrocephalus*, however, is larger (33% of HL) than the one of *B. dainellii* (25%) and that of Bh (20-26%). The number of scales on the lateral line is also larger in *B. dainellii macrocephalus* (35) than in *B. dainellii* (31-32) or Bh (29-34). One of the illustrations of *B. dainellii* (Appendix: fig. 38) and the one of *B. dainellii macrocephalus* (Appendix: fig. 40) show great similarities with Bh. Another illustration of *B. dainellii* with an expanded head (Appendix: fig. 39) is difficult to compare. The oral gape in this illustration appears to be terminal, but the description states explicitly that the mouth can be easily protruded and that the mouth is opening in a downward direction. Therefore we conclude that Bighead is synonymous to *B. dainellii* Bini.

Bigmouth big-eye (Be)

The only description and illustration that fit this morphotype are, without any doubt, those of Bini's *B. gorguari macrophtalmus*. All quantitative and qualitative characters from Bini's text match those from our measurements. Most conspicuous are the large eye (ED 29% of HL for *B. gorguari macrophtalmus*, 20-30% for Be), the short barbels (smaller than the eye diameter for *B. gorguari macrophtalmus* , 33-66% of ED for Be), the terminal oral gape, the nuchal hump and the rostrally extending lower jaw in larger specimens. The illustration (Appendix: fig. 42) is very convincing and therefore we assign Bigmouth big-eye to *B.macrophtalmus* Bini.

Carplike (Ca) and Zurki (Zu)

Rüppell described a barb that was called 'surkis', by the local fishermen and called it *B. surkis*. We found, however, that two morphotypes are called 'surkis' by the local people. One of these is Zu and the other Ca. Both morphotypes are characterized by a relatively short head (HL 21-23% and 22-26% of SL for Zu and Ca respectively), a deep body (BD 28-33% and 26-32% of SL for Zu and Ca respectively, BD > HL) and a small, downward oral gape (gape width is 4-6% of fork length for Zu, 5-8% for Ca). Zu, however, is dark green (as is Rüppell's *B. surkis*) and has relatively small and thin barbels compared with the golden-yellowish Ca (ABL 50-113% of eye diameter for Zu, 109-175% for Ca). Ca has the smaller eye (at least 1.6 times in snout length, less than 1.7 times in Zu).

Carplike (Ca)

Rüppell does not mention a fish that resembles Ca. Boulenger's description and illustration of *B. surkis* (Appendix: fig. 14) however, is based on a specimen which is similar to Carplike: it has a yellow colour and long barbels (ABL is 1.75 times the eye diameter). The specimen has a small eye (2.1 times in snout length) and 32 scales on the lateral line (30-36 in Ca, 33-38 in Zu). Moreover, Banister's revision (1973: 69) contains an illustration (fig. 57) of the pharyngeal jaw of a fish, previously identified as *B. surkis*. This figure shows a very heavy pharyngeal jaw with large crushing teeth, which was found typical for Ca and not for Zu (Nagelkerke et al. 1994): another indication that Boulenger mistook Ca for *B. surkis*. He also mentions the molluscivory of 'his' *B. surkis*. Nagelkerke et al. (1994) show that Ca is to a large extent molluscivorous and Zu macrophytovorous.

There are two descriptions by Bini that resemble Ca, but neither matches exactly. *B. duchesnii s.* Bini (Appendix: fig. 24) matches Ca in most morphometric parameters. The short head (24-27% of SL), deep body (27-33% of SL), long barbels (1 to 2 times the eye diameter), and grey colour with yellow nuances, combined with dark fins match Ca. The problem is, however, that the syntype of *B. duchesnii* Boulenger from Lake Tana (Appendix: fig. 7) differs from Ca and from *B. duchesnii s.* Bini (e.g. the interorbital width of the latter is 33-40% of the HL, while it is 30% in the syntype). It is likely that Bini included several different morphotypes in *B. duchesnii*.

Bini's description and illustration of *B. intermedius gorgorensis* (Appendix: fig. 29) resemble Ca closely. He describes the short (HL 24-27% of SL), wide head, the deep body (BD 25-29% of SL, BD>HL), the thick barbels and the golden colour. Moreover, the illustration shows the large anal opening which was found to be typical for Ca. However, the length of the anterior barbels is given as 0.75 to 1.25 times the eye diameter, while in Ca it is 1.1-1.75 times. This can be caused by the larger eye diameter of Bini's animals (22-29% of HL, while this is 14-20% in Ca), which, in turn, is probably caused by the fact that Bini studied animals of maximally 315 mm total length, while we studied fish of at least 365 mm TL and the eye is relatively bigger in small fish. The details of the thick barbels (which is stressed in Bini's text), and the large anal opening convinced us that *B. intermedius gorgorensis* is most close to Ca. Therefore we assign Carplike to the species *B. gorgorensis* Bini.

Zurki (Zu)

Rüppell's description of *B. surkis* (Appendix: fig. 2) mentions the dark green colour and the thin barbels, which proves that Rüppell described Zu and not Ca (which is golden-yellowish and has thick barbels). Boulenger's description is based on a specimen of Ca, as was discussed before.

Bini does not give a description, but his illustration of *B. surkis* (Appendix: fig. 30) resembles Zu accurately, especially because of the thin barbels, the eye (which is larger in comparison with the snout length than in Ca) and the voluminous, bulging abdomen which is very typical for Zu. In conclusion, Zu is synonymous with *B. surkis* Rüppell.

Dark (Da) and Bigmouth small-eye (Se)

None of the previous descriptions distinguish between specimens of these two morphotypes and call them both *B. gorguari* Rüppell (Bini misspelled the name as 'gorguarii'). However, Boulenger's illustrations from his 1907 work even show both morphotypes as different forms of *B. gorguari* (Appendix: figs 16&17). The descriptions of *B. gorguari* by Rüppell and Boulenger largely match both Da and Se. The morphometric characters do not distinguish between the two morphotypes in these authors' descriptions: large mouth, long head (26-31% of SL), small barbels (≤ED) and short gut (1½ times SL, only mentioned by Rüppell, but in accordance with our results). The qualitative characters and illustrations are more important for distinguishing Da and Se, as will be discussed next.

Dark (Da)

Examination of Rüppell's type specimen of *B. gorguari* (Fig. 5.10, Appendix: fig. 3) shows, without any doubt, that it is synonymous with Da only. It is of a dark colour, has a steeply rising nuchal hump (more gradual in Se), and its jaws close equally (ExLJ=3, in Se specimens larger than 25 cm SL the lower jaw always extends clearly beyond the upper jaw). Moreover its head is wider than that of Se (HW is 53% of head length, 45-56% in Da, and 41-48% in Se) and its upper jaw fits less than 1.3 times in its lower jaw (more than 1.3 times in Da).

Boulenger only used the illustration (Appendix: fig. 16) of the Da specimen for his "Catalogue of fresh-water fishes" (1911), but an extra illustration (Appendix: fig. 17) from his "Zoology of Egypt" (1907) clearly shows a Se specimen with the gradual hump and the projecting lower jaw. The BMNH collection of barbs labelled as *B. gorguari* by Boulenger even contains specimens belonging to Barbel and possibly other morphotypes, or species.

Bini does not describe *B. gorguari*, but his illustration (Appendix: fig. 41) clearly shows a specimen of Se, with a gradual nuchal hump and the projecting lower jaw.

In conclusion, we synonymise Da with *B. gorguari* Rüppell.

Bigmouth small-eye (Se)

As was discussed in the previous section, Se was included in *B. gorguari* Rüppell by Boulenger and Bini. We therefore have to assign a new species name for Bigmouth small-eye: *B. megastoma* spec. nov.

Intermedius (In)

This name was given to the most abundant morphotype during our first visit at Lake Tana (48% of the total number of cyprinids, cf. Nagelkerke et *al.*, 1994), because it superficially resembles *B. intermedius* Rüppell (Appendix: fig. 1), since it did not seem to have any conspicuous special characters, and as it is intermediate in body shape compared to the other barbs. This seems to have been an unfortunate choice, however, because (1) the Intermedius morphotype is not synonymous with *B. intermedius* after all, and (2) the name Intermedius implies a non-distinct morphotype, whereas it is distinct.

The *B. intermedius* type specimen only marginally matches the ranges of the morphometric characters of In, and it even mismatches when it is compared with In specimens of the same standard length (c. 300 mm). The head of In specimens of c. 300 mm SL is longer than that of the *B. intermedius* type (HL is 25-27% of SL in In, 24% of SL in *B. intermedius*); while the eye diameter of these specimens is much less than 20% of HL, while it is 20% in the *B. intermedius* type. Moreover, Rüppell describes a yellow-green fish, while In is silvery-white, with a darker grey back. Boulenger describes *B. intermedius* (Appendix: fig. 13) as being vivid or bluish green, greenish, olive, and golden-yellow. The BMNH collection of *B. intermedius* contains about 60 specimens that belong to several morphotypes: there are some clear Intermedius, but also Shorthead was found. The largest part however, probably belongs to the group of variable barbs that inhabit the shore area of Lake Tana (cf. Nagelkerke et al. 1995*b*) that indeed show the greenish hues described by Boulenger. Rüppell's type specimen probably also belongs to this group, which leads to the conclusion that *B. intermedius* belongs to this 'shore-complex'.

One of the three syntypes of *B. leptosoma* Boulenger (field n° 291) (Appendix: fig. 10) resembles In quite well in general appearance, including its colour (silvery), but it has 35 lateral line scales, while In has 29-32 lateral line scales, and it has a shorter head (23% of SL, 24-27% in In). Boulenger states that *B. intermedius* has an interrupted lower lip, like in our morphotype, while that in *B. leptosoma* is continuous. He regards lower lip continuity as a very important character (e.g. in his identification keys, 1902, 1907, 1911). Two of the syntypes of *B. leptosoma* show continuous lower lips, but the one resembling *B. intermedius* does not. The three syntypes also differ in general appearance (e.g. in head profile) which casts doubts on the syntyping of all three specimens.

In the "descriptive part" of his work, Bini states explicitly that it was difficult for him to distinguish the separate *Barbus* species from the previous descriptions. He especially mentions *B. intermedius* and *B. leptosoma*. To solve this problem he rearranges *B. intermedius* Rüppell and *B. leptosoma* Boulenger and describes 3 new subspecies: *B. intermedius leptosoma* Boulenger, *B. i. microstoma* Bini and *B. i. gorgorensis* Bini (the latter is already synonymised with Ca). The description and illustration of *B. intermedius leptosoma* (Appendix: fig. 27) are most like our In morphotype. The eye diameter of the latter is smaller though (17-21% of HL in In, 21-27% of HL in *B. intermedius leptosoma*), but this could be caused by the small specimens that Bini examined (less than c. 200 mm SL). Bini states that this subspecies is similar to both *B. intermedius* Rüppell and *B. leptosoma* Boulenger, but does not match either of them perfectly, which is exactly what we

found for the In morphotype. *B. intermedius leptosoma* therefore is the most likely synonym for In. Bini, however, erred by using this name for a newly described form, because both the names *intermedius* and *leptosoma* were already in use. Therefore we have to assign a new name to Intermedius: *B. tsanensis* spec. nov.

Lip (Li)

This morphotype is mainly distinguished by its highly-developed lips with a distinct, fleshy lobe on the lower lip and often large flaps on the upper lip and/or a fleshy 'nose'. There are several descriptions which apply to Li. Rüppell described *Labeobarbus nedgia* (Appendix: fig. 6), with a large lobe on the lower jaw and a large flap on the upper lip. Boulenger called this fish *B. nedgia* (Appendix: fig. 12) and Bini *B. affinis nedgia* (Appendix: fig. 20,21). The latter author considers lip development as a very plastic character and therefore also includes fishes in *B. affinis nedgia* that lack the lip flaps considering them as young animals. We, however, also found small Li (c. 110 mm SL) with conspicuous lip flaps (cf. Nagelkerke et al. 1995*b*).

The form without pronounced flaps on the upper lip, but with a lower lip lobe and a fleshy 'nose' is called *B. degeni*, by Boulenger (Appendix: fig. 11) and Bini (Appendix: fig. 22). Bini also describes the related subspecies *B. degeni leptorhinus* (Appendix: fig. 23), which only differs from the former in details of lip and snout development. We consider all these fishes to belong to the Li morphotype (cf. Figs 5.14-5.16)and therefore to be conspecific. All five (sub)species descriptions are valid synonyms for Li, so the senior one gets priority. Therefore Li is assigned to *B. nedgia* Rüppell.

Bigmouth mini-eye (Mi)

This morphotype was not found to be synonymous with any of the described (sub)species, and is therefore assigned to a new species: *B. longissimus* spec. nov.

Shorthead (Sh)

Shorthead was the last morphotype to be described (Nagelkerke et al. 1995*b*), as it was originally included in Intermedius (Nagelkerke et al. 1994). Although there are some similarities between Sh and the description of *B. intermedius microstoma* Bini, neither this, nor any other previous (sub)species description matches Sh convincingly. Therefore Sh is assigned to a new species: *B. brevicephalus* spec. nov.

Troutlike (Tr)

This morphotype resembles the description of *B. platystomus prognathus* Bini in most morphometric measures, although Tr has a shorter head than the latter (25-27% of SL and 29% respectively). The illustration (Appendix: fig. 35), however shows that the head shape (especially the irregular 'bump' in the dorsal head profile, caused by the premaxillaries) of *B. platystomus prognathus* is very different. The illustration of *B. platystomus dagà* Bini (Appendix: fig. 33) resembles Tr better, but its eyes are generally larger over the whole size range (17-23%, while only

14-17% of HL in Tr). The anterior barbels are just as long, or a bit longer than the eye diameter, while the barbels are at most 82% of the eye diameter in Tr.

In conclusion, we did not find a convincing synonym for Troutlike and assign it to the new species: *B. truttiformis* spec. nov.

White hunch (Wh)

It is remarkable that a fish that is so abundant and important in fisheries (Nagelkerke et al. 1994) could not be synonymised convincingly with any of the previous descriptions of (sub)species. The only (doubtful) similarities were found in the description and illustration of Bini's *B. platystomus platystomus* (Appendix: fig. 32), especially concerning the shape of the head and lower jaw. Its head, however, is shorter (HL 22-25% of SL, 27-30% of SL in Wh) and the body deeper (BD 29-33% of SL, 26-29% of SL in Wh). The colour of *B. platystomus platystomus* is slaty grey to dark blue according to Bini, while Wh is silvery white. Bini's description of *B. platystomus platystomus* was meant to add information to Boulenger's description of *B. platystomus*. Wh however, does not agree with the description nor with the illustration of Boulenger's *B. platystomus* (Appendix: fig. 35) nor with the studied type material. We therefore conclude that there is no convincing synonym for White hunch and assign it to the new species: *B. platydorsus* spec. nov.

Species descriptions

Originally, 13 morphotype distinctions were based on general appearance, when sorting around 14,000 kg of fish from commercial catches in the field in 1990 (Nagelkerke et al. 1994). These distinctions were adjusted, extended to small specimens (for 11 morphotypes), and an extra morphotype was added (Nagelkerke et al. 1995*b*). Therefore, the morphotype distinction was based on many more fishes than used for the present formal species description (for which 10 specimens of each species were measured). This study focuses on larger specimens (SL > 15 cm) with a relatively narrow size range to prevent size effects to obscure species differences. All meristic, metric, angular, and coded qualitative characters are listed in Table 5.5.

The descriptions will focus on diagnostic characters, as it did not appear to be useful to copy all the information already listed in Table 5.5 and in the above sections. Most meristic characters are not discussed in the species descriptions (except for some scale counts) as they are not diagnostic. All localities are in Lake Tana, Ethiopia, and are listed in Table 5.1 and Fig 5.1.

Table 5.5. Characters of 14 *Barbus* species.

	B. acutirostris						*B. brevicephalus*					
	Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
Meristic measures												
Dorsal fin rays (simple)	4.0	4.0	4	4	0.0	10	4.0	4.0	4	4	0.0	10
Dorsal fin rays (branched)	8.7	9.0	8	9	0.5	10	8.0	8.0	8	8	0.0	10
Anal fin rays (simple)	3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10
Anal fin rays (branched)	5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
Pectoral fin rays (total)	16.7	17.0	16	18	0.7	10	16.5	17.0	15	17	0.7	10
Ventral fin rays (total)	11.4	11.0	11	12	0.5	10	10.6	10.5	10	12	0.7	10
Scales on lateral line (total)	34.1	35.0	31	36	1.9	10	33.3	33.5	29	36	1.9	10
Predorsal scales	13.9	14.0	13	16	1.0	10	13.5	13.0	13	15	0.8	10
Scales from dorsal fin to lateral line	6.4	6.5	5.5	7.0	0.4	10	5.6	5.5	5.5	6.0	0.2	10
Scales from anal fin to lateral line	4.6	4.8	4.0	5.0	0.5	10	3.9	4.0	3.0	4.0	0.3	10
Scales from ventral fin to lateral line	3.0	3.0	3.0	3.0	0.0	10	2.8	2.8	2.5	3.0	0.3	10
Circumpeduncular scales	12	12	12	12	0.0	10	12	12	12	12	0.0	10
Circumference scales	25.6	26.0	24	26	0.7	10	22.6	22.0	22	24	1.0	10
Metric measures												
In % of standard length:												
Head length	29.5	29.6	28.3	30.6	0.9	10	22.0	22.0	20.9	23.3	0.6	10
Body depth	23.9	24.0	22.8	25.6	1.0	10	26.2	26.6	23.6	27.9	1.2	10
Body width	12.1	11.9	11.3	13.3	0.6	10	12.3	12.2	11.1	13.5	0.8	10
Caudal peduncle length	17.6	17.6	16.6	18.1	0.4	10	21.4	21.3	19.3	23.8	1.3	10
Caudal peduncle depth	9.2	9.1	8.3	10.4	0.7	10	10.7	10.7	9.6	11.5	0.6	10
Predorsal length	52.4	52.3	51.5	53.8	0.8	10	46.2	46.1	45.0	47.6	0.8	10
Preanal length	76.3	76.2	74.6	77.3	0.8	10	72.1	71.7	69.9	76.3	1.8	10
Preventral length	54.1	54.1	52.6	55.6	0.9	10	46.8	46.6	45.8	49.3	1.0	10
Pectoral-ventral length	25.3	25.3	23.9	26.2	0.7	10	25.3	25.0	24.1	27.2	1.1	10
Ventral anal length	23.6	23.9	21.9	24.7	1.0	10	26.5	26.2	24.3	28.4	1.4	10
Dorsal spine length	17.3	17.5	14.4	19.9	2.1	10	23.7	23.8	18.4	28.2	3.1	10
Dorsal fin base length	13.6	13.6	12.9	14.4	0.5	10	14.6	14.6	13.0	15.5	0.8	10
Anal fin length	18.2	18.6	15.7	19.5	1.2	10	19.3	18.8	17.6	22.2	1.4	10
Anal fin base length	6.8	6.7	6.4	7.5	0.4	10	7.2	7.1	6.4	8.4	0.6	10
Pectoral fin length	19.8	19.7	19.1	21.1	0.6	10	19.8	19.8	18.7	20.9	0.7	10
Ventral fin length	16.0	16.0	15.3	16.9	0.5	10	17.3	17.4	16.1	18.1	0.7	10
Upper lobe length of caudal fin	28.0	28.0	24.9	30.4	2.0	10	30.3	30.3	28.7	32.6	1.2	9
Lower lobe length of caudal fin	27.9	27.6	25.8	29.9	1.6	10	29.9	30.0	27.0	31.7	1.4	10
In % of head length:												
Head depth at occiput	52.7	52.1	49.9	55.2	2.0	10	70.4	69.9	68.6	73.8	1.6	10
Head width	39.9	39.6	38.4	42.5	1.3	10	52.8	53.0	48.9	55.8	2.4	10
Snout length	29.8	29.6	29.3	31.4	0.7	10	29.4	29.6	28.2	30.3	0.7	10
Snout width	23.0	23.0	20.8	25.0	1.3	10	34.7	34.2	32.5	38.3	1.7	10
Eye diameter	17.4	17.8	15.0	19.7	1.6	10	23.9	24.0	21.4	26.2	1.5	10
Orbit diameter	22.1	22.2	17.6	24.8	2.2	10	26.9	26.8	24.4	29.3	1.7	10
Postorbital length	46.9	46.6	44.4	49.1	1.6	10	45.0	44.6	42.7	48.0	1.8	10
Interorbital width	18.6	18.6	16.9	20.6	1.2	10	33.6	33.9	29.4	36.3	2.0	10
Operculum depth	28.2	28.5	26.9	29.4	0.8	10	39.1	39.7	34.6	42.4	2.1	10
Anterior barbel length	9.7	10.0	5.9	12.4	2.1	10	16.2	15.5	13.8	20.6	2.3	10
Upper jaw length	28.5	28.6	27.5	28.9	0.4	10	28.3	28.2	27.2	29.5	0.7	10
Lower jaw length	41.3	41.1	40.1	42.9	0.8	10	38.1	38.2	36.1	40.3	1.2	10
Gut length/fork length	1.70	1.66	1.43	2.32	0.19	32	2.02	1.92	1.55	3.07	0.37	17
Angular measures												
Dorsal head inclination	18.2	18.0	16	21	1.5	10	28.6	29.0	23	35	4.4	10
Gape inclination	49.3	49.5	37	59	7.0	10	38.5	39.5	28	49	7.2	10
Coded qualitative measures												
Head profile	3.8	4.0	3	5	0.8	10	2.6	3.0	2	3	0.5	10
Nuchal hump development	2.3	2.5	1	3	0.8	10	1.2	1.0	1	2	0.4	10
Upper lip development	1.8	2.0	1.0	2.0	0.4	10	1.0	1.0	1.0	1.0	0.0	10
Lower lip development	1.1	1.0	1.0	2.0	0.3	10	1.0	1.0	1.0	1.0	0.0	10
Anterior extension of lower jaw	3.9	4.0	3.0	4.0	0.3	10	2.2	2.0	2.0	3.0	0.4	10
Protrusion measures												
In % of head length:												
Protrusion length	26.0	25.9	22.3	30.2	2.0	44	29.9	29.5	23.7	37.1	3.7	24
Horizontal oral gape	27.6	27.6	24.3	32.9	1.8	44	24.1	24.4	20.0	27.7	1.8	24
Vertical oral gape	32.3	32.6	23.1	37.0	3.2	44	35.0	35.7	28.5	41.5	3.2	24
Protrusion angle	65.1	66.0	41	80	7.7	44	50.7	50.5	44	57	3.9	24

B.crassibarbis						*B. dainellii*						*B.gorgorensis*					
Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
3.9	4.0	3	4	0.3	10	4.0	4.0	4	4	0.0	10	3.9	4.0	3	4	0.3	10
8.0	8.0	8	8	0.0	10	8.5	8.5	8	9	0.5	10	8.0	8.0	8	8	0.0	10
3.0	3.0	3	3	0.0	10	2.9	3.0	2	3	0.3	10	3.0	3.0	3	3	0.0	10
5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
16.9	17.0	16	19	0.9	10	16.6	16.5	16	18	0.7	10	16.3	16.5	15	17	0.8	10
10.4	10.0	10	11	0.5	10	10.6	11.0	10	11	0.5	10	10.5	10.5	10	11	0.5	10
32.8	32.5	31	35	1.2	10	31.2	31.0	29	34	1.4	10	32.8	33.0	30	36	1.9	10
13.4	13.0	12	15	0.8	10	12.8	13.0	11	15	1.0	10	13.9	14.0	13	15	0.7	10
5.9	5.5	5.5	7.0	0.6	10	5.3	5.5	4.5	5.5	0.4	10	5.7	5.5	5.5	6.0	0.3	10
4.3	4.0	4.0	5.5	0.5	10	3.7	4.0	3.0	4.0	0.5	10	4.0	4.0	4.0	4.0	0.0	10
3.4	3.3	3.0	4.0	0.5	10	2.6	2.5	2.0	3.0	0.3	10	3.0	3.0	3.0	3.0	0.0	10
12	12	12	12	0.0	10	12	12	12	12	0.0	10	12	12	12	12	0.0	10
24.5	24.0	23	26	1.1	10	21.8	22.0	20	23	1.0	10	22.9	22.5	22	24	1.0	10
27.5	27.4	26.4	29.1	0.9	10	30.2	29.9	28.0	33.7	1.8	10	24.2	24.3	22.2	25.5	1.0	10
26.9	27.0	24.9	28.5	1.2	10	22.6	22.0	20.7	25.6	1.5	10	29.1	28.9	26.0	32.2	1.9	10
13.9	13.5	12.8	16.0	1.1	10	12.2	12.4	10.0	14.3	1.4	10	14.7	14.8	13.3	16.7	1.1	10
20.2	20.4	19.2	21.2	0.7	10	18.0	17.9	17.2	18.9	0.6	10	19.7	20.1	17.0	21.5	1.5	10
11.0	10.9	9.7	11.9	0.6	10	9.4	9.4	8.9	9.9	0.3	10	11.0	10.9	10.5	11.7	0.5	10
51.6	51.8	49.6	53.4	1.2	10	51.7	51.7	49.6	54.0	1.5	10	50.2	49.9	47.9	53.2	2.0	10
73.9	73.7	72.3	75.1	0.8	10	76.0	76.3	74.4	77.4	0.9	10	74.1	73.9	73.0	76.7	1.0	10
50.9	51.0	49.1	53.0	1.2	10	53.3	53.0	51.3	55.4	1.3	10	49.6	49.6	47.6	52.4	1.5	10
24.5	24.7	22.3	25.9	1.0	10	24.7	24.6	23.2	25.9	0.8	10	25.9	25.3	24.4	27.7	1.2	10
24.3	23.9	22.4	26.8	1.4	10	24.0	24.4	21.6	25.4	1.1	10	27.0	26.9	25.0	28.8	1.5	10
20.5	20.3	16.2	25.7	2.9	10	16.6	17.0	12.2	20.1	2.5	10	16.2	15.6	13.4	21.1	2.4	10
14.1	14.0	12.9	15.0	0.7	10	13.9	13.9	12.4	15.2	0.7	10	14.2	14.2	12.6	15.1	0.8	10
19.5	19.7	18.5	20.5	0.8	10	18.8	19.4	16.9	19.9	1.2	9	20.4	20.5	18.7	21.7	0.9	10
7.2	7.2	6.4	7.8	0.4	10	7.1	7.1	6.6	8.2	0.5	10	7.5	7.5	7.0	8.0	0.3	10
21.3	21.0	19.9	22.9	1.0	10	19.6	19.3	17.8	21.1	1.0	10	21.0	20.8	18.8	24.0	1.3	10
17.4	17.3	16.2	19.1	1.0	10	16.3	16.3	14.6	18.1	1.0	10	16.7	16.6	15.4	19.2	1.0	10
29.8	30.3	27.7	31.5	1.3	9	28.4	28.4	26.2	30.3	1.2	8	27.4	27.5	25.6	29.1	1.2	9
29.4	29.5	27.5	31.8	1.5	8	27.6	28.4	24.7	29.4	1.9	7	27.8	27.8	26.3	29.2	1.0	10
69.7	68.8	66.2	76.0	3.2	10	54.0	54.5	47.9	60.2	4.0	10	73.9	74.0	69.1	81.3	3.6	10
51.0	51.0	48.8	52.8	1.4	10	41.5	40.8	36.6	47.1	3.4	10	62.0	61.8	55.7	68.4	3.4	10
33.6	33.8	32.2	34.6	0.7	10	36.9	36.4	34.8	39.7	1.6	10	33.8	34.2	31.8	35.4	1.1	10
33.7	33.6	32.2	35.9	1.3	10	26.3	26.3	24.6	29.3	1.4	10	36.6	36.7	33.8	38.3	1.2	10
16.1	16.0	13.6	19.2	1.8	10	13.9	14.3	10.8	17.3	1.7	10	16.3	15.9	13.7	20.3	1.9	10
21.0	20.2	18.7	24.2	2.1	10	17.9	18.2	14.9	20.1	1.7	10	20.7	20.3	18.1	23.3	1.6	10
47.7	48.3	44.4	50.8	2.0	10	45.7	45.7	42.1	48.4	1.9	10	47.8	48.0	46.3	49.8	1.2	10
28.0	28.3	24.9	29.9	1.7	10	23.5	23.4	20.2	26.3	1.8	10	34.9	34.7	32.3	38.0	1.9	10
38.5	38.4	36.3	40.5	1.4	10	30.6	30.6	25.5	35.7	2.8	10	39.8	39.4	38.4	42.5	1.6	10
22.7	23.2	18.5	26.1	2.2	10	12.8	12.5	10.4	16.0	1.9	10	22.3	22.4	17.0	28.5	3.7	10
32.9	32.9	31.9	33.9	0.7	10	33.8	33.8	30.5	36.2	1.8	10	30.4	30.5	28.9	31.6	1.0	10
44.1	43.9	42.3	47.1	1.6	10	40.3	41.1	36.4	42.4	2.0	10	37.4	37.3	35.1	40.2	1.5	10
2.27	2.32	1.89	2.70	0.25	10	1.54	1.52	1.13	2.20	0.29	27	3.33	3.24	2.65	3.91	0.42	8
27.2	27.0	21	35	5.0	10	21.9	22.5	15	26	3.6	10	32.8	33.5	26	38	4.4	10
40.7	41.0	28	53	7.6	10	34.1	35.0	22	45	7.2	10	37.4	40.0	29	46	6.3	10
1.5	1.0	1	3	0.7	10	2.7	3.0	2	4	0.7	10	2.9	3.0	2	3	0.3	10
1.3	1.0	1	2	0.4	10	1.2	1.0	1	2	0.4	10	1.8	2.0	1	3	0.6	10
1.1	1.0	1.0	1.5	0.2	10	2.8	3.0	2.0	3.0	0.3	10	1.6	1.5	1.0	2.0	0.4	10
1.2	1.0	1.0	2.0	0.4	10	2.2	2.0	1.5	3.0	0.5	10	1.8	2.0	1.0	2.0	0.3	10
2.0	2.0	2.0	2.0	0.0	10	1.1	1.0	1.0	2.0	0.3	10	2.0	2.0	2.0	2.0	0.0	10
36.7	37.3	29.5	41.1	3.4	18	37.7	37.6	27.4	51.3	5.5	29	31.0	30.8	27.4	35.4	2.1	12
28.8	29.1	24.1	32.0	2.1	18	28.0	28.0	21.5	33.6	2.8	29	26.8	27.1	22.8	30.9	2.1	12
34.3	34.9	28.8	38.5	2.8	18	38.4	38.8	30.4	45.6	4.1	29	32.0	31.7	29.0	36.5	2.5	12
46.0	46.0	35	64	7.9	18	46.2	45.0	19	70	13.0	29	53.8	55.0	43	63	5.8	12

Table 5.5. Characters of 14 *Barbus* species (continued).

	B. gorguari						*B.longissimus*					
	Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
Meristic measures												
Dorsal fin rays (simple)	4.0	4.0	4	4	0.0	10	4.1	4.0	4	5	0.3	10
Dorsal fin rays (branched)	8.1	8.0	8	9	0.3	10	8.1	8.0	8	9	0.3	10
Anal fin rays (simple)	3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10
Anal fin rays (branched)	5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
Pectoral fin rays (total)	16.7	16.5	16	18	0.8	10	16.8	17.0	16	18	0.8	10
Ventral fin rays (total)	9.9	10.0	9	11	0.7	10	10.5	10.5	10	11	0.5	10
Scales on lateral line (total)	33.6	34.0	29	37	2.2	10	34.8	34.5	31	39	2.0	10
Predorsal scales	13.5	13.5	13	14	0.5	10	14.7	15.0	13	16	1.0	9
Scales from dorsal fin to lateral line	5.7	5.5	5.5	6.5	0.3	10	6.0	6.0	5.5	6.5	0.5	10
Scales from anal fin to lateral line	4.0	4.0	4.0	4.0	0.0	10	4.1	4.0	4.0	4.5	0.2	10
Scales from ventral fin to lateral line	3.0	3.0	3.0	3.0	0.0	10	3.0	3.0	3.0	3.0	0.0	10
Circumpeduncular scales	12	12	12	12	0.0	10	12	12	12	12	0.0	10
Circumference scales	23.0	23.0	22	24	0.9	10	23.9	24.0	22	26	1.2	10
Metric measures												
In % of standard length:												
Head length	29.4	29.2	27.3	32.4	1.3	10	26.8	26.8	25.5	28.8	1.0	10
Body depth	24.9	24.9	22.8	26.5	1.1	10	23.8	23.9	20.8	25.8	1.4	10
Body width	14.7	14.3	11.9	17.0	1.7	10	13.1	12.8	11.8	15.4	1.3	10
Caudal peduncle length	19.0	19.0	18.4	19.8	0.4	10	20.6	20.7	18.8	21.7	0.9	10
Caudal peduncle depth	9.7	9.8	8.8	10.7	0.7	10	10.5	10.6	9.6	11.4	0.6	10
Predorsal length	51.0	50.9	49.2	52.9	1.1	10	48.3	48.5	45.1	50.1	1.6	10
Preanal length	75.2	75.3	73.3	77.1	1.3	10	73.0	73.1	71.1	74.5	1.0	10
Preventral length	53.5	53.6	51.5	55.7	1.4	10	50.6	50.4	48.5	52.4	1.1	10
Pectoral-ventral length	25.4	25.7	23.7	26.7	1.1	10	25.0	25.1	22.9	27.1	1.2	10
Ventral anal length	24.0	24.0	21.6	27.7	1.8	10	24.7	24.6	23.4	25.9	1.0	10
Dorsal spine length	15.1	14.7	11.6	21.2	3.0	10	16.0	15.3	13.9	19.0	1.7	10
Dorsal fin base length	13.7	13.9	12.2	14.8	0.9	10	13.5	13.5	12.7	14.0	0.4	10
Anal fin length	18.9	18.8	17.1	20.3	0.9	10	17.8	17.6	15.7	19.4	1.2	10
Anal fin base length	7.2	7.0	6.8	8.0	0.4	10	7.2	7.2	6.6	7.9	0.4	10
Pectoral fin length	19.7	19.8	17.8	22.3	1.3	10	17.7	17.5	16.8	19.2	0.8	10
Ventral fin length	15.3	15.3	13.5	17.9	1.3	10	14.8	14.8	13.5	16.4	0.8	10
Upper lobe length of caudal fin	26.9	25.7	23.8	30.3	2.4	10	27.8	27.8	24.7	30.8	2.0	9
Lower lobe length of caudal fin	26.3	26.0	24.1	29.4	2.0	10	27.3	26.6	25.3	31.7	2.2	8
In % of head length:												
Head depth at occiput	61.5	61.7	56.7	65.0	2.7	10	63.9	64.5	58.8	67.0	2.7	10
Head width	50.6	49.8	45.4	55.9	3.0	10	49.2	50.2	44.0	52.5	3.2	10
Snout length	32.4	32.3	30.6	34.1	1.2	10	33.9	33.9	32.5	35.0	0.8	10
Snout width	29.6	29.2	27.9	32.9	1.6	10	31.7	31.7	29.3	33.8	1.7	10
Eye diameter	15.6	15.6	13.1	18.5	1.8	10	13.7	13.6	12.0	15.6	1.1	10
Orbit diameter	20.1	20.4	17.3	22.6	1.8	10	17.0	17.0	15.0	18.8	1.2	10
Postorbital length	48.3	48.0	46.5	51.2	1.7	10	49.2	48.9	48.1	51.6	1.2	10
Interorbital width	27.6	27.9	24.7	31.1	2.1	10	27.6	27.4	26.1	29.1	1.0	10
Operculum depth	33.2	33.2	31.2	37.2	1.9	10	34.4	34.2	32.7	36.1	1.1	10
Anterior barbel length	12.3	12.0	9.3	15.4	2.2	10	9.0	8.7	7.7	11.6	1.4	10
Upper jaw length	33.1	33.4	30.6	35.0	1.6	10	33.5	33.5	32.0	36.4	1.3	10
Lower jaw length	41.6	41.6	39.5	43.9	1.4	10	44.1	44.5	40.7	46.0	1.9	10
Gut length/fork length	1.70	1.65	1.21	2.44	0.29	20	1.79	1.73	1.35	2.33	0.29	7
Angular measures												
Dorsal head inclination	17.1	17.0	10	23	4.1	10	19.5	19.0	16	23	1.9	10
Gape inclination	64.6	63.5	55	80	7.6	10	57.8	59.5	47	65	5.8	10
Coded qualitative measures												
Head profile	3.6	4.0	3	4	0.5	10	3.1	3.0	2	4	0.7	10
Nuchal hump development	4.6	4.8	4	5	0.5	10	1.6	2.0	1	2	0.5	10
Upper lip development	1.9	2.0	1.0	2.0	0.3	10	1.5	1.5	1.0	2.0	0.3	10
Lower lip development	1.8	2.0	1.0	2.0	0.3	10	1.1	1.0	1.0	1.5	0.2	10
Anterior extension of lower jaw	3.0	3.0	2.0	3.5	0.4	10	3.6	4.0	3.0	4.0	0.5	10
Protrusion measures												
In % of fork length:												
Protrusion length	31.7	31.8	25.2	35.2	2.4	25	23.9	24.4	19.9	27.3	2.6	14
Horizontal oral gape	29.7	29.5	23.8	35.2	3.2	25	31.1	31.7	28.4	32.6	1.3	14
Vertical oral gape	39.0	39.2	31.3	44.0	3.0	25	39.0	38.7	34.8	44.8	3.0	14
Protrusion angle	64.9	62.0	51	82	7.2	25	77.3	77.0	70	90	5.1	14

B. macrophtalmus						*B. megastoma*						*B.nedgia*					
Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
4.0	4.0	4	4	0.0	10	4.0	4.0	4	4	0.0	10	3.9	4.0	3	4	0.3	10
8.1	8.0	8	9	0.3	10	8.4	8.0	8	9	0.5	10	8.8	9.0	8	9	0.4	10
3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10
5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
16.7	16.5	15	18	1.1	10	17.3	17.0	16	18	0.7	10	17.5	18.0	16	18	0.7	10
10.3	10.0	10	11	0.5	10	10.4	10.0	10	11	0.5	10	10.4	10.0	10	11	0.5	10
32.5	33.0	30	34	1.1	10	35.1	35.0	33	37	1.4	10	33.4	33.0	30	37	2.0	10
13.5	13.5	13	14	0.5	10	14.9	15.0	13	16	0.9	10	13.0	13.0	12	14	0.7	9
5.9	6.0	5.5	6.5	0.4	10	5.9	5.8	5.5	6.5	0.5	10	5.8	5.8	5.5	6.0	0.3	10
4.0	4.0	4.0	4.0	0.0	10	4.0	4.0	4.0	4.0	0.0	10	4.0	4.0	4.0	4.0	0.0	10
3.0	3.0	3.0	3.0	0.0	10	3.0	3.0	3.0	3.0	0.0	10	2.9	3.0	2.5	3.0	0.2	10
12	12	12	12	0.0	10	12	12	12	13	0.3	10	12	12	12	12	0.0	10
23.9	24.0	23	26	1.0	10	23.8	24.0	22	25	0.8	10	22.6	22.0	22	24	0.8	10
27.6	27.3	26.0	29.8	1.2	10	27.4	28.6	24.3	30.0	2.2	10	27.4	27.1	24.8	30.3	1.6	10
27.1	27.2	25.7	29.6	1.2	10	23.4	23.6	21.5	24.2	0.8	10	25.9	26.0	24.3	27.3	0.9	10
13.6	13.4	11.9	15.4	1.0	10	12.4	12.4	10.8	14.2	1.0	10	13.6	13.3	12.2	15.9	1.2	10
20.9	21.0	20.1	21.9	0.7	10	19.4	19.3	18.4	20.4	0.6	10	20.3	20.0	19.1	22.2	1.0	10
10.2	10.2	9.6	11.2	0.4	10	9.6	9.7	8.9	10.1	0.4	10	10.6	10.5	10.1	11.4	0.5	10
48.8	48.8	47.3	50.3	0.9	10	49.0	49.0	46.3	51.7	1.8	10	50.7	50.5	48.5	52.5	1.2	10
73.0	72.8	71.7	74.8	1.0	10	73.9	73.9	71.6	76.2	1.3	10	73.5	73.3	71.0	76.3	1.7	10
51.7	51.5	49.8	53.9	1.4	10	51.7	51.6	49.8	53.7	1.5	10	50.3	50.5	47.0	51.9	1.4	10
25.5	25.6	24.0	27.5	1.0	10	25.6	25.8	24.0	26.7	0.9	10	24.2	24.1	22.7	26.1	1.0	10
23.2	23.4	21.7	24.7	0.9	10	24.7	24.3	21.7	28.1	2.1	10	24.9	25.0	22.2	28.4	1.8	10
19.0	20.0	14.9	25.8	3.5	10	15.8	14.5	12.5	24.2	3.5	10	18.2	18.3	12.3	23.9	3.9	10
14.0	13.9	12.2	16.2	1.1	10	13.3	13.5	12.3	14.3	0.6	10	14.4	14.4	13.5	15.2	0.5	10
19.9	19.8	19.0	21.1	0.8	10	18.3	18.2	17.4	19.3	0.7	10	19.9	19.8	18.3	22.2	1.4	10
7.4	7.4	6.9	7.7	0.2	10	7.0	7.0	6.5	8.4	0.5	10	7.1	7.1	5.9	8.5	0.7	10
22.4	22.4	21.2	23.3	0.6	10	19.2	19.1	18.1	20.3	0.7	10	20.4	20.3	17.9	22.4	1.2	10
17.8	17.8	17.0	18.8	0.6	10	15.7	15.5	14.7	16.7	0.6	10	16.6	16.7	14.9	18.1	1.1	10
29.6	29.8	26.8	31.1	1.4	9	27.9	28.1	25.4	31.1	1.8	10	29.0	29.3	25.6	31.7	2.0	10
30.1	30.1	27.3	32.3	1.4	10	27.5	27.8	25.3	30.1	1.7	9	28.8	29.1	26.5	30.5	1.4	8
63.9	63.6	57.9	68.8	3.5	10	59.0	59.3	55.6	62.0	2.0	10	65.4	64.7	60.1	71.5	3.6	10
48.9	48.6	45.3	53.1	2.7	10	43.9	43.1	41.0	47.7	2.3	10	50.1	49.4	46.6	55.8	3.2	10
29.7	30.3	26.3	31.1	1.6	10	31.5	31.9	28.2	33.6	1.9	10	36.9	37.5	32.5	39.3	2.1	10
29.8	29.8	28.0	32.8	1.4	10	26.7	26.4	24.9	29.9	1.5	10	30.2	30.1	28.7	33.0	1.2	10
23.1	22.3	20.1	29.8	2.9	10	16.0	15.6	14.2	20.4	1.8	10	16.4	16.3	12.1	20.0	2.7	10
26.5	25.7	25.0	31.8	2.0	10	19.4	19.1	17.7	23.8	1.7	10	21.0	21.0	17.1	24.6	2.7	10
43.9	43.8	41.5	46.3	1.3	10	45.9	46.3	43.2	49.4	2.0	10	43.2	43.1	39.1	46.6	2.5	10
20.9	21.0	19.2	22.7	1.3	10	22.1	21.5	19.6	26.2	2.1	10	29.7	29.1	27.4	36.1	2.4	10
34.9	34.9	32.0	38.9	2.1	10	31.7	31.5	29.8	34.2	1.5	10	36.6	36.4	34.8	38.9	1.2	10
10.7	10.6	8.1	13.3	1.6	10	10.0	8.6	8.0	15.2	2.6	10	19.9	21.0	12.4	22.8	3.4	10
30.1	30.2	26.8	31.5	1.3	10	31.3	31.5	28.1	33.3	1.4	10	32.8	32.8	28.4	36.4	2.5	10
42.4	42.4	40.8	44.4	1.2	10	45.6	45.9	41.9	48.6	2.5	10	37.3	37.1	33.6	40.7	2.6	10
1.82	1.77	1.46	2.38	0.27	18	1.98	1.92	1.39	2.61	0.30	40	2.44	2.43	1.77	3.43	0.40	48
18.1	19.0	13	23	3.2	10	11.8	10.5	6	19	4.3	10	27.1	28.5	22	32	3.6	10
57.7	54.5	50	70	8.1	10	69.6	70.5	54	81	8.0	10	28.8	26.0	18	48	9.9	10
3.7	4.0	2	5	0.9	10	4.3	4.5	3	5	0.8	10	2.9	3.0	2	4	0.7	10
4.3	4.5	2	5	0.9	10	4.0	4.0	3	5	0.7	10	1.8	2.0	1	3	0.6	10
1.3	1.0	1.0	2.0	0.4	10	2.0	2.0	1.5	2.0	0.2	10	3.6	3.5	3.0	4.0	0.4	10
1.3	1.0	1.0	2.0	0.4	10	1.8	2.0	1.0	2.0	0.4	10	3.8	4.0	3.0	4.0	0.4	10
3.7	4.0	3.0	4.0	0.5	10	4.0	4.0	4.0	4.0	0.0	10	1.0	1.0	1.0	1.0	0.0	10
28.0	28.9	20.1	33.4	3.4	25	28.2	29.4	17.2	34.5	4.5	48	39.0	38.3	30.7	59.4	4.8	55
28.6	29.1	20.8	33.5	2.8	25	29.1	29.1	15.3	38.4	3.9	48	23.1	22.6	15.9	32.1	3.3	55
39.2	39.2	34.8	45.0	2.5	25	40.4	39.5	32.2	49.0	4.3	48	36.2	37.1	21.9	55.7	6.5	55
68.0	67.0	51	89	8.3	25	83.7	81.5	61	111	11.4	48	47.4	48.0	21	63	9.4	55

Table 5.5. Characters of 14 *Barbus* species (continued).

	B. platydorsus						*B. surkis*					
	Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
Meristic measures												
Dorsal fin rays (simple)	3.9	4.0	3	4	0.3	10	4.0	4.0	4	4	0.0	10
Dorsal fin rays (branched)	8.5	8.5	8	9	0.5	10	8.3	8.0	8	9	0.5	10
Anal fin rays (simple)	3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10
Anal fin rays (branched)	5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
Pectoral fin rays (total)	16.9	17.0	15	19	1.1	10	16.2	16.0	15	17	0.8	10
Ventral fin rays (total)	10.7	11.0	10	11	0.5	10	10.1	10.0	10	11	0.3	10
Scales on lateral line (total)	32.6	32.5	31	34	1.0	10	36.0	36.5	33	38	1.5	10
Predorsal scales	14.4	14.0	13	16	0.8	10	14.6	14.0	14	16	0.8	10
Scales from dorsal fin to lateral line	5.8	5.5	5.5	6.5	0.4	10	6.4	6.5	5.5	7.0	0.5	10
Scales from anal fin to lateral line	4.0	4.0	4.0	4.0	0.0	10	4.1	4.0	4.0	5.0	0.3	10
Scales from ventral fin to lateral line	3.1	3.0	3.0	3.5	0.2	10	3.1	3.0	3.0	4.0	0.3	10
Circumpeduncular scales	12	12	12	12	0.0	10	12	12	12	12	0.0	10
Circumference scales	23.7	23.5	22	26	1.2	10	24.4	24.5	22	26	1.5	10
Metric measures												
In % of standard length:												
Head length	28.1	28.0	27.1	30.0	0.9	10	22.0	22.1	20.9	22.7	0.6	10
Body depth	27.3	27.0	25.8	28.8	1.0	10	29.5	29.0	27.6	32.9	1.7	10
Body width	14.6	14.6	13.3	16.4	1.2	10	14.0	13.8	11.2	17.0	2.0	10
Caudal peduncle length	19.0	18.7	18.1	21.2	1.0	10	20.7	20.5	19.5	23.1	1.1	10
Caudal peduncle depth	10.1	10.2	9.0	11.2	0.7	10	10.6	10.6	9.8	11.0	0.4	10
Predorsal length	51.7	51.8	50.5	53.2	0.9	10	47.0	47.1	44.9	48.5	1.1	10
Preanal length	74.7	74.7	72.4	75.9	1.0	10	73.8	73.6	71.4	76.3	1.5	10
Preventral length	52.8	52.7	51.6	55.0	1.2	10	48.2	48.0	45.8	50.0	1.6	10
Pectoral-ventral length	25.9	26.1	24.2	27.3	1.0	10	26.7	26.2	25.2	29.7	1.5	10
Ventral anal length	23.7	23.8	21.9	25.4	1.2	10	27.9	27.6	26.1	30.1	1.4	10
Dorsal spine length	18.4	18.5	13.2	22.5	3.0	10	19.2	19.2	14.9	23.3	3.0	10
Dorsal fin base length	14.5	14.4	13.9	15.8	0.6	10	14.5	14.4	13.5	16.2	0.9	10
Anal fin length	20.3	20.2	18.4	21.9	1.0	10	18.9	18.9	17.0	20.5	1.1	10
Anal fin base length	7.1	7.2	6.5	7.8	0.3	10	7.5	7.4	7.0	8.7	0.5	10
Pectoral fin length	22.2	22.1	20.3	23.5	1.0	10	20.5	20.3	19.4	22.4	0.9	10
Ventral fin length	18.0	17.7	16.9	19.6	0.9	10	17.0	17.1	16.1	17.7	0.5	10
Upper lobe length of caudal fin	30.2	29.9	28.5	33.1	1.7	10	29.0	28.9	26.2	31.2	1.7	9
Lower lobe length of caudal fin	31.0	30.8	29.5	34.1	1.4	10	29.2	29.2	28.7	30.2	0.5	9
In % of head length:												
Head depth at occiput	66.9	66.7	62.9	72.2	2.5	10	73.3	72.8	65.6	81.6	4.5	10
Head width	51.5	50.9	47.2	54.9	2.5	10	58.3	57.8	54.7	63.8	3.2	10
Snout length	32.1	32.3	29.3	33.6	1.4	10	30.1	29.7	27.3	33.5	2.2	10
Snout width	31.5	31.7	29.0	34.5	1.9	10	34.3	34.3	33.0	35.4	0.8	10
Eye diameter	17.1	17.7	13.9	19.1	1.7	10	21.8	21.5	19.0	25.8	2.4	10
Orbit diameter	21.6	22.0	16.9	25.5	2.4	10	26.0	26.2	22.8	29.7	2.5	10
Postorbital length	48.3	47.8	46.2	51.2	1.7	10	45.5	45.2	43.5	47.6	1.4	10
Interorbital width	27.4	26.2	25.6	31.5	2.1	10	36.0	35.9	33.7	39.6	1.8	10
Operculum depth	36.2	36.6	32.4	38.1	1.9	10	40.9	40.4	37.8	46.1	2.4	10
Anterior barbel length	17.0	16.9	14.1	21.6	2.3	10	17.2	17.3	12.2	21.9	2.7	10
Upper jaw length	32.0	31.8	29.6	33.4	1.3	10	27.8	27.9	26.6	29.3	0.9	10
Lower jaw length	40.4	40.8	38.4	41.8	1.2	10	37.8	37.7	35.4	39.4	1.0	10
Gut length/fork length	1.86	1.83	1.45	3.05	0.32	39	2.90	2.82	1.91	4.52	0.62	36
Angular measures												
Dorsal head inclination	24.4	25.5	19	27	2.9	10	29.3	28.0	23	40	4.9	10
Gape inclination	54.7	55.0	47	64	5.5	10	45.2	47.0	25	62	10.7	10
Coded qualitative measures												
Head profile	3.5	3.0	3	5	0.7	10	2.9	3.0	2	4	0.6	10
Nuchal hump development	4.5	4.5	4	5	0.5	10	1.4	1.3	1	2	0.5	10
Upper lip development	1.7	1.8	1.0	2.0	0.4	10	1.3	1.0	1.0	2.0	0.4	10
Lower lip development	1.4	1.3	1.0	2.0	0.4	10	1.1	1.0	1.0	1.5	0.2	10
Anterior extension of lower jaw	2.8	3.0	2.0	3.0	0.4	10	2.1	2.0	2.0	3.0	0.3	10
Protrusion measures												
In % of fork length:												
Protrusion length	28.5	29.0	21.6	34.0	2.8	46	29.3	29.0	24.8	36.0	2.8	41
Horizontal oral gape	31.1	31.5	22.6	37.6	3.3	46	23.7	24.0	18.7	30.0	2.6	41
Vertical oral gape	36.1	35.9	28.5	41.6	3.4	46	32.4	32.5	25.7	38.3	3.1	41
Protrusion angle	66.8	66.0	56	82	5.7	46	58.7	58.0	36	77	8.4	41

B. truttiformis						*B.tsanensis*					
Mean	Median	Min	Max	Std	n	Mean	Median	Min	Max	Std	n
4.1	4.0	4	5	0.3	10	4.0	4.0	4	4	0.0	10
8.7	9.0	8	10	0.7	10	8.0	8.0	8	8	0.0	10
3.0	3.0	3	3	0.0	10	3.0	3.0	3	3	0.0	10
5.0	5.0	5	5	0.0	10	5.0	5.0	5	5	0.0	10
18.3	18.0	17	19	0.7	10	17.0	17.0	16	18	0.5	10
11.0	11.0	10	12	0.5	10	10.8	11.0	10	11	0.4	10
34.8	35.0	32	38	1.7	10	30.7	31.0	29	32	0.8	10
13.2	13.0	12	15	1.0	10	13.2	13.0	12	14	0.6	10
6.2	6.0	5.5	7.0	0.4	10	5.9	6.0	5.5	6.0	0.2	10
4.0	4.0	4.0	4.0	0.0	10	3.9	4.0	3.0	4.0	0.3	10
3.0	3.0	3.0	3.0	0.0	10	3.0	3.0	3.0	3.0	0.0	10
12	12	12	12	0.0	10	12	12	12	12	0.0	10
24.3	24.0	22	26	1.1	10	23.0	23.0	22	24	0.9	10
26.1	26.1	24.9	27.3	0.8	10	25.7	25.7	23.7	27.3	0.9	10
27.0	27.2	24.1	29.3	1.6	10	28.7	28.7	27.5	29.7	0.7	10
14.8	14.8	13.3	17.9	1.3	10	14.5	14.8	13.0	15.5	0.9	10
21.0	21.1	20.0	21.8	0.6	10	19.9	19.8	19.0	21.4	0.9	10
11.3	11.5	10.1	12.1	0.6	10	10.9	10.9	10.2	11.6	0.4	10
47.0	46.6	45.7	49.8	1.3	10	50.1	49.9	48.2	53.1	1.5	10
73.7	73.5	72.1	76.1	1.2	10	74.1	73.8	72.0	75.5	1.2	10
50.2	50.3	48.6	52.7	1.3	10	49.4	49.6	47.6	50.2	0.8	10
25.4	25.3	23.5	26.8	1.0	10	25.5	25.7	23.6	26.6	0.9	10
26.4	26.4	25.0	27.5	0.9	10	26.0	26.4	24.2	27.6	1.1	10
19.3	19.3	16.3	22.7	1.8	10	22.5	22.0	17.2	26.7	3.0	10
15.0	15.1	13.1	16.2	1.0	10	14.9	15.0	13.7	15.8	0.8	10
19.1	19.3	17.0	20.9	1.2	10	18.4	18.3	17.0	19.8	1.0	9
7.7	7.7	7.2	8.4	0.4	10	7.4	7.4	7.0	7.9	0.3	10
19.6	19.7	18.7	20.2	0.5	10	21.7	21.6	20.6	22.9	0.8	10
16.6	16.6	14.7	18.0	0.8	10	17.4	17.4	16.1	18.8	0.9	10
29.7	30.0	26.6	31.8	1.7	10	30.2	30.3	27.5	33.6	2.2	8
29.3	28.9	28.0	32.2	1.3	10	29.8	29.9	26.8	32.7	2.1	8
67.8	67.3	64.3	71.5	2.3	10	71.8	71.3	66.5	77.8	3.5	10
53.1	52.8	49.3	58.8	3.0	10	54.7	54.4	51.5	61.3	2.9	10
31.4	31.0	29.5	33.9	1.4	10	32.9	32.7	30.6	35.6	1.6	10
32.1	31.8	30.1	36.2	1.7	10	34.0	33.8	31.3	36.6	1.6	10
15.2	14.9	14.2	16.6	0.9	10	18.6	18.3	17.1	21.4	1.3	10
19.1	19.2	17.7	20.3	1.0	10	22.5	22.1	20.4	24.7	1.5	10
50.1	50.3	46.7	52.0	1.6	10	47.5	47.2	45.7	50.1	1.4	10
26.6	26.2	24.5	31.6	2.0	10	30.4	30.6	28.1	32.8	1.6	10
35.5	35.2	34.0	38.1	1.2	10	38.6	38.6	36.3	41.2	1.3	10
9.7	9.2	7.2	13.4	1.9	10	18.9	18.2	14.8	23.6	2.5	10
31.9	32.2	29.3	34.8	1.8	10	29.6	29.4	28.0	31.9	1.2	10
41.1	40.6	39.7	44.1	1.2	10	37.4	37.7	34.5	40.4	1.8	10
1.92	1.84	1.59	2.47	0.23	15	2.26	2.24	1.76	2.78	0.29	32
18.0	17.0	13	23	3.2	10	30.5	30.0	25	37	4.1	10
60.8	60.0	54	69	4.5	10	33.0	33.0	23	45	6.4	10
3.7	3.8	3	5	0.7	10	2.9	3.0	2	4	0.9	10
1.6	1.5	1	2	0.4	10	2.6	3.0	2	3	0.5	10
1.4	1.0	1.0	2.0	0.5	10	1.0	1.0	1.0	1.0	0.0	10
1.0	1.0	1.0	1.0	0.0	10	1.2	1.0	1.0	2.0	0.3	10
3.7	4.0	3.0	4.0	0.4	10	2.0	2.0	2.0	2.0	0.0	10
24.5	23.8	19.2	29.5	2.5	20	34.5	34.9	24.7	40.4	3.3	43
33.1	32.9	28.3	37.1	2.3	20	26.4	26.3	20.3	31.5	2.4	43
38.4	39.4	31.7	44.9	3.3	20	33.5	33.4	28.0	39.1	2.4	43
66.5	63.5	55	83	8.3	20	49.4	49.0	23	71	10.0	43

B. acutirostris Bini, 1940
(fig. 5.4)

Barbus brunellii acutirostris: Bini, 1940: 174-175, plate 10.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Acute': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Neotype, 327 mm, RMNH 32870, Debre Mariam (locality 1), Lake Tana , Ethiopia, 11.ii.1993, S.P.L.M. van Gaans, L.A.J. Nagelkerke & G.M.J. van Snik; other material (9), 205.5-326 mm, RMNH 32871-32879, localities 1, 2, 5, 13, and 19, Lake Tana, Ethiopia, 26.i.1993 - 26.ix.1994, S.P.L.M. van Gaans, M.H. Helmes, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the neotype and the 9 other specimens mentioned above, 205.5-326 mm SL (Table 5.5).
Habitus and diagnosis.- A medium-sized (maximally 411 mm FL), shallow- (BD<HL), and narrow-bodied species, sometimes with a slight nuchal hump (in larger specimens). The head is relatively long and narrow, with a small head depth and a tapering, narrow snout. The head inclination is relatively small (< 20°), with a straight to concave dorsal profile. The eyes are relatively large, with a small interorbital width. The operculum depth is small. The lower jaw is relatively long and is equal to the upper jaw or protrudes (usually in larger specimens). The oral gape is relatively large and (sub)terminal. The mouth has thin lips, the lower one interrupted or continuous. The barbels are relatively short and thin (ABL<<ED). The lateral scale count is average (31-36), but the number of scales from the dorsal fin to the lateral line is relatively high (5.5-7), as is the circumference scale count (24-26).
Colouration.- Live specimens are very light, silvery white with a slightly darker (silvery grey) back. The fins are whitish, often the pectoral, and sometimes the caudal fins are tinged pink or red at their bases. In alcohol the light colour, with the slightly darker back can still be observed, the basic colour being light yellowish brown.
Size range.- Specimens from 32 to 411 mm FL have been observed.
Distribution, habitat and ecology.- *B. acutirostris* is only known from Lake Tana. It occurs over muddy, sandy and rocky substrates all over the lake, preferably in water deeper than 6 m. Based on the contents of 67 intestines, *B. acutirostris* is a real piscivore. Specimens smaller than 15 cm FL mainly eat zooplankton and insect larvae, but already start feeding on fish. When growing larger the importance of fish in the diet increases rapidly, while zooplankton disappears; the amount of insect larvae decreases. Adult insects are more prominent in the diet of fish larger than 25 cm FL; macrophytes are also sometimes found.

B. brevicephalus spec. nov.
(fig. 5.5)

'Shorthead': Nagelkerke et al., 1995*b*: 437-439, table 1, fig.3.
Material.- Holotype, 185 mm, RMNH 32880, Yigashu (locality 10), Lake Tana , Ethiopia, 14.xi.1995, L.A.J. Nagelkerke & F.A. Sibbing; paratypes (9), 146-225 mm, RMNH 32881-32889, localities 4, 6, 10, 26, and 29, Lake Tana, Ethiopia, 1.ii.1993 - 14.xi.1995, A.B. van den Burg, S.P.L.M. van Gaans, M.H. Helmes, S. Kranenbarg, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Etymology.- The name is derived from the Latin 'brevis' (short) and the Latinized form of the Greek 'κεφαλη' (head), referring to the short head of this species.

Description.- Based on the holotype and paratypes, 146-225 mm SL (Table 5.5).
Habitus and diagnosis.- A small-sized (maximally 317 mm FL), deep-bodied (BD>HL) species, without a nuchal hump. The head is very short, of average width, and relatively deep with a wide snout. The head inclination is relatively large (> 20°), with a straight to slightly convex dorsal profile. The eyes are relatively large (ED≈SnL), with a relatively large interorbital width. The operculum is quite deep. The upper and lower jaw are relatively short; the lower jaws is shorter than, or equal to the upper jaw, when the mouth is closed. The gape is relatively small and (sub)inferior. The lips are thin, the lower one is interrupted. The barbels are of average size and thin, but short compared to the eye diameter (ABL<ED). All scale counts are average.
Colouration.- Live specimens are light yellow-green, sometimes with a bluish tinge on the (slightly darker) back. The fins are greenish, and especially the pectoral is often tinged orange or reddish (especially at the bases). In alcohol the basic colour is a dull yellow, the back being darker, often with a greenish tinge.
Size range.- Specimens from 89 to 317 mm FL have been observed (specimens larger than 250 mm FL are rare).
Distribution, habitat and ecology.- *B.brevicephalus* is only known from Lake Tana and its tributaries. It occurs over muddy, sandy and rocky substrates all over the lake, preferably in water of less than 6 m deep. Based on the contents of 24 intestines, *B. brevicephalus* is the only large *Barbus* species in the lake that eats considerable amounts of zooplankton when adult. Small specimens rely almost completely on zooplankton and insects; larger fish also eat some molluscs and macrophytes.

B. crassibarbis spec. nov.
(fig. 5.6)

'Barbel': Nagelkerke et al., 1994, table 1, fig.3.
Material.- Holotype, 295 mm, RMNH 32890, Angara (locality 14), Lake Tana , Ethiopia, 5.v.1995, L.A.J. Nagelkerke & J.E. van Oostenbrugge; paratypes (9), 182-324 mm, RMNH 32891-32899, localities 2, 5, 8, 12, 14, 18, and 24, Lake Tana, Ethiopia, 21.i.1993 - 2.xi.1995, A.B. van den Burg, S.P.L.M. van Gaans, M.H. Helmes, S. Kranenbarg, L.A.J. Nagelkerke, J.E. van Oostenbrugge, F.A. Sibbing & G.M.J. van Snik.

Etymology.- The name is derived from the Latin 'crassus' (thick, fat) and 'barba' (beard), referring to the thick barbels of this species.

Description.- Based on the holotype and paratypes, 182-324 mm SL (Table 5.5).
Habitus and diagnosis.- A medium- to large-sized (maximally 505 mm FL) species, without a nuchal hump. The head is relatively deep, of average width and depth, with a wide snout. The head inclination is relatively large (> 20°). The premaxillaries form a 'bump'in the dorsal head profile, while caudally the head is straight to strongly convex. This combination results in a very irregular dorsal head profile. The eyes are relatively small. The lower jaw is relatively long and is shorter than the upper jaw when the mouth is closed; it makes a clear, sharply edged angle with the ventral head profile. The gape is relatively large and inferior, with a large protrusion. The lips are thin, the lower one interrupted or continuous. The barbels are long (18-26% of HL) and very thick and darkly coloured (ABL>ED). The lateral scale count is average (31-35), but the number of scales from the dorsal, anal and ventral fin to the lateral line are relatively high (5.5-7, 4-5.5, and 3-4 respectively), as is the circumference scale count (23-26).
Colouration.- Live specimens are silvery white on the sides, darker grey, with some brown nuances on the back. The conspicuous barbels are dark grey. The fins are whitish; often the pectoral, and sometimes the caudal, ventral and dorsal fins are tinged pink or red at their bases. In alcohol the basic colour is yellowish brown, with a darker back. The dark colour of the barbels is preserved.
Size range.- Specimens from 73 to 505 mm FL have been observed.
Distribution, habitat and ecology.- *B. crassibarbis* is only known from Lake Tana. It occurs over muddy, sandy and rocky substrates all over the lake, preferably in water deeper than 6 m. Based on the contents of 20 intestines, *B. crassibarbis* is a real benthivore, mainly feeding on insect larvae, small molluscs, detritus and substratum.

B. dainellii Bini, 1940
(fig. 5.7)

Barbus dainellii: Bini, 1940: 175-176, plate 11.
Barbus dainellii macrocephalus Bini, 1940: 176-177, plate 11.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Bighead': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Neotype, 308 mm, RMNH 32900, South-Dek (locality 27), Lake Tana , Ethiopia, 7.iii.1993, S.P.L.M. van Gaans, G.M.J. van Snik & L.A.J. Nagelkerke; other material (9), 229-396 mm, RMNH 32901-32909, localities 13, 17, 20, 22, 25, and 27, Lake Tana, Ethiopia, 9.xi.1990 - 8.xi.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, M.H. Helmes, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the neotype and the 9 other specimens mentioned above, 229-396 mm SL (Table 5.5).

Habitus and diagnosis.- A medium- to large-sized (maximally 490 mm FL), shallow- (BD<HL), and narrow-bodied species, without a nuchal hump. The head is very long (up to 1/3 of SL!), narrow, and has a small depth, with a long, narrow snout. The dorsal head profile ranges from slightly concave to convex. The eyes are relatively small (more than 2 times in SnL), with a large interorbital width. The lower jaw is of average length, but is much shorter than the upper jaw when the mouth is closed. The gape is relatively large and inferior, with a large protrusion and thick lips, the lower one continuous, sometimes with a small median lobe. The barbels are slightly shorter than average, approximately the same length as the eye diameter, and thin. The lateral scale count is lower than average (29-34), as is the number of scales from the lateral line to the dorsal, anal and ventral fins (4.5-5.5, 3-4, and 2-3 respectively). The circumference scale count is also relatively low (20-23).
Colouration.- Live specimens are variable in colour, but rather dark. The ground colour varies from greenish yellow, to olive- and coppery brown. The back is darker, often slaty grey or dark green, the ventral parts light, or even white. The fins are dark, green or grey, sometimes with an orange or pinkish tinge in the pectoral and ventrals. In alcohol the rather dark colour, with the even darker back can still be observed, the basic colour being brown.
Size range.- Specimens from 119 to 490 mm FL have been observed.
Distribution, habitat and ecology.- *B. dainellii* is only known from Lake Tana. It has a preference for rocky substrates, but also lives over sandy and muddy parts, especially in the shore areas. This species is absent from water which is deeper than 6 m. In contrast with the impression based on its morphology (especially the inferior mouth) *B. dainellii* is a real piscivore, that also eats small amounts of insects (based on 22 intestines).

B. gorgorensis Bini, 1940
(fig. 5.8)

Barbus intermedius gorgorensis: Bini, 1940: 168-169, plate 6.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Carplike': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Neotype, 379 mm, RMNH 32910, Debre Mariam (locality 1), Lake Tana , Ethiopia, 26.i.1993, S.P.L.M. van Gaans, G.M.J. van Snik & L.A.J. Nagelkerke; other material (9), 299-420 mm, RMNH 32911-32919, localities 3, 16, 17, 19, 21, and 29, Lake Tana, Ethiopia, 12.xi.1990 - 5.xi.1995, J.G.M. van den Boogaart, S.P.L.M. van Gaans, M.H. Helmes, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the neotype and the 9 other specimens mentioned above, 299-420 mm SL (Table 5.5).
Habitus and diagnosis.- A medium- to large-sized (maximally 618 mm FL), deep- (BD>HL), and wide-bodied species, sometimes with a slight nuchal hump. The belly of this species often feels rather soft and usually shows a large anal opening. The head is relatively deep, wide and short with a wide snout. The head inclination is relatively large (> 20°), with a straight to slightly convex

dorsal profile. The eyes are relatively small, with a large interorbital width. The operculum is deep. The upper and lower jaw are relatively short, the latter being shorter than the upper jaw when the mouth is closed. The oral gape is relatively small and (sub)inferior, with thin lips, the lower one interrupted or continuous. The barbels are relatively long and thick (ABL>>ED). This species has very heavy pharyngeal jaws, with large molariform teeth (cf. Nagelkerke et al. 1994). The lateral scale count is average (30-36), as are the other scale counts.
Colouration.- Live specimens usually show bright golden-yellowish sides, with a darker (olive-green) back. The fins are variable in colour, ranging from light yellow to dark grey and green, sometimes with a pinkish tinge. In alcohol the basic colour is yellowish brown, the back being darker than the ventral parts.
Size range.- Specimens from 199 to 618 mm FL have been observed. Real small specimens have never been obtained.
Distribution, habitat and ecology.- *B. gorgorensis* is only known from Lake Tana. It occurs over muddy, sandy and rocky substrates, especially in the shore areas of the lake, almost exclusively in water shallower than 6 m. Based on the contents of 23 intestines, *B. gorgorensis* is a specialized macro-molluscivore. Especially bivalves, up to 5 cm in length, and to a lesser extent gastropod snails have been found in its intestine.

B. gorguari Rüppell, 1836
(figs 5.9, 5.10)

Barbus gorguari: Rüppell, 1836: 9-11, plate 1, fig. 4.
Luciobarbus gorguari: Heckel, 1846: 324.
Barbus gorguari: Günther, 1868: 100.
Barbus gorguari (part): Boulenger, 1907: 237-239, plate 44.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Dark': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 399 mm SL, SMF 2586, Goraza, Zana-See, Abyssinien (locality 9), 1832, E. Rüppell; other material (10), 195-410 mm, RMNH 32920-32929, localities 13, 19, 20, 27, 28, and 29, Lake Tana, Ethiopia, 10.xi.1990 - 6.xi.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the holotype and the 10 other specimens mentioned above, 195-410 mm SL (Table 5.5).
Habitus and diagnosis.- A medium- to large-sized (maximally 532 mm FL), shallow-bodied (BD<HL) species, with a conspicuous, steeply rising nuchal hump. The head is relatively long, with a small depth; the snout is of average length and width. The head inclination is relatively small (< 20°), with a straight to concave dorsal profile. The eyes are a little smaller than average, with an average interorbital width. The operculum depth is also average. The upper and lower jaw are relatively long and the latter is equal to the upper jaw or extends slightly beyond (usually in larger specimens). The oral gape is large, round and (sub)terminal, with moderately developed lips, the

lower one usually continuous. The barbels are relatively short and thin (ABL<ED). The lateral scale count has a large range (29-37), the other scale counts are quite average.
Colouration.- Live specimens are very dark green, dark brown, coppery or blackish red or black. Usually the ventral parts are lighter. The head and fins are generally of the same colour as the rest of the body, but often even darker. In alcohol the very dark colour persists, usually becoming dark brown.
Size range.- Specimens from 91 to 532 mm FL have been observed.
Distribution, habitat and ecology.- *B. gorguari* is only known from Lake Tana. It prefers rocky substrates in waters less than 6 m deep, especially in the shore areas, but it also occurs over muddy and sandy substrates. Based on the contents of 16 intestines, *B. gorguari* has a mixed diet of mainly fish, insects, and macrophytes.

B. longissimus spec. nov.
(fig. 5.11)

'Bigmouth mini-eye': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 373 mm SL, RMNH 32930, Kentefami (locality 11), Lake Tana, Ethiopia, 31.x.1995 , L.A.J. Nagelkerke & F.A. Sibbing; paratypes (9), 220-406 mm, RMNH 32931-32939, localities 1, 13, 17, 20, and 31, Lake Tana, Ethiopia, 12.xi.1990 - 17.x.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Etymology.- The Latin word 'longissimus' means 'very long' and refers to the elongated and slender body of this species.

Description.- Based on the holotype and paratypes, 220-406 mm SL (Table 5.5).
Habitus and diagnosis.- A medium- to large-sized (maximally 610 mm FL), shallow- (BD<HL), and narrow-bodied species, sometimes with a very slight nuchal hump. The body makes a very slender impression, because the differences between head depth, body depth and caudal peduncle depth are relatively small in this species, giving it an elongated shape. The head is of average depth and length with a long, rather wide snout. The head inclination is relatively small (< 20°), with a slightly convex to slightly concave dorsal profile. The eyes are relatively small (more than 2 times in SnL), with an average interorbital width. The operculum depth is small. The upper and lower jaw are relatively long and the latter is equal to the upper jaw when the mouth is closed, or even extends beyond it. The oral gape is relatively large and terminal, with a short protrusion. The lips are thin, the lower one is usually interrupted. The barbels are short and thin (ABL<<ED). The lateral scale count is high (31-39), the rest of the scale counts is average.
Colouration.- Live specimens are generally yellowish green, or greenish grey, with a darker back (olive-green) and whitish ventral parts. The fins are usually slightly darker than the body: olive- to dark green. In alcohol the basic colour is yellowish brown, with a slightly darker back and fins.

Size range.- Specimens from 171 to 548 mm FL have been observed. This is another species for which no real small specimens have been found.
Distribution, habitat and ecology.- *B. longissimus* is only known from Lake Tana. It occurs mostly over rocky substrates in relatively shallow water (less than 6 m deep). Based on the contents of 14 intestines, *B. longissimus* is a real piscivore, with almost 100% of its food consisting of fish.

B. macrophtalmus Bini, 1940
(fig. 5.12)

Barbus gorguari macrophtalmus: Bini, 1940: 177-178, plate 12.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Bigmouth big-eye': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Neotype, 282 mm, RMNH 32940, Bet Menzo (locality 4), Lake Tana , Ethiopia, 21.i.1993, S.P.L.M. van Gaans, G.M.J. van Snik & L.A.J. Nagelkerke; other material (9), 144.5-290 mm, RMNH 32941-32949, localities 1, 5, 8, 11, and 19, Lake Tana, Ethiopia, 21.i.1993 - 26.ix.1994, S.P.L.M. van Gaans, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the neotype and the 9 other specimens mentioned above, 144.5-290 mm SL (Table 5.5).
Habitus and diagnosis.- A medium-sized (maximally 425 mm FL) species of average body depth (BD≈HL) and width, usually with a clear nuchal hump in larger specimens. The head is a bit longer and narrower than average, with a short snout of average width. The head inclination is relatively small (< 20°), with a slightly convex to concave dorsal profile. The eyes are very large (ED≈SnL), with a small interorbital width (IOW<ED). The operculum depth is average. The upper and lower jaw are of average length, the latter being equal to the upper jaw when the mouth is closed, or even extending beyond it (usually in larger specimens). The oral gape is of average size and (sub)terminal. The mouth has thin lips, the lower one interrupted or continuous. The barbels are relatively short and thin (ABL<<ED). The lateral scale count is average (30-34), but the circumference scale count is relatively high (23-26).
Colouration.- Live specimens have a yellowish or brownish silvery ground colour, darker brown on the back. The fins are brownish, the pectoral sometimes with some dark markings on the edges. In alcohol the basic pattern of lighter sides and darker back is preserved, the ground colour being yellowish brown.
Size range.- Specimens from 53 to 425 mm FL have been observed.
Distribution, habitat and ecology.- *B. macrophtalmus* is only known from Lake Tana. It occurs all over the lake, over muddy, sandy and rocky substrates (with a slight preference for rocks), usually in water deeper than 3 m. Based on the contents of 17 intestines, *B. macrophtalmus* mainly feeds on insects (both larvae and adults); small specimens also eat zooplankton, while larger ones sometimes exclusively feed on fish.

B. megastoma spec. nov.
(fig. 5.13)

Barbus gorguari (part) Boulenger, 1907: 237-239, plate 44.
Barbus gorguari (part) Bini, 1940: 177, plate 12.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Bigmouth small-eye': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 402 mm SL, RMNH 32950, Rema (locality 25), Lake Tana, Ethiopia, 15.xi.1990 , J.G.M. van den Boogaart, E.H.R.R. Lammens, L.A.J. Nagelkerke & F.A. Sibbing; paratypes (9), 198-366 mm, RMNH 32951-32959, localities 1, 11, 20, 21, 22, and 29, Lake Tana, Ethiopia, 10.xi.1990 - 15.xi.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Etymology.- The name is derived from the Latinized forms of the Greek words 'μεγας' (great) and 'στομη' (mouth), referring to the very large mouth of this species.

Description.- Based on the holotype and paratypes, 198-402 mm SL (Table 5.5).
Habitus and diagnosis.- A medium to very large-sized (maximally 824 mm FL), shallow- (BD<HL), and narrow-bodied species, with a clear nuchal hump that rises more gradually than in *B. gorguari*, and which becomes increasingly pronounced in larger specimens. The head is relatively long and narrow, with a small head depth and a relatively narrow snout. The head inclination is relatively small (< 20°), with a straight to concave dorsal profile. The eyes are relatively small, with a smaller than average interorbital width. The operculum depth is of average size. The lower jaw is very long and prominent, making a pronounced sharply-hooked angle with the ventral head profile; it is longer than the upper jaw, and almost always extends significantly beyond it. The oral gape is large and terminal. The mouth has well-developed, but rather thin lips, the lower one usually being continuous. The barbels are relatively short and thin (ABL<ED). The lateral scale count is relatively high (33-37), but the other counts are quite average, although one specimen showed 13 scales round its caudal peduncle, which is the only specimen of any *Barbus* species of Lake Tana, in which this was found.
Colouration.- Live specimens have a ground colour which is light yellowish brown, with a silvery sheen, sometimes just silvery grey. The back is darker and can be brownish to dark grey, sometimes with a blue tinge. The fins are whitish, yellowish or brownish, the pectoral often with a clear red base; also the other fins may have a pinkish or reddish tinge.
Size range.- Specimens from 75 to 824 mm FL have been observed.
Distribution, habitat and ecology.- *B. megastoma* is only known from Lake Tana and its tributaries. It has a small preference for rocky substrates and waters less than 6 m deep. Based on the contents of 91 intestines, *B. megastoma* is a (partial) piscivore. Specimens smaller than 15 cm FL mainly eat insect larvae and zooplankton, but also some fish. With size the amount of fish in the diet increases, as does the amount of plant material, while the amount of insects decreases and zooplankton disappears altogether.

B. nedgia (Rüppell, 1836)
(figs 5.14-5.16)

Labeobarbus nedgia: Rüppell, 1836: 14-16, plate 2, fig. 3.
Barbus nedgia: Günther, 1868: 104.
Barbus degeni: Boulenger, 1902: 435.
Barbus affinis nedgia: Bini, 1940: 163, plate 2.
Barbus degeni leptorhinus: Bini, 1940: 164, plate 3.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
Tor nedgia: Fowler, 1976: 384.
'Lip': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 480 mm SL, SMF 2619, Goraza, Zana-See, Abyssinien (locality 9), 1832, E. Rüppell; other material (10), 181-426 mm, RMNH 32960-32969, localities 1, 16, 17, 18, 27, and 29, Lake Tana, Ethiopia, 9.xi.1990 - 6.xi.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the holotype and the 10 other specimens mentioned above, 181-480 mm SL (Table 5.5).

Habitus and diagnosis.- A medium to very large-sized (maximally 707 mm FL) species with an average body depth and width (BD≈HL), sometimes with a very slight nuchal hump. The head is of average length and depth, and has a relatively long snout of average width. The head inclination is relatively large (> 20°), with a slightly convex to concave dorsal profile. The eyes are relatively small, with a slightly larger than average interorbital width. The operculum depth is average. The oral gape is relatively small and inferior, with a large upper jaw protrusion. The mouth has very thick lips, the lower one with a fleshy median lobe. The upper lip sometimes has a fleshy median flap that curls back over the snout. If such a flap is absent the snout often forms a triangular pointed 'nose', which overhangs the lip (fishes of this type were called *B. degeni* by Boulenger, 1902). The barbels are relatively long (ABL>ED) and thick, and are sometimes slightly branched. The lateral scale count has a large range and is average (30-37), as are the rest of the scale counts.

Colouration.- Live specimens are variable in colour, from light yellowish brown with a silvery sheen to golden brown, olive-green and dark brown. The back is always darker than the sides. The fins also vary. In the lightest specimens they are whitish, sometimes with a red tinge, but usually they are darker: brown or slaty grey. In alcohol the ground colour is yellowish brown, with a darker back.

Size range.- Specimens from 103 to 707 mm FL have been observed.

Distribution, habitat and ecology.- *B. nedgia* has been described not only from Lake Tana and its tributaries, but also from another lake and several rivers in the Ethiopian region (Boulenger 1907: 225). However, we have indications that all Lake Tana *Barbus* species originated within the lake and form a species flock (Nagelkerke et al. 1994, 1995*b*, 1996). The occurrence of *B. nedgia* outside Lake Tana could imply dispersion after the species originated in the lake. Most probably, however, it is based on parallel lip development in separate *Barbus* populations. In Lake Tana, *B.*

nedgia occurs especially over rocky substrates in water of no more than 6 m deep. Based on the contents of 75 intestines, *B. nedgia* is a real macro-benthivore. Specimens smaller than 15 cm FL mainly eat insect larvae, but switch to a more diverse diet when their size increases: adult insects, molluscs and detritus become more important, and large specimens of this species are the only barbs in Lake Tana that eat fresh-water crabs of the genus *Potamonautes* MacLeay, 1838. Large *B. nedgia* also eat some fish.

B. platydorsus spec. nov.
(fig. 5.17)

'White hunch': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 351 mm SL, RMNH 32970, Rema (locality 25), Lake Tana, Ethiopia, 10.xi.1990, J.G.M. van den Boogaart, E.H.R.R. Lammens, L.A.J. Nagelkerke & F.A. Sibbing; paratypes (9), 193-336 mm, RMNH 32971-32979, localities 2, 4, 7, 8, 11, 23, and 27, Lake Tana, Ethiopia, 21.i.1993-6.x.1993, S.P.L.M. van Gaans, L.A.J. Nagelkerke & G.M.J. van Snik.

Etymology.- The name is derived from the Latinized form of the Greek 'πλατυς' (broad, wide) and the Latin 'dorsum' (back), referring to the wide back of this species.

Description.- Based on the holotype and paratypes, 193-336 mm SL (Table 5.5).
Habitus and diagnosis.- A medium to large-sized (maximally 635 mm FL), relatively deep- (BD≈HL), and wide-bodied species, with a clear, gradually starting, wide nuchal hump (already present in very small specimens). The head is slightly longer than average and of average width and depth. The snout is of average length, but relatively wide. The head inclination is average (≈ 20°), with a straight to concave dorsal profile. The eyes are relatively small, with an average interorbital width. The operculum depth is average. The upper and lower jaws are of average length, with the latter slightly shorter, or equal to the upper jaw, when the mouth is closed. The oral gape is relatively large and (sub)terminal. The mouth has thin lips, the lower one interrupted or continuous. The barbels are a little longer than average and thin (ABL≈ED). The lateral scale count is average (31-34), as are the rest of the scale counts.
Colouration.- Live specimens are very light, comparable to *B. acutirostris*, i.e. silvery white with a slightly darker (silvery grey) back. The fins are whitish, often the pectoral, and sometimes the caudal fins are tinged pink or red at their bases. In alcohol the light colour, with the slightly darker back can still be observed, the basic colour being light yellowish brown.
Size range.- Specimens from 66 to 635 mm FL have been observed.
Distribution, habitat and ecology.- *B. platydorsus* is only known from Lake Tana. It occurs especially over muddy and sandy substrates all over the lake, preferably in water deeper than 6 m. Based on the contents of 116 intestines, *B. platydorsus* is a benthivore that at larger size turns into a piscivore. Specimens smaller than 15 cm FL mainly eat insect larvae. Molluscs and plant material

become more important with increased size. When the fishes reach sizes of 25 cm FL or more, fish is their main food item, while also some plants and insect larvae are consumed.

B. surkis Rüppell, 1836
(fig. 5.18)

Barbus surkis: Rüppell, 1936: 5-7, plate 1, fig. 1.
Barbus intermedius (part): Banister, 1973: 47-75, figs 30-33, 36-44, 46, 56-58.
Barbus intermedius intermedius (part): Banister, 1973: 74-75.
'Zurki': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Neotype, 295 mm, RMNH 32980, Entos (locality 17), Lake Tana, Ethiopia, 8.ii.1993, S.P.L.M. van Gaans, L.A.J. Nagelkerke & G.M.J. van Snik; other material (9), 194-318 mm, RMNH 32981-32989, localities 1, 13, 16, and 17, Lake Tana, Ethiopia, 8.ii.1993-10.x.1995, A.B. van den Burg, S.P.L.M. van Gaans, S. Kranenbarg, L.A.J. Nagelkerke , F.A. Sibbing & G.M.J. van Snik.

Description.- Based on the neotype and the 9 other specimens mentioned above, 194-318 mm SL (Table 5.5).
Habitus and diagnosis.- A medium-sized (maximally 430 mm FL), deep-bodied (BD>HL) species, without a nuchal hump. The large abdomen of this species usually feels very soft. The head is short, deep and wide with a relatively short and wide snout. The head inclination is relatively large (> 20°), with a slightly convex to slightly concave dorsal profile. The eyes are relatively large, with a large interorbital width. The operculum is deep. The upper and lower jaws are short, the latter being shorter or equal to the upper jaw, when the mouth is closed. The oral gape is relatively small and inferior. The mouth has thin lips, the lower one interrupted. The barbels are longer than average (ABL≈ED). The lateral scale count is relatively high (33-37), as is the number of scales from the dorsal and ventral fins to the lateral line (5.5-7, and 3-4 respectively).
Colouration.- Live specimens are dark green (often with a golden sheen) on the sides, with yellowish green or yellow ventral parts, and a very dark sea-green back. The fins are dark green. In alcohol the dark colour, with the slightly darker back can still be observed, the basic colour being dark green-brown.
Size range.- Specimens from 107 to 430 mm FL have been observed.
Distribution, habitat and ecology.- *B. surkis* has been described not only from Lake Tana, but also from the Didessa River (Ethiopia)(Boulenger 1907: 227). However, we have indications that all Lake Tana *Barbus* species originated within the lake and form a species flock (Nagelkerke et al. 1994, 1995*b*, 1996). The occurrence of *B. surkis* outside Lake Tana would suggest dispersion after the species originated in the lake, or a parallel development in separate *Barbus* populations (cf. *B. nedgia*). In Lake Tana, *B. surkis* occurs over muddy, sandy and rocky substrates all over the lake, preferably in water of no more than 3 m deep. Based on the contents of 64 intestines, *B. surkis* is a real macrophytivore. Specimens smaller than 15 cm FL do not eat a lot of plant material yet, but mainly feed on zooplankton and insect larvae. The amount of insect larvae and zooplankton

decreases with fish size, while macrophytes increase in importance, finally making up most of this species' diet.

B. truttiformis spec. nov
(fig. 5.19)

'Troutlike': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 338 mm SL, RMNH 32990, Wanzaie (locality 30), Gumara River, tributary of Lake Tana, Ethiopia, 15.ix.1994, L.A.J. Nagelkerke & F.A. Sibbing; paratypes (9), 266-344 mm, RMNH 32991-32999, localities 11, 18, 21, 29, and 30, Lake Tana, Ethiopia, 15.xi.1990 - 12.x.1995, J.G.M. van den Boogaart, A.B. van den Burg, S.P.L.M. van Gaans, M.H. Helmes, S. Kranenbarg, E.H.R.R. Lammens, L.A.J. Nagelkerke, F.A. Sibbing & G.M.J. van Snik.

Etymology.- The name is derived from the the Latin 'trutta' (trout) and 'forma' (form), referring to the troutlike appearance of this species.

Description.- Based on the holotype and paratypes, 266-344 mm SL (Table 5.5).
Habitus and diagnosis.- A medium-sized (maximally 442 mm FL), wide-bodied species of average depth (BD≈HL), sometimes with a very slight nuchal hump (in larger specimens). The head is shorter than average, wide, and of average depth, with an averagely long and relatively wide snout. The head inclination is average (≈ 20°), with a straight to concave dorsal profile. The eyes are relatively small, with an average interorbital width. The operculum depth is average. The upper and lower jaws are of average length . The lower jaw is at least as long as the upper jaw, and often extends (especially in larger specimens) when the mouth is closed. The oral gape is relatively large and (sub)terminal, with a very short upper jaw protrusion. The mouth has thin lips, the lower one is interrupted. The barbels are short and thin (ABL<ED). The lateral scale count is high (32-38), as is the number of scales from the dorsal fin to the lateral line (5.5-7).
Coloration.- Live specimens are silvery, with a yellowish, or brownish sheen, with a whitish belly. The back is slightly darker: brownish or greenish. The fins are whitish, often with a pinkish tinge. In alcohol the light colour, with the slightly darker back can still be observed, the basic colour being yellowish brown.
Size range.- Specimens from 104 to 442 mm FL have been observed.
Distribution, habitat and ecology.- *B. truttiformis* is only known from Lake Tana and its tributaries. It occurs mainly over rocky substrates all over the lake (but never very abundant), both in shallow and deep water. Based on the contents of 16 intestines, *B. truttiformis* is mainly piscivorous. Smaller specimens also eat considerable amounts of insects, but the larger ones almost completely switch to fish.

B. tsanensis spec. nov.
(fig. 5.20)

'Intermedius': Nagelkerke et al., 1994: table 1, fig.3.

Material.- Holotype, 250 mm SL, RMNH 33000, Blue Nile (locality 13), Lake Tana, Ethiopia, 8.x.1993, S.P.L.M. van Gaans & L.A.J. Nagelkerke; paratypes (9), 198-294 mm, RMNH 33001-33009, localities 1, 4, 5, 8, 11, and 13, Lake Tana, Ethiopia, 21.i.1993 - 8.x.1993, S.P.L.M. van Gaans & L.A.J. Nagelkerke.

Etymology.- 'tsanensis' is the latinized genitive case of tsana, the name which is also used for Lake Tana, distinguishing it from the Tana river in Kenya. The name refers to the abundance of this species in Lake Tana.

Description.- Based on the holotype and paratypes, 198-294 mm SL (Table 5.5).
Habitus and diagnosis.- A small to medium-sized (maximally 394 mm FL), deep-bodied (BD>HL) species, sometimes with a slight nuchal hump (in larger specimens). The head is relatively short, deep, and wide, with an averagely long, relatively wide snout. The head inclination is relatively large (> 20°), with a slightly convex to slightly concave dorsal profile. The eyes are of average size, with a larger than average interorbital width. The operculum is averagely deep. The upper and lower jaws are shorter than average, with the latter being shorter than the upper jaw, when the mouth is closed. The oral gape is smaller than average and inferior, with a large upper jaw protrusion. The mouth has thin lips, the lower one usually interrupted. The barbels are relatively long (ABL≥ED). The lateral scale count is low (29-32), as is the number of scales from the anal fin to the lateral line (3-4).
Coloration.- Live specimens are silvery white with a grey back, sometimes with a greenish or brown sheen. The fins are whitish, often the pectoral, and sometimes the dorsal and caudal fins are tinged pink or red at their bases. In alcohol the ground colour is yellowish brown: slightly darker on the back than on the sides.
Size range.- Specimens from 52 to 394 mm FL have been observed.
Distribution, habitat and ecology.- *B. tsanensis* is only known from Lake Tana. It occurs over muddy, sandy and rocky substrates all over the lake, preferably in water deeper than 6 m. Based on the contents of 166 intestines, *B. tsanensis* is a real benthivore. Specimens smaller than 10 cm FL already mainly eat insect larvae, although zooplankton and ostracods also are important food items. With size increase, insect larvae remain the most abundant food items, but adult insects, molluscs and detritus also become important.

Key to the 'large' Lake Tana *Barbus* (*Labeobarbus*) species

For rapid identification in the field we suggest using the photographs and characters as summarized in Nagelkerke et al. (1994, 1995*b*), referring to the initial morphotypes and comparing the morphotype name with Table 5.4 of this paper.

This key is designed for accurate identification of an estimated 90-95% of the barb specimens larger than 15 cm SL, caught from the deep water (> 6 m). Catches from the shore areas may include the variable 'shore-complex', to which *B. intermedius* Rüppell belongs. This species is excluded from this key (cf. Discussion). Note that barbel lengths are for fresh specimens; they can be shorter in preserved specimens, complicating use of this key.

1. Lower lip forming a distinct median lobe (LLD≥3); upper lip well developed, often with a median fleshy lobe (DLD ≥3); if lobes are absent, often a fleshy 'nose' is present; operculum depth about as large as (0.9 to 1.1 times) ventral cheek length; head length less than 1.2 times in body depth — *B. nedgia*
   - Lower lip interrupted or continuous, but not forming a distinct median lobe (LLD≤2); upper lip always without lobes (DLD≤3); (in few cases a small lobe can be present [LLD=3], but then the operculum depth is clearly smaller than ventral cheek length , and head length is at least 1.2 times body depth: *B.dainellii*, see 6.) — 2

2. Head length shorter than body depth; upper and lower lips thin (DLD≤2 and LLD≤2); inferior mouth with downward protrusion ; lower jaw does not extend anteriorly of the upper jaw (ExLJ≤3); eye diameter more than 1.1 times in interorbital width; anterior barbel length less than 2 times in gape width — 3
   - Not showing the above combination of characters — 6

3. Eye diameter at least 1.6 times in snout length and interorbital width; anterior barbel longer than 1.1 times eye diameter; golden yellowish; heavy pharyngeal bones, with large crushing teeth; often a large anal opening — *B. gorgorensis*
   - Eye diameter less than 2 times in snout length and interorbital width; anterior barbel length less than 1.3 times in eye diameter; silvery, or light or dark green — 4

4. Head length less than 4.2 times in standard length; head longer than pectoral-ventral length; anal fin length less than 0.75 times in head length; lower lobe of caudal fin less than 1.25 times in head length; eye diameter at least 5 times in head length; maximally 32 scales on lateral line; silvery — *B.tsanensis*
   - Head length more than 4.2 times in standard length; head shorter than pectoral-ventral length; anal fin length more than 0.75 times in head length; lower lobe of caudal fin more than 1.25 times in head length; eye diameter less than 5 times in head length; maximally 38 scales on lateral line; light or dark green — 5

5. Head width less than 1.8 times in head length; head length more than 1.3 times in body depth; body depth less than 3.6 times in standard length; eye diameter more than 1.3 times in inteorbital width; dark green; often with an extended, soft abdomen — *B. surkis*
   -Head width more than 1.8 times in head length; head length less than 1.3 times in body depth; body depth more than 3.6 times in standard length; eye diameter less than 1.6 times in interorbital width; standard length usually less than 25 cm; body spindle-shaped; light yellowish green — *B. brevicephalus*

6. Lower jaw falls inside upper jaw by at least the thickness of the lower lip (ExLJ=1); lower and upper lip well developed (LLD and DLD≥2); head length less than 3.5 times in standard length; body depth at least 1.2 times in head length; no clear nuchal hump; eye diameter at least 2 times in snout length — *B. dainellii*
   - Not showing the above combination of characters — 7

7.	Eye diameter less than 1.5 times in snout length, less than 1.1 times in interorbital width, and less than 5 times in head length; head length the same as body depth (HL is 0.9 to 1.1 times BD); lower and upper jaw close equally or lower jaw extends anteriorly from the upper jaw (ExLJ≥3); usually a well developed nuchal hump (Nhu≥3)	*B. macrophtalmus*
	- Not showing the above combination of characters	8
8.	Snout width more than 4 times in head length; interorbital width more than 2 times in head width; head depth more than 1.8 times in head length; operculum depth more than 3.4 times in head length; silvery white	*B. acutirostris*
	- Snout width less than 4 times in head length; interorbital width less than 2 times in head width; head depth less than 1.8 times in head length; operculum depth less than 3.4 times in head length	9
9.	Nuchal hump present (Nhu≥3)	10
	- No clear nuchal hump (Nhu≤2)	12
10.	Lower jaw extending anteriorly of the upper jaw by at least the thickness of the upper lip (ExLJ=4); upper jaw length more than 1.3 times in lower jaw	*B. megastoma*
	- Lower jaw and upper jaw close equally, or lower jaw extends slightly anteriorly or falls inside upper jaw (2 ≤ExLJ≤3.5); upper jaw length less than 1.3 times in lower jaw	11
11.	Body depth at least 1.1 times in head length; ventral fin length at least 1.7 times in head length; nuchal hump steeply rising at occiput; black, blackish red, dark brown or dark green	*B. gorguari*
	- Body depth 1 to 1.1 times in head length; ventral fin length less than 1.7 times in head length; nuchal hump starts gradually at occiput; silvery white	*B. platydorsus*
12.	Anterior barbels very thick and dark, length less than 5.5 times in head length, less than 2 times in gape height, longer than eye diameter; oral gape inferior; dorsal head profile irregular, convex caudally and with a 'bump' caused by the premaxillaries	*B. crassibarbis*
	- Anterior barbels thin, length more than 5.5 times in head length, more than 2 times in gape height, shorter than eye diameter; oral gape terminal; dorsal head profile without premaxillary 'bump'	13
13	Very slender build: head length longer than body depth; body depth more than 4 times in standard length; ventral fin length more than 1.8 times in head length; eye diameter more than 2 times in snout length, more than 1.8 times in interorbital width; greenish or greenish grey	*B. longissimus*
	- Rather deep-bodied: head length shorter or equal to body depth (HL is 0.9 to 1 times BD); body depth less than 4 times in standard length; ventral fin length less than 1.7 times in head length; eye diameter less than 2.2 times in snout length, less than 2 times in interorbital width; silvery or yellowish	*B. truttiformis*

DISCUSSION

What are the criteria for species distinction? The essential criterion for the 'biological species' is genetic isolation under natural circumstances (Mayr 1942). In practice this definition is very difficult to work with (Løvtrup 1987, Mina 1992, Witte & Witte-Maas 1987), as it requires extensive field observations of the (sympatric) organisms in question. Mina (1992: 33) used the term 'taxonomic species' for species that are distinguished by their phenotype only. A taxonomic species may or may not coincide with a biological species. Usually this cannot even be tested, as the biological species concept is not operational when groups of allopatric individuals are compared. Mina takes a pragmatic view, considering the distinction of taxonomic species primarily as a tool to get a grip on organismal diversity, and accepts that classifications of taxonomic species are not final.

Male colouration rather than morphological difference is often considered to be of great importance for species distinction (in e.g. some haplochromine cichlids van Oijen et al. 1981, Witte & Witte-Maas 1981, 1987, Goldschmidt & Witte 1990), because of its role in the specific mate recognition system (Greenwood, 1974). In this way the 'taxonomic' and 'biological'species concepts are integrated.

In the case of the Lake Tana barbs we have long avoided referring to species and used the term morphotype (Nagelkerke et al. 1994, 1995*a*, 1995*b*, 1996, Sibbing et al. 1994), because of the uncertainties about their reproductive segregation, caused by: (1) the impossibility to observe the barbs in the turbid (Secchi-depth < 1m) Lake Tana water, (2) the inability to study their breeding behaviour in laboratory conditions (partly because of their large size), and (3) the absence of sexual dimorphism and breeding colours.

However, the growing body of evidence from morphological, ontogenetic, ecological, genetic, and spawning data strongly suggests that the morphotypes behave as biological species (see Introduction). Actually, more and better evidence for the validity of their species status is present than in many other cases. A pragmatic reason to elevate the morphotypes to species rank is that only (sub)species names are scientifically valid, providing the proper reference for the description of the *Barbus* diversity of Lake Tana.

In a previous paper (Nagelkerke et al. 1995*b*) we showed that for 11 of the 14 species juveniles (less than 10 cm fork length) could be distinguished, which we considered a strong argument for the validity of the species distinction. No juveniles of the other three species (*B. gorgorensis*, *B. longissimus*, and *B. truttiformis*) were caught by that time. Since then small specimens of *B. truttiformis* (c. 10 cm FL) have been caught, while juveniles of the other two species are still absent from the collection. However, because of their specific morphologies and ecological characters we also consider these three morphotypes as 'good' species.

'Missing' and new *Barbus* species

Species that are described from Lake Tana by previous authors, but which we did not find in the lake are called 'missing'. The most conspicuous 'missing' species is *B. intermedius*. Unfortunately we initially called the most abundant morphotype 'Intermedius', because we expected it to be synonymous to *B. intermedius* Rüppell, 1836. After studying the holotype of this species, which has a generalized *Barbus* shape and 'intermediate' characters (explaining the name Rüppell gave it), we concluded that *B. intermedius* is not synonymous to our 'Intermedius' morphotype (which is described as *B. tsanensis* spec.nov. in this paper), but belongs to the variable group of barbs, mainly found in the shore area. We suspect these shore-barbs to be very close to the ancestor of the Lake Tana barbs and therefore to the riverine barbs from the Ethiopian high plateau (Nagelkerke et al. 1995*b*, 1996). This variable group (the 'shore-complex') also posed problems for the previous authors. This is especially clear when reading Bini's (1940) (sub)species descriptions, who explicitly states the problems he had using Boulenger's (1902, 1911) descriptions. Bini described *B. intermedius* Rüppell, *B. affinis* Rüppell, *B. duchesnii* Boulenger and *B. platystomus* Boulenger with 4, 3, 3, and 5 (usually ill-defined) subspecies respectively. He even re-used the names and descriptions of *B. brevibarbis* Boulenger and *B. leptosoma* Boulenger to define some of his subspecies. Most probably Bini described fishes from the (easily accessible) 'shore-complex' and tried to deal with the variability he found by describing many (sub)species. His inclusion of *B. ilgi* Pellegrin in the Lake Tana ichthyofauna can be interpreted in the same way. In conclusion, 'missing' *Barbus* species can be explained by previous descriptions of the variable 'shore-complex'. The holotype of *B. intermedius* Rüppell is part of this group, and therefore the 'shore-complex' might be synonymous with this species. However, we do not know whether the whole 'shore-complex' belongs to *B. intermedius* or that also other variable species are present.

We have described seven new species. There are several probable reasons why previous authors have not described these fishes. The first is that they have only collected small numbers of fishes, compared to the numbers in this study (there are c. 2,000 specimens in our collection and an estimated 40,000 have been handled). This would explain the absence of descriptions of rare species such as *B. truttiformis* and *B. longissimus*. Another reason can be that only recently (since the start of the fishery project in Bahar Dar in 1986) fishermen use motorized boats and shoot their nets in deep water, far from the shore, where typical deep water species such as *B. crassibarbis*, *B. platydorsus* , and *B. tsanensis* are found.

We have found three to four additional *Barbus* morphotypes in Lake Tana, that could also represent new species. We did not include them in this study, as they could not be studied in sufficient numbers yet. The most remarkable of them has a narrow, tweezer-like lower jaw, slightly reminding of the genus *Mandibulacra* Herre 1924 from Lake Lanao, which shows remarkable similarities with Lake Tana (Nagelkerke et al. 1994, Mina et al. 1996).

The status of the subgenus *Barbus* (*Labeobarbus*)

As with the description of species, there are both biological and pragmatic reasons for the assignment of genus names to a subgeneric group. The 'large', hexaploid African barbs have recently been described as a monophyletic group (Berrebi 1995) that are probably more closely related to other hexaploid genera such as *Varicorhinus* than to the European barbs. The genus *Barbus* is most probably paraphyletic and so large (c. 800 species) that it is hardly meaningful anymore to assign a species to this genus. Therefore we propose to reelevate the subgenus *Barbus (Labeobarbus)* Rüppell 1836, as discussed by Berrebi (1995) to full generic rank, i.e. to *Labeobarbus* Rüppell 1836.

Concluding remarks

The study of the evolutionary mechanisms producing the unique *Barbus* species flock of Lake Tana not only requires insight into the taxonomic and phylogenetic relations within this group, but also into the ecological relations over time and space. Species distinction is the first step in this integrated approach. Besides its scientific significance, species distinction is also crucial for identifying the exploited fish stocks. Monitoring the effects of fisheries on the species and size composition of the fish stocks (e.g. by catch-effort recording) can help in developing a rational management of fisheries, which is a prerequisite for sustainable fisheries, protecting biodiversity as much as posible (Sibbing et al. 1994) .

We do not expect our species distinctions to be final. It is evident from this, and our previous studies (Nagelkerke et al. 1994, 1995*b*, 1996, Sibbing et al. 1994), however, that species cannot be described from museum collections alone (at least for some groups of organisms, such as the large African barbs). It is essential to understand at least something of the biology and environment of these organisms. The local population structure, the relative numbers of discrete morphs and intermediates, the distribution during spawning, all these factors provide essential information on the biology and therefore on the taxonomic status and evolution of these organisms. To obtain this information considerable time in the field has to be spent (Nagelkerke et al. 1994), or, to put it in other words, researchers have to become intimately involved with their study organisms (Cresko & Baker 1996). This suggests that biologically meaningful species descriptions will take considerably more time than presently usual. The description and explanation of the rapidly diminishing biodiversity in poorly studied (tropical) areas, and the development of strategies to conserve it are hampered by this phenomenon.

ACKNOWLEDGEMENTS

We would like to thank D.J. Siebert, F. Krupp and S.M. Wernet, and G. Duhamel for the opportunity they gave us to study the specimens from the Natural History Museum, the Senckenberg Museum and the Musée nationale d'Histoire Naturelle. P.G. Bianco is acknowledged for his efforts in tracing Bini's collection and M.V. Mina for stimulating discussions. W.N. Eschmeyer checked whether the new species names were available; Martien v. Oijen helped us with the taxonomic methodology. Heleen Zwennes is much acknowledged for making the drawings of the *Barbus* specimens. The Bureau of Agriculture of the Amhara National Regional State in Bahar Dar (especially Dr. Belay Demisse and Mr. Girma Mengistu) and the Fisheries Resources Development Department of the Ministry of Agriculture in Addis Ababa (Mr. Tarekegn Mengistu, Ms. Mebrat Alem and Mr. Tesfaye Wudneh) are acknowledged for their continuing support in implementing the project in Ethiopia. The students Geert van Snik, Michiel Helmes, Hans van Oostenbrugge, Arnold van den Burg and Sander Kranenbarg contributed in the collection. Suzanne van Gaans is acknowledged for help and support in fishing, administration and social aspects during the field work. Special thanks goes to Asfaw Berhe, who helped greatly with the field work, but we are especially grateful for his friendship. Unfortunately he is not with us anymore.

This research was funded by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W 88-176, the Interchurch Foundation Ethiopia (ISE, Urk) and the Interchurch Coordination Commission of Development Projects (ICCO, Zeist).

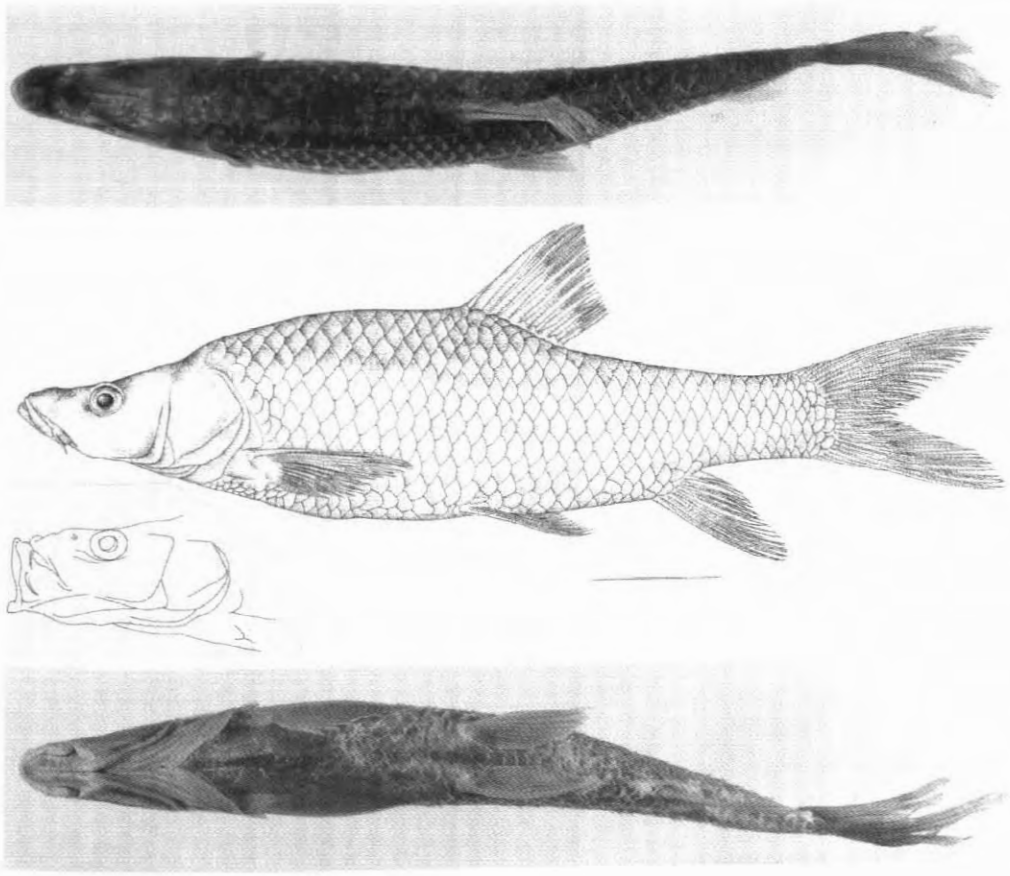


Fig. 5.4. *Barbus acutirostris* Bini. Neotype, RMNH 32870, SL 327 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

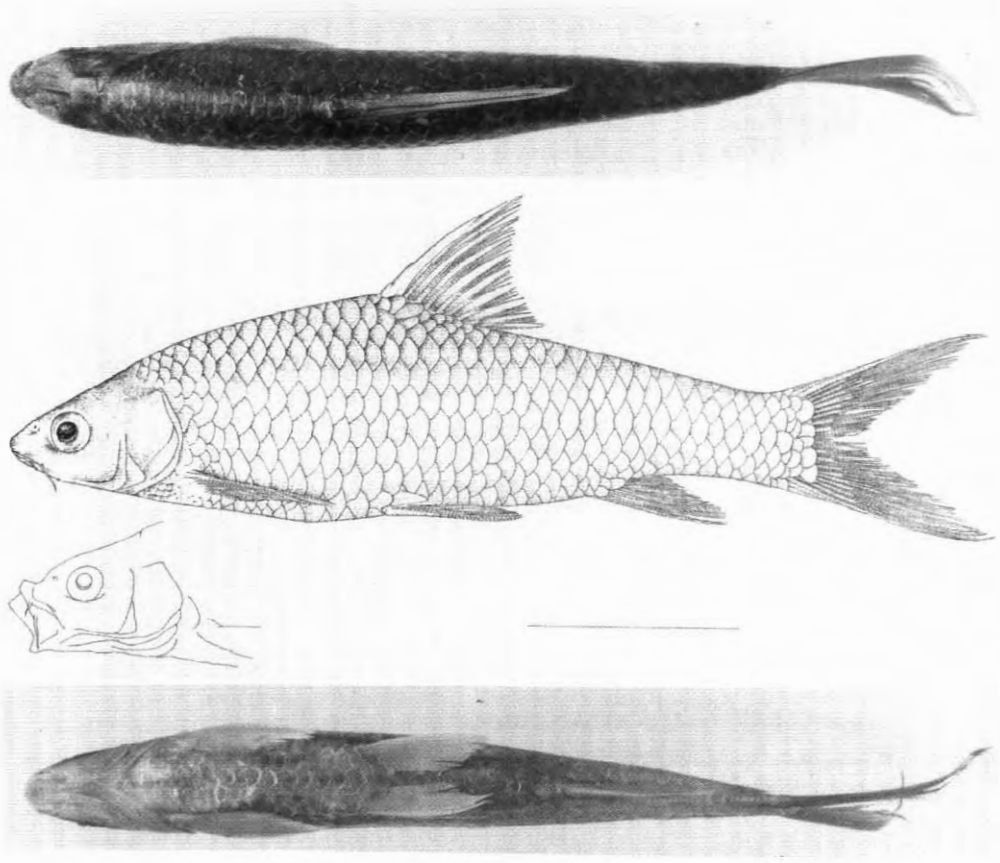


Fig. 5.5. *Barbus brevicephalus* spec. nov. Holotype, RMNH 32880, SL 185 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

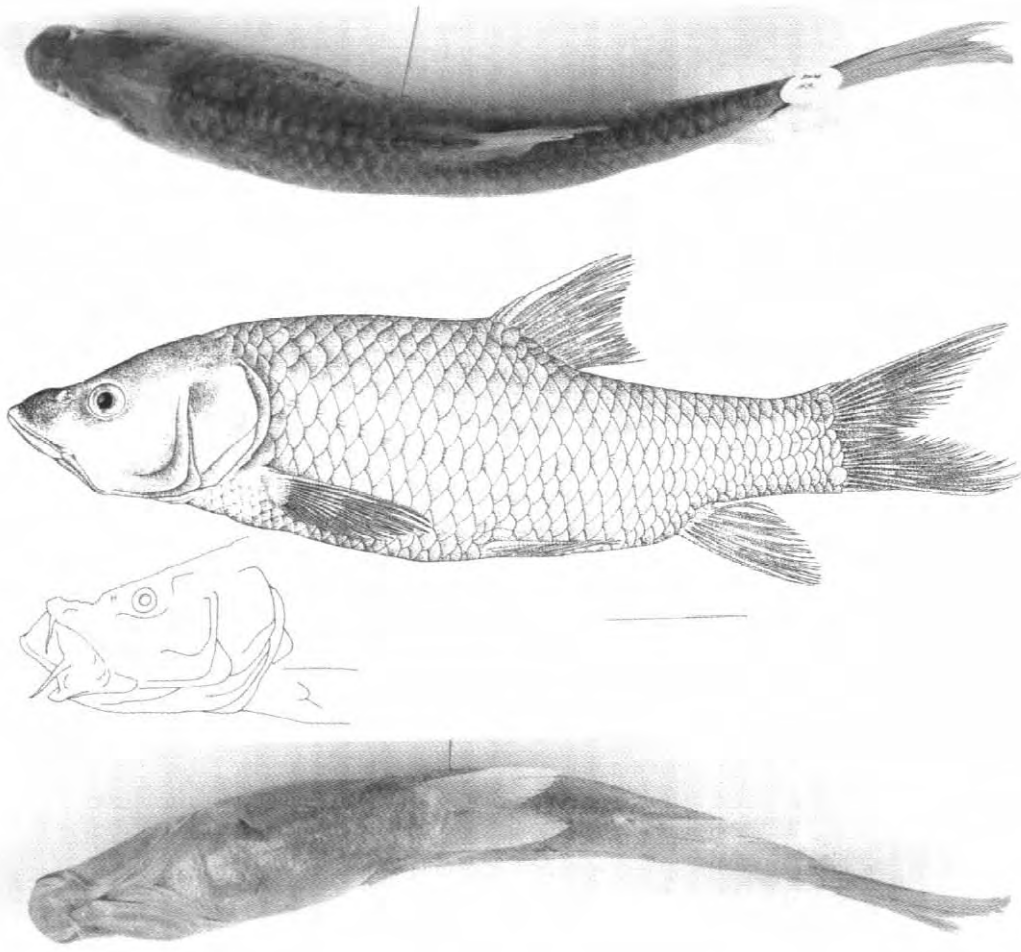


Fig. 5.6. *Barbus crassibarbis* spec. nov. Holotype, RMNH 32890, SL 295 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

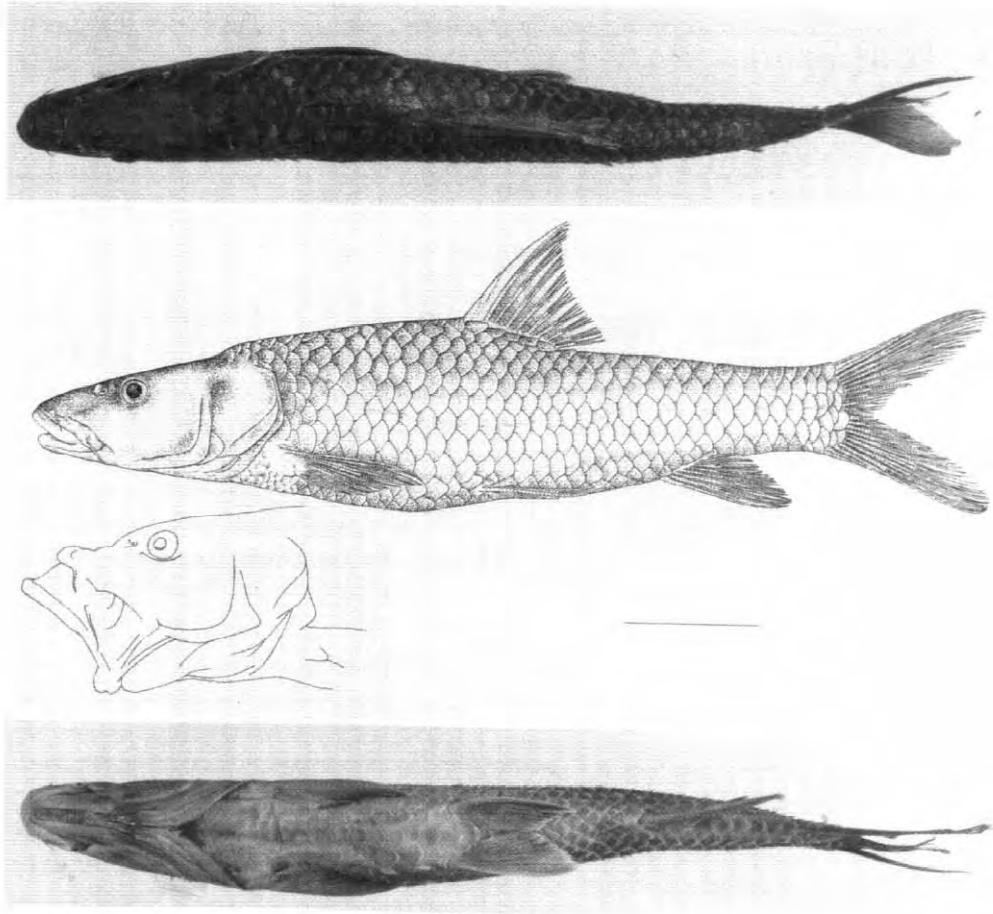


Fig. 5.7. *Barbus dainellii* Bini. Neotype, RMNH 32900, SL 308 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

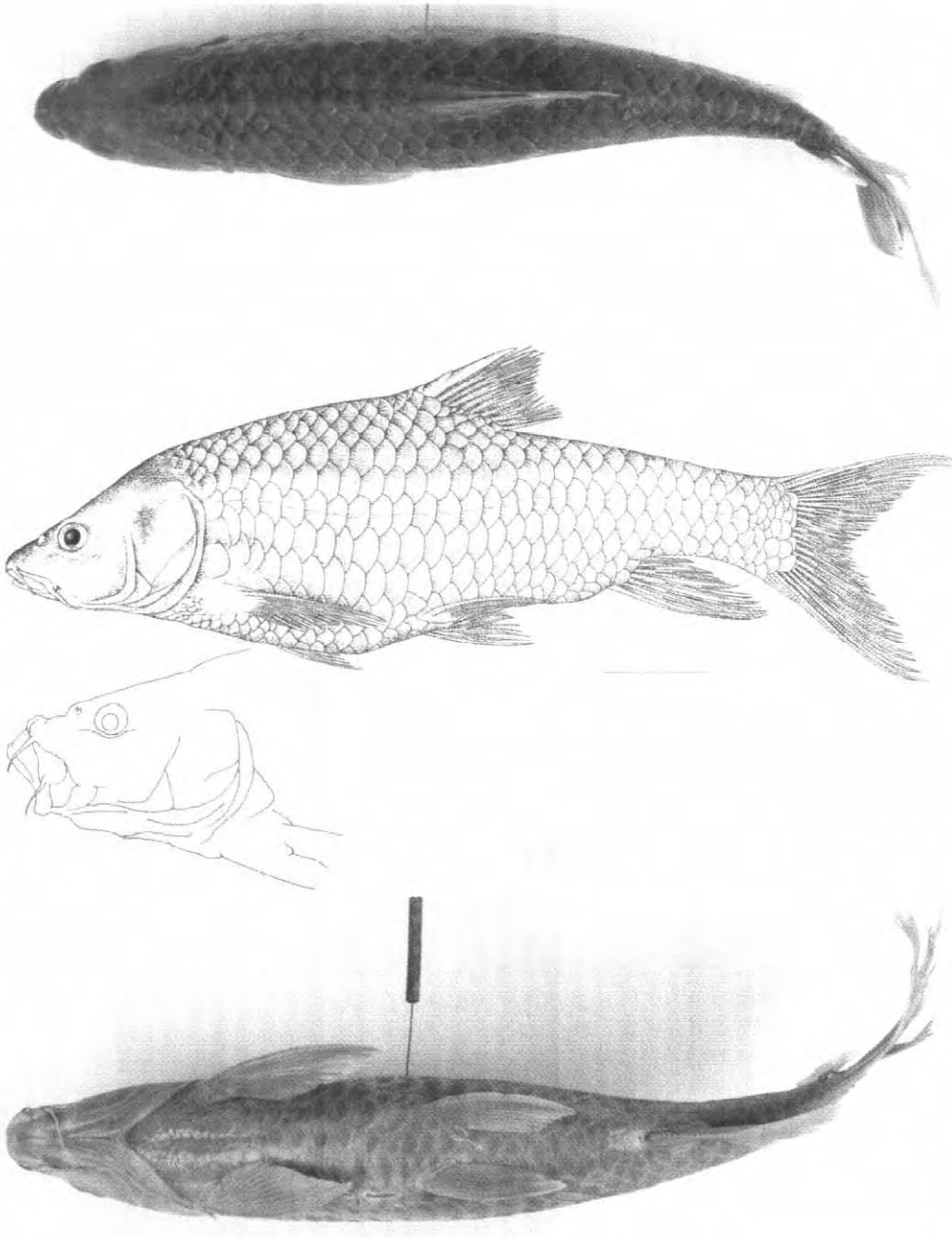


Fig. 5.8. *Barbus gorgorensis* Bini. Neotype, RMNH 32910, SL 379 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

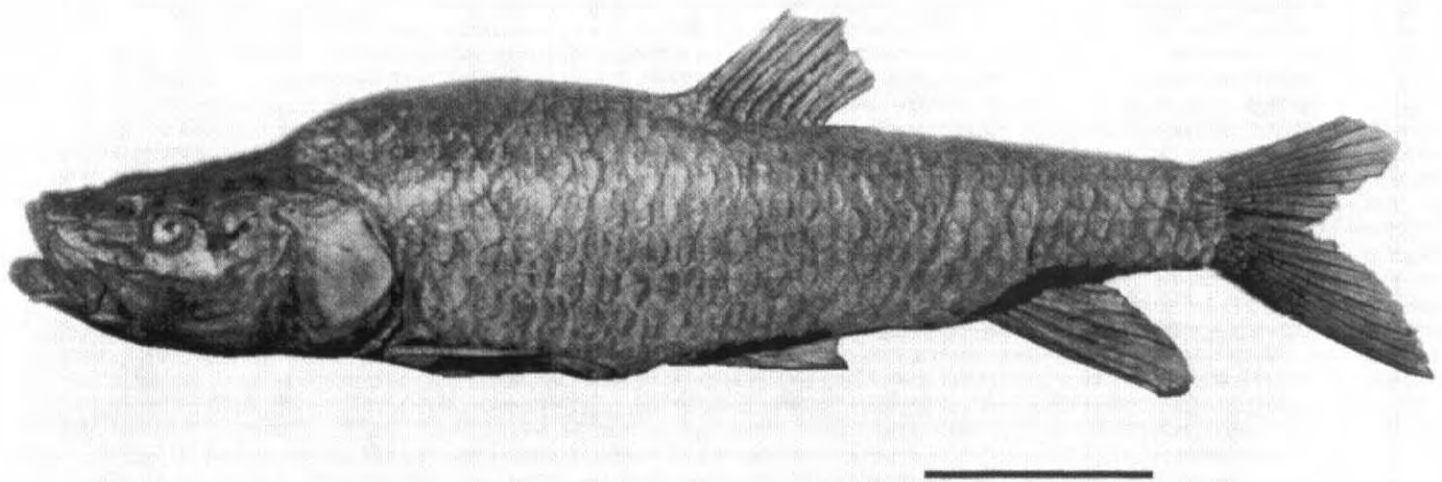


Fig. 5.9. *Barbus gorguari* Rüppell. Holotype, SMF 2586, SL 399 mm, lateral view. Scale equals 50 mm.

Fig. 5.10. *Barbus gorguari* Rüppell. RMNH 32920, SL 395 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

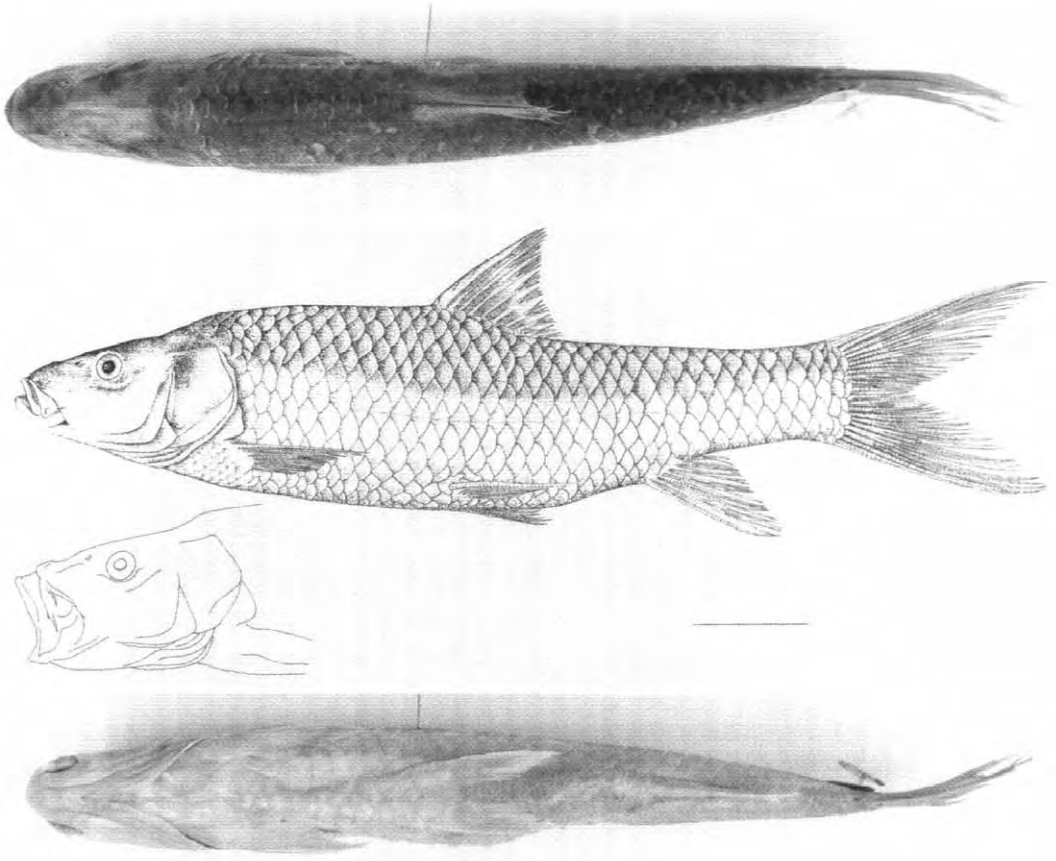


Fig. 5.11. *Barbus longissimus* spec. nov. Holotype, RMNH 32930, SL 373 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

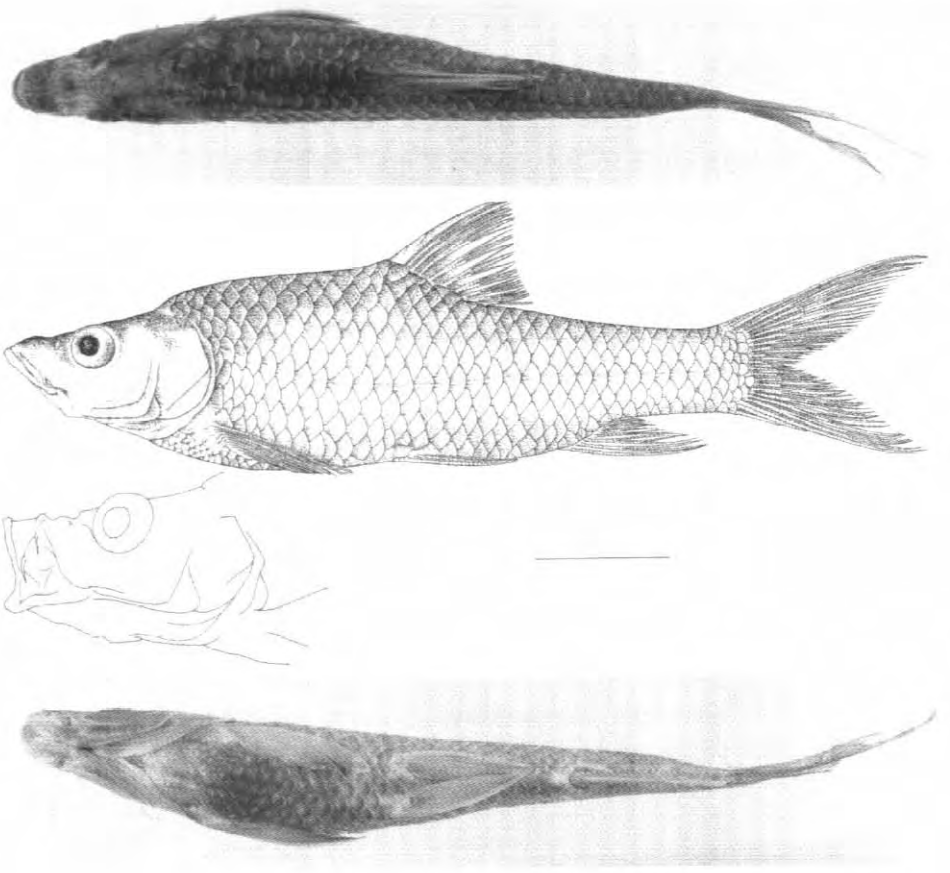


Fig. 5.12. *Barbus macrophtalmus* Bini. Neotype, RMNH 32940, SL 282 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

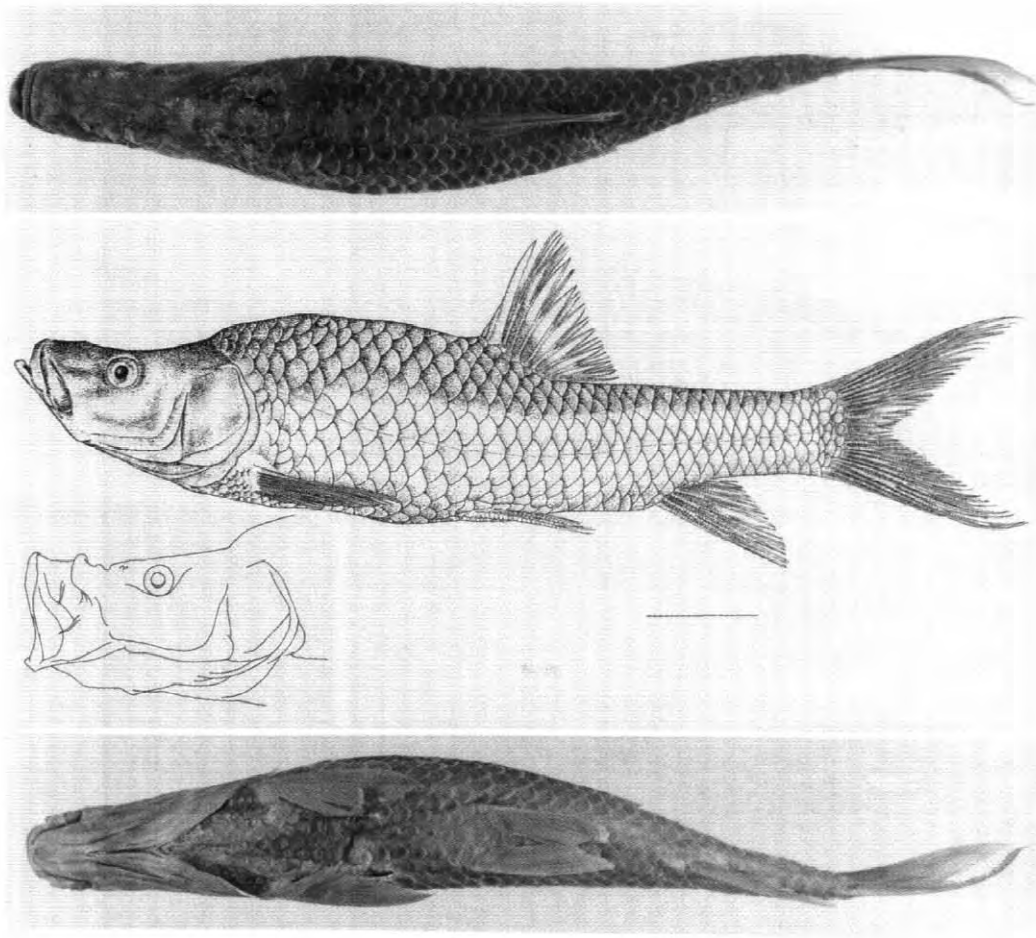


Fig. 5.13. *Barbus megastoma* spec. nov. Holotype, RMNH 32950, SL 402 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

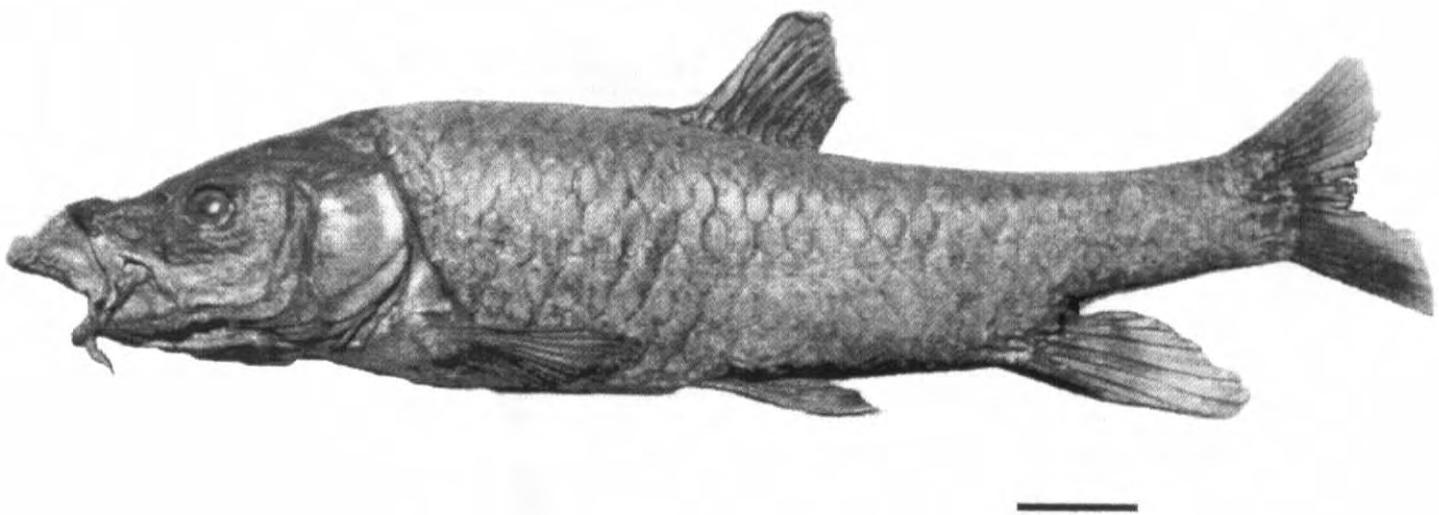


Fig. 5.14. *Barbus nedgia* (Rüppell). Holotype, SMF 2619, SL 480 mm, lateral view. Scale equals 50 mm.

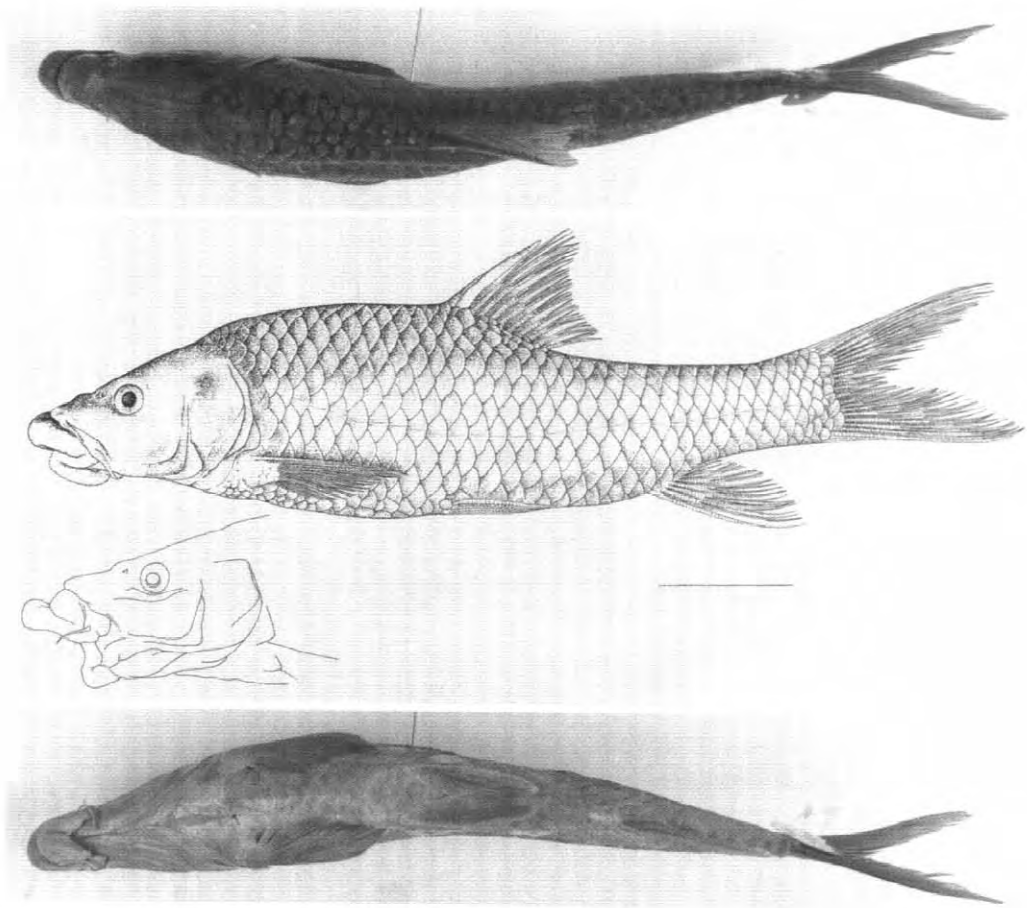


Fig. 5.15. *Barbus nedgia* (Rüppell). RMNH 32960, SL 303 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

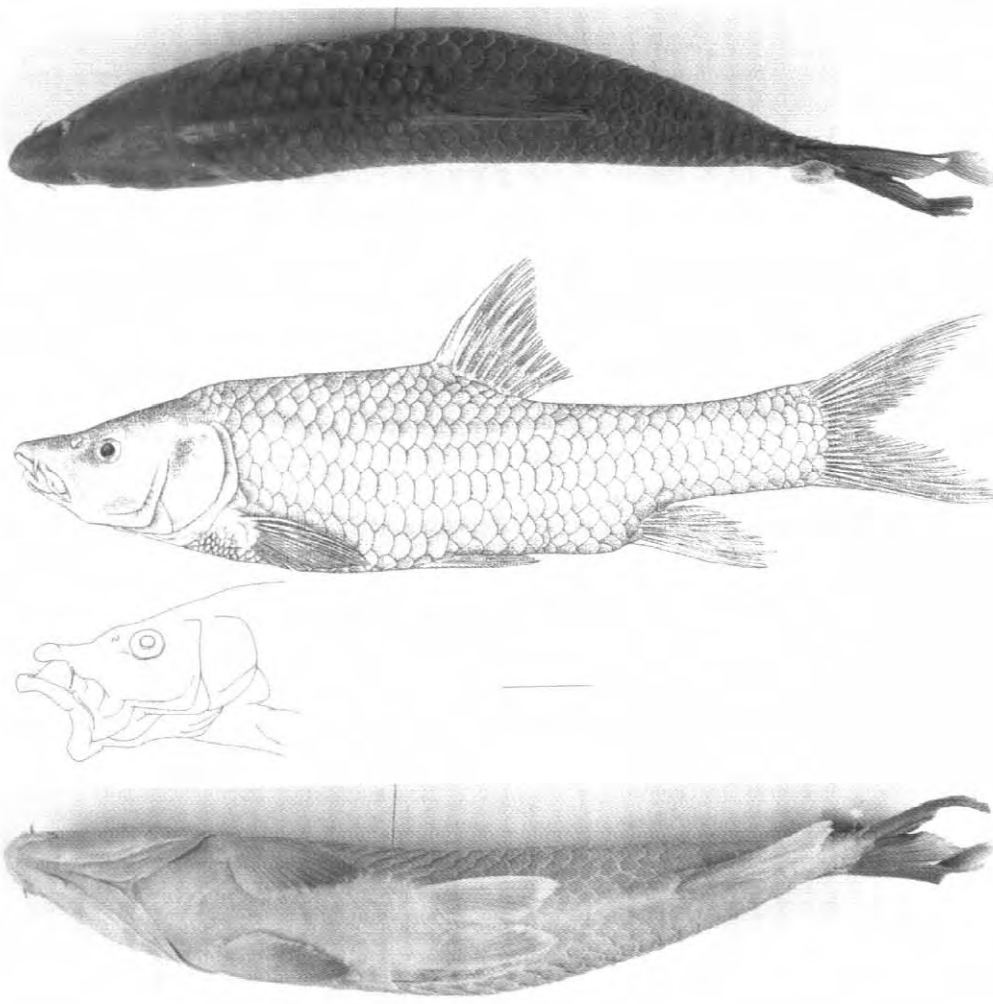


Fig. 5.16. *Barbus nedgia* (Rüppell). RMNH 32961, SL 426 mm, dorsal, lateral and ventral view. Scale equals 50 mm. This specimen resembles *Barbus degeni* Boulenger.

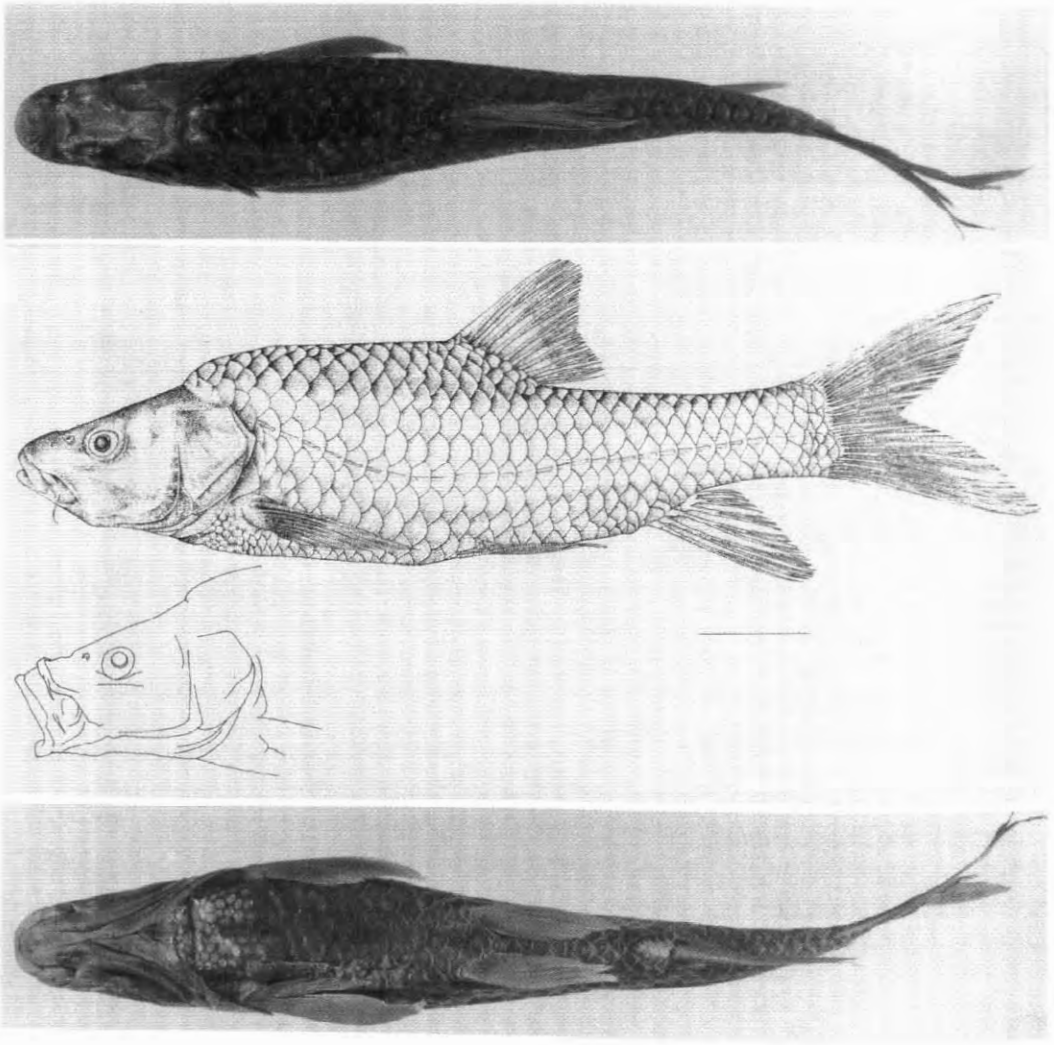


Fig. 5.17. *Barbus platydorsus* spec. nov. Holotype, RMNH 32970, SL 351 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

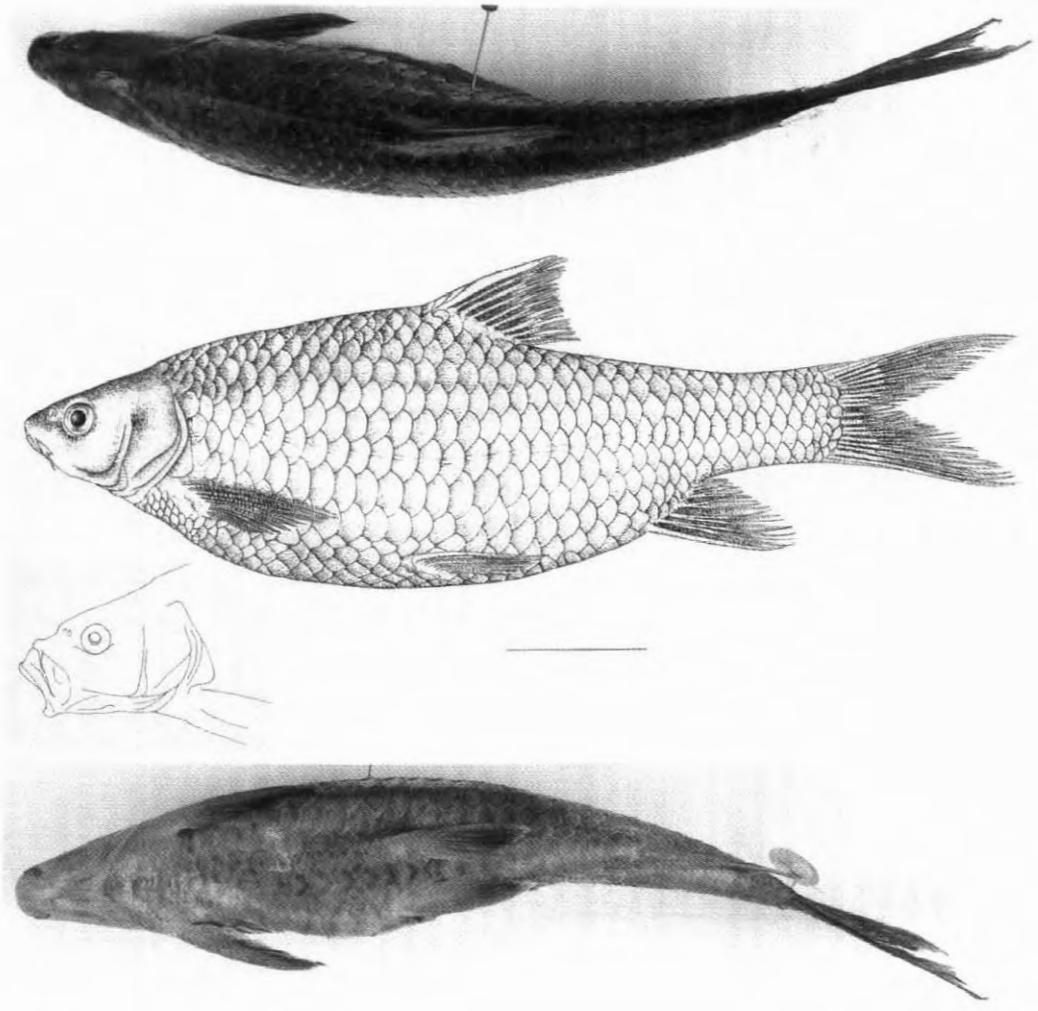


Fig. 5.18. *Barbus surkis* Rüppell. Neotype, RMNH 32980, SL 295 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

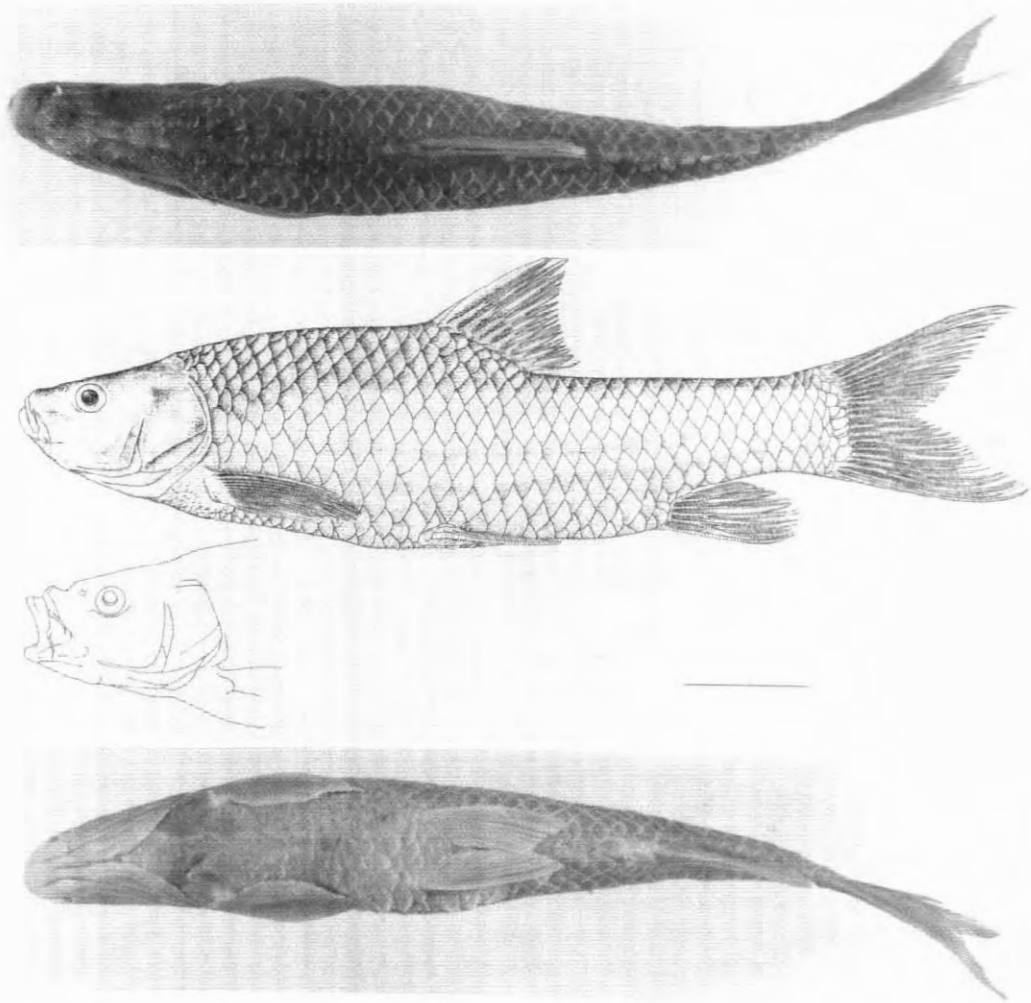


Fig. 5.19. *Barbus truttiformis* spec. nov. Holotype, RMNH 32990, SL 338 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

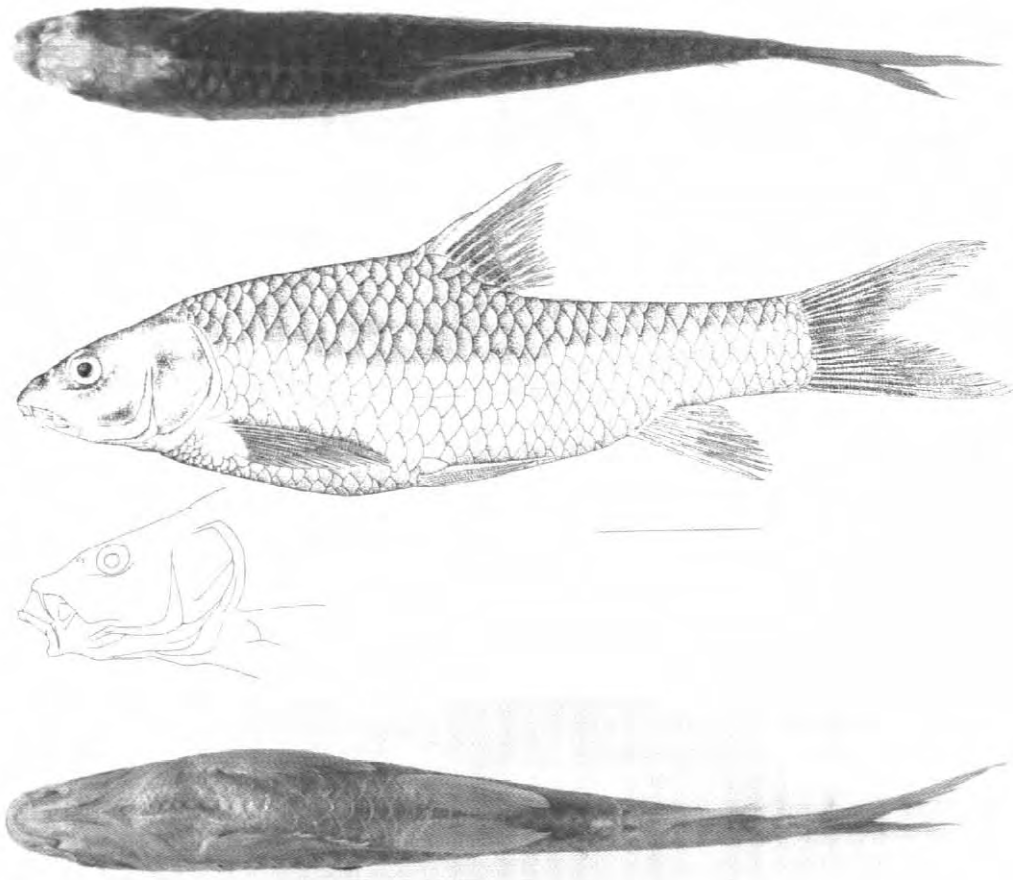


Fig. 5.20. *Barbus tsanensis* spec. nov. Holotype, RMNH 33000, SL 250 mm, dorsal, lateral and ventral view. Scale equals 50 mm.

Appendix.

Compilation of the illustrations, published by Rüppell (1836), Boulenger (1907, 1911), and Bini (1940).

Plate 1 (Rüppell 1836)

1. *B. intermedius* Rüppell, 1836
2. *B. surkis* Rüppell, 1836
3. *B. gorguari* Rüppell, 1836
4. *B. affinis* Rüppell, 1836
5. *B. elongatus* Rüppell, 1836
6. *Labeobarbus nedgia* Rüppell, 1836

Plate 2 (Boulenger 1907, 1911)

7. *B. duchesnii* Boulenger, 1902
8. *B. affinis* Rüppell, 1836
9. *B. brevibarbis* Boulenger, 1902
10. *B. leptosoma* Boulenger, 1902
11. *B. degeni* Boulenger, 1902
12. *B. nedgia* (Rüppell, 1836)
13. *B. intermedius* Rüppell, 1836
14. *B. surkis* Rüppell, 1836
15. *B. platystomus* Boulenger, 1902
16. *B. gorguari* Rüppell, 1836
17. *B. gorguari* Rüppell, 1836

Plate 3 (Bini 1940)

18. *B. affinis affinis* Rüppell, 1836
19. *B. affinis brevibarbis* (Boulenger, 1902)
20. *B. affinis nedgia* (Rüppell, 1836)
21. *B. affinis nedgia* (Rüppell, 1836)
22. *B. degeni* Boulenger, 1902
23. *B. degeni leptorhinus* Bini, 1940
24. *B. duchesnii* Boulenger, 1902
25. *B. duchesnii maximus* Bini, 1940
26. *B. duchesnii ibridus* Bini, 1940
27. *B. intermedius leptosoma* (Boulenger, 1902)
28. *B. intermedius microstoma* Bini, 1940
29. *B. intermedius gorgorensis* Bini, 1940

Plate 4 (Bini 1940)

30. *B. surkis* Rüppell, 1836
31. *B. ilgi* Pellegrin, 1905
32. *B. platystomus platystomus* Boulenger, 1902
33. *B. platystomus dagà* Bini, 1940
34. *B. platystomus dekkensis* Bini, 1940
35. *B. platystomus prognathus* Bini, 1940
36. *B. brunellii* Bini, 1940
37. *B. brunellii acutirostris* Bini, 1940
38. *B. dainellii* Bini, 1940
39. *B. dainellii* Bini, 1940
40. *B. dainellii macrocephalus* Bini, 1940
41. *B. gorguari* Rüppell, 1836
42. *B. gorguari macrophtalmus* Bini, 1940

Plate 1 (after Rüppell, 1836)

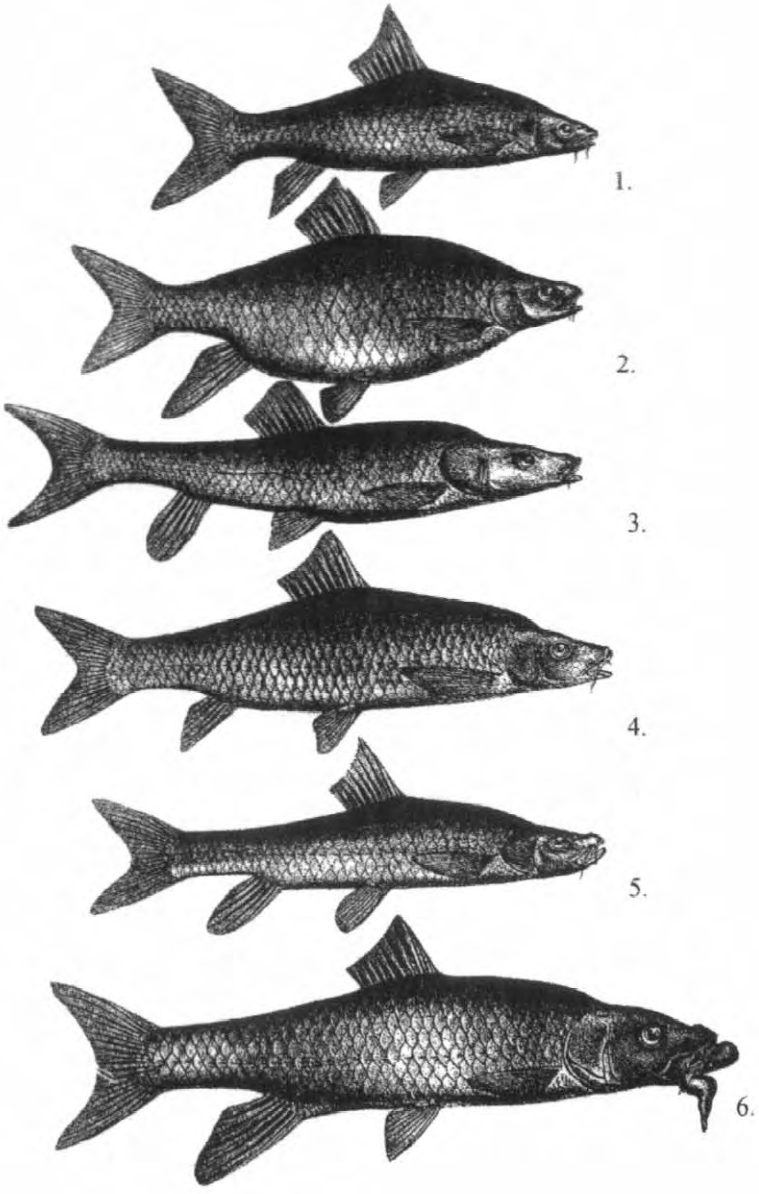


Plate 2 (after Boulenger, 1907, 1911)

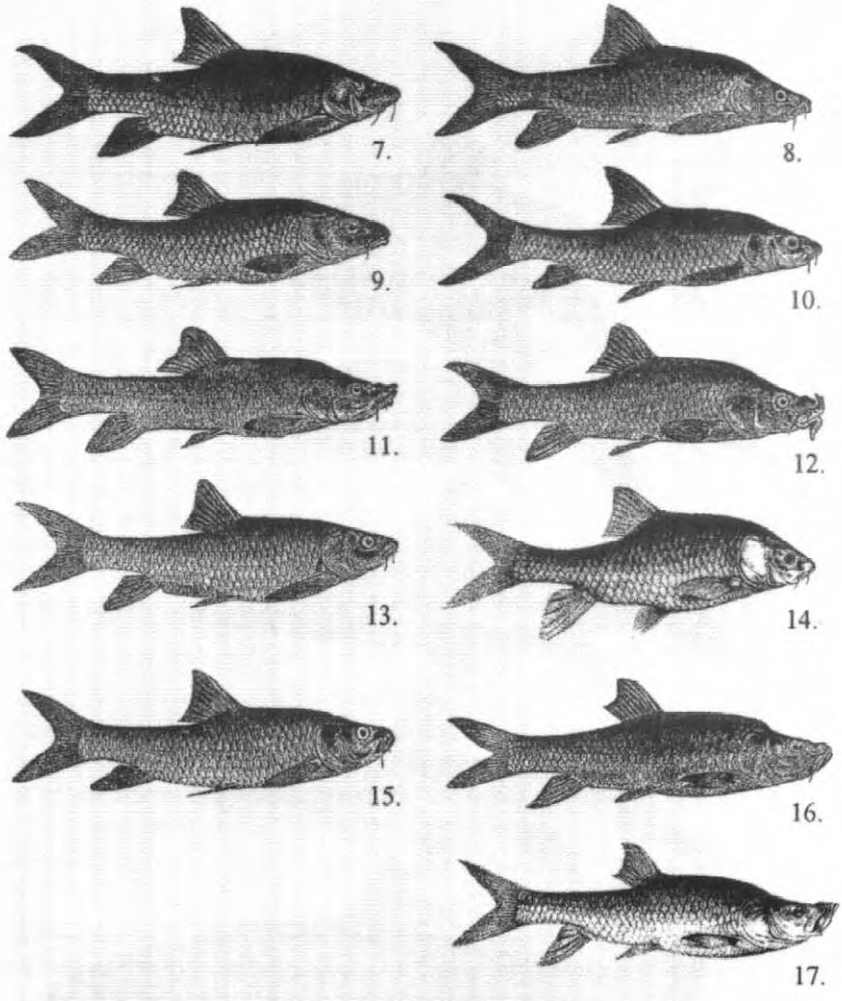


Plate 3 (after Bini, 1940)

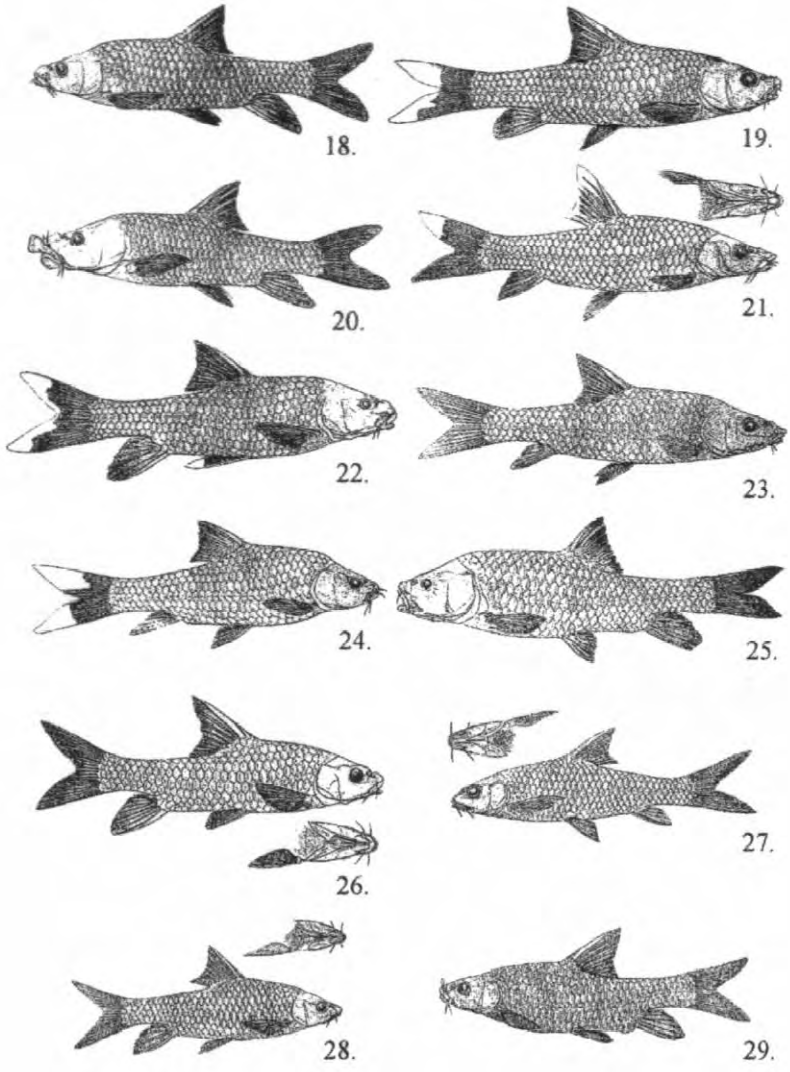
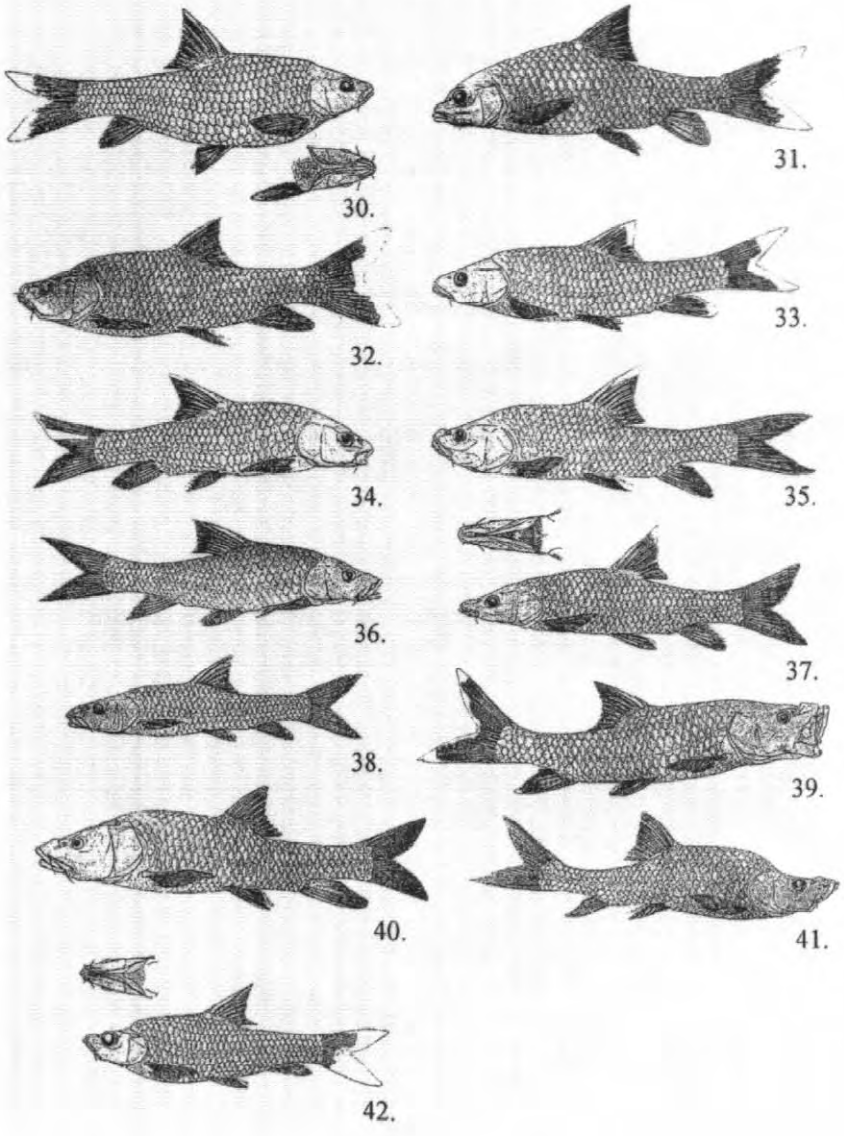


Plate 4 (after Bini, 1940)



Chapter 6

Trophic segregation within the *Barbus* species flock of Lake Tana, Ethiopia: 1. Diets predicted from food properties and fish morphology

Ferdinand A. Sibbing[1] & Leo A.J. Nagelkerke[1]

[1] *Agricultural University, Wageningen Institute of Animal Sciences (WIAS), Experimental Zoology Group, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

ABSTRACT

A food-fish model is developed relating properties of aquatic food types (size, shape, velocity, habitat, strength, compliance, fibrousness, chemical quality) to structural characters of cyprinid fish. The model is based on functional morphological principles and experiments on food detection, approach, intake, size- and taste selection, transport, mastication and digestion. It provides a set of 33 parameters which together predict foraging and food processing abilities and inabilities of fish. By the cumulative effect of the character set the food niche is gradually narrowed. The *Barbus* species flock of Lake Tana is a case study to test this model, since its structural diversity most probably reflects adaptations to (trophic) niches and not phylogenetic differences. If food types are clustered according to their compatible structural demands to fish, following the model, a food-hierarchy becomes apparent: (a) size separates micro-particles from larger items, (b) velocity divides between large evasive prey and slow or sedentary organisms, (c) habitat distinguishes pelagic from benthic prey, or between food organisms from complex environments and open water (d) mechanical properties differentiate within several benthic groups (e) chemical properties (animal versus plants) separate only at the level of subgroups. The present Lake Tana barbs are predicted to partition their resources as follows: (1) Phyto- and zooplankton are utilised best by pump filter-feeding *B. brevicephalus*. Phytoplankton best by *B. tsanensis*, zooplankton best by *B. macrophtalmus*. (2) Specialised piscivores are *B. dainellii, B. gorguari and B. longissimus.* Specific pursuit hunters are *B. acutirostris* and *B. megastoma*, a specific ambush hunter is *B. platydorsus*. (3) Detritivores also utilising insect larvae are *B. tsanensis* (also phytoplankton and molluscs) and *B. nedgia* (also phytoplankton) and *B. crassibarbis* (incl. macro-insects). (4) Seeds and molluscs are best utilised by *B. gorgorensis*. (5) Sessile algae, macrophytes and seeds will be taken by *B surkis* (6) True polyphagous barbs are *B. macrophtalmus* (best in micro-crustaceans) and *B. truttiformis* (best in macrophytes). The cyprinid food-fish model will have its highest predicting value in comparison among species and therefore in predicting resource partitioning in fish communities. However, present predictions first must be tested against intestinal contents of the above barbs.

INTRODUCTION

Feeding strategies are important for survival and reproduction of organisms, and therefore natural selection will favour body constructions that effectively enhance these strategies. This point of view must have been underlying all studies tracing correlations between morphological diversity of fish species and environmental factors (reviews in Barel et al. 1989, Douglas & Matthews 1992, Gatz 1979, Keast & Webb 1966, Norton 1995, Wainwright & Reilly 1994, Wainwright & Richard 1995, Winnemiller 1991, Witte & van Oijen 1990, and many others). However, studies of correlations between the morphology of fish and patterns of food resource and microhabitat use

Table 6.1. Properties of major aquatic food categories (cf. Fig. 6.2). Maximum food diameter categories are: 1: < 0.5 mm, 2 : 0.5-2.0 mm, 3: 2.0-5.0 mm, 4: 5.0-20 mm, 5: > 20 mm. In order to formulate feeding demands to fish, food diameter and (escape) velocity (mm s^{-1}) should be compared to predator gape-size and velocity. Qualifications of food such as 'micro' and 'macro' in this table refer to feeding fish larger than 15 cm fork length. Relative mechanical properties (per unit of volume) refer to the most demanding components of such heterogeneous biomaterials as fish skin, mollusc shell, or arthropod exoskeleton. Codes separated by a slash indicate varied properties within a single food category: --: very low value, -: low value, 0: average value, +: high value, ++: very high value

Food type	Maximum diameter	Relative velocity	Shape	Habitat	Chemical composition	Relative mechanical properties				Need for post-oral macro-diminution	Need for post-oral micro-diminution
						Strength	Compliance	Fibrousness	Toughness		
Plant foods											
Phytoplankton	1	0		pelagic	carbohydrates	-/+	-/0	-	-/0	--	++
Sessile algae	1-(3)	0		rocks, plants	carbohydrates	0	-/0	-	-/0	-	+
Filamentous algae	1	0	elongate	all	carbohydrates	-/0	0	-	-/0	-	+
Macrophytes	2-5	0	elongate	vegetation	carbohydrates	+	0	0/++	0/+	+	++
Seeds	3-4	0		benthic, vegetation	carbohydrates	+/++	-	0	0/+	+	0
Detritus	1-3	0		benthic	carbohydrates	0	0	0/+	0	0	0
Animal foods											
Zooplankton	1-2	1-2		pelagic	proteins	0	0	0	0	--	+
Macro-crustaceans	4-5	3-4		benthic, rocks, vegetation	proteins	0	-/0	0	0	+	-
Benthic larvae/worms	2	1		benthic	proteins	0	+	0/+	0/+	0	0
Macro-insects	3-4	4	elongate	benthic, rocks, vegetation	proteins	+	0/+	+	+	+	-
Molluscs	3-4	1		benthic, rocks, vegetation	proteins	+/++	--	0	0/+	+	-
Fish	5	5	elongate	pelagic	proteins	+	++	++	++	+	-

thus far yielded varied success (e.g. Felley 1984, Goulding 1985, Grossman 1986, Kotrschal 1989, Motta et al. 1995).

In this paper we will make quantitative predictions about the diets of the 14 Lake Tana *Barbus* species, and about partitioning of aquatic food sources among them. We will base these predictions on the properties of aquatic food types (Table 6.1) and the (structural) options the barbs have to deal with these properties in order to feed effectively. We are not interested in purely correlative relationships between structures and performance, but we will only consider structures that have been shown - from performance and biomechanical studies - to be causally and quantitatively linked with a function to deal with a particular food type (e.g. it has been proven that the higher the density of taste buds on the palatal organ is, the more effective the internal sorting between food and non-food). We called these mechanistic links between food properties and fish structures the food-fish model (FFM, Fig. 6.1*a*).

If the quantitative relation between a structural parameter and feeding performance is known, it can be predicted what the optimum value (or value range) of the parameter must be for effective utilization of particular food types (e.g. for an effective retention of small food particles from ingested debris, the taste bud density on the palatal organ should be high). If there are several or many structural parameters that can thus be linked with feeding performance this results in a morphological profile for effective feeding on each particular food type (Table 6.2).

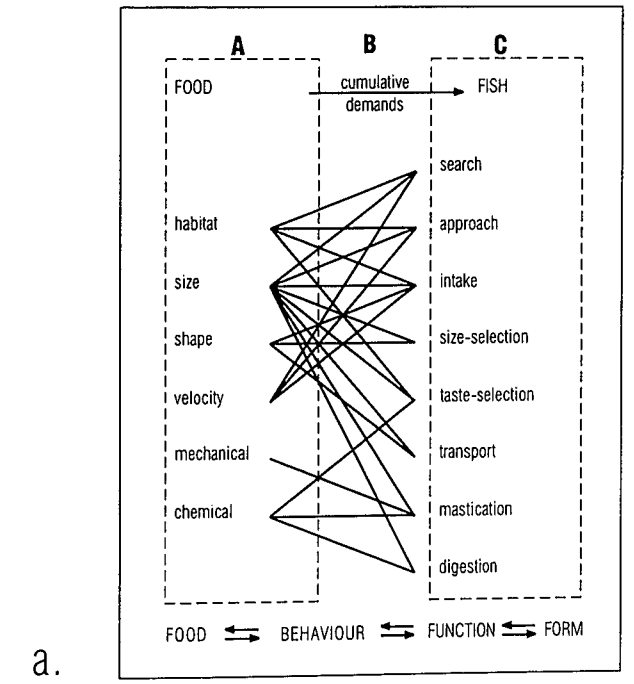
Only the parameters which could be linked quantitatively with feeding performance were selected from the morphological data set we measured on the Lake Tana barbs during this and previous studies. This resulted in two independent sets of 33 parameters: the first containing the predicted values for effective feeding on particular food types (Tables 6.2 and 6.4), and the other with the measured values for each *Barbus* species (Table 6.5). Subsequently, each separate species was matched with each profile for effective feeding on particular food types. If a match was good, the species was predicted to be good at eating that food type, if the match was poor, it was predicted to be bad at feeding on that food type.

In the following sections we will first discuss the bottlenecks in ecomorphological studies, and will try to explain why they met with various amounts of success. In the Methodology part we will discuss in detail the food-fish model, the food properties and the choice of the fish parameters, as we think it crucial in evaluating the whole method of this study.

In the Material & Techniques section the measurements are explained, but most attention is given to the processing of the large data-sets and the matching of profiles for effective feeding on particular food types with the measurements of the 14 species.

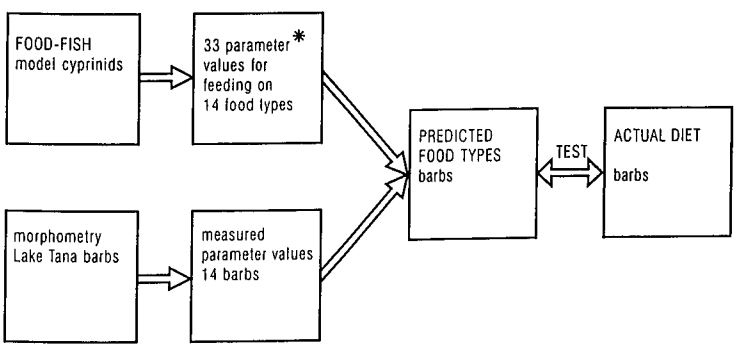
What are the major bottle-necks, obscuring clear form-function relations in many studies:

1) The large phylogenetic distances between the compared species (e.g. Douglas & Matthews 1992, Felley 1984, Findley & Black 1983, Strauss 1987). Morphological differences as a result of long separate evolutionary histories may dominate, obscure and even constrain the tuning between structural and ecological features. For example, one may expect biting jaws in fish feeding on



a.

FOOD-FISH model cyprinids



b. * *parameters selected from mechanistic studies (FOOD-FISH model)*

Fig. 6.1. Methodology of this study. (**a**) The food-fish model (FFM) for cyprinid fish describes, based on experimental knowledge, the structural options cyprinids have to deal with the cumulative demands that specific food types impose on them (e.g. if the fish is confronted with a very strong food item, such as a large snail, it can cope with such properties [within the cyprinid 'Bauplan'] by developing heavy pharyngeal jaws and teeth for crushing). The FFM enables us to select a cumulative set of fish parameters as a response to a cumulative set of food parameters, all based on experimental research. (**b**) The same parameters were measured in the Lake Tana barbs. By comparison of the measured parameters with the parameter values that were predicted to be optimal for utilization of particular food types it can be predicted which food types can be handled effectively by the barbs (e.g. a barb with heavy pharyngeal jaws is predicted to be good at snail crushing, a barb with a short gut is predicted to be bad at eating plants). These predicted diets should be tested against actual diets (see Chapter 7).

Table 6.2. Demands on shape and relative sizes of elements of the feeding apparatus, derived for cyprinid fish to enhance feeding on specific categories of aquatic food types. Food types, the appropriate feeding modes and the fish's relative parameter values fitted for these feeding modes on the food types are listed. Relative parameter values are compared among food types (columns), for each parameter (row) separately. Note that for phytoplankton, micro-crustaceans and fish two separate feeding modes are defined. Masticatory operations in italics refer to microdiminution, others to macrodiminution. Fish parameters between parentheses are relevant, but have not been measured in this study. The total number of parameters exceeds 33, but some parameters did not differ among species (such as OLJ/ILJ and were not used in the further analysis) If not stated differently, fork length (FL) was taken as a reference in standardizing the measurements over size classes (cf. Table 6.3). Two codes for a single food category refer to its widely varying properties. Parameters marked with ' * ' refer to different teeth from the heterodont pharyngeal dentition and can not be averaged. Codes: '--' = very low value demanded; '-'= low value demanded; '+'= high value demanded; '++'= very high value demanded; '0'=no specific demands, neutral parameter. Blanks have been analyzed as '0' in further analysis.

Food type		Phytoplankton		Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans		Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish	
Feeding mode		townet	pump	scraping	biting	particulate	particulate	townet	pump	particulate	particulate	particulate	particulate	pursuit	ambush
Fish parameter	Abbreviation														
Search and detection															
barbel length	ABL						++				++				
eye diameter	ED								+						
Approach															
body depth/length	BD/FL	-			+	+	+	-			+		+	--	
body depth/width	BD/BW	0/+						0/+						1	
oral gape area/cross body area	GAr/BAr	1						1						1	
(perc. white tail muscles)		--						--				+		--	++
(aspect ratio caudal fin)		+						+				-		++	--
caudal peduncle depth	CPD	-						-				+		--	++
anal fin area	AFAr	-				0/+	0/+	-			0/+	+	0/+	--	++
Intake															
oral gape position	PrA	term					inf	term			inf	term/sup		term	
protrusion size	Prot				--	+	++			+	++	+	+		++
lower jaw length	LJL			-	--							+		++	++
kinem. eff. closing lower jaw	OLJ/ILJ			-	--							+	0/-	++	++
pharyngo-opercular volume	PhOpV		+						+			+		+	++
head length	HL	+	+	-	-			+	+			+		+	++
hyoid length	HyL														+
hyoid/jaw ratio	HyL/LJL														0.71
operculum length/depth	POrL/OpD		+						+			+		+	++
opercular membrane width	OpMW											+			++
(internal streamline)														++	+
gill raker length / interraker distance	RLI/IRI	++	++					++	++			0			
(jaws)				scraping	robust										

Table 6.2. (continued)

Food type		Phytoplankton		Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans		Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish
Feeding mode		townet	pump	scraping	biting	particulate	particulate	townet	pump	particulate	particulate	particulate	particulate	pursuit/ambush
Fish parameter	Abbreviation													
Size selection														
oral gape diameter	OG	++						++						++ +
pharyngeal gape diameter	PhG					0/+				+		+	+	++
lateral gill raker length	RLl		++	+			+		++					
medial interraker distance	IRm		--	-			-		--					+
secondary profile gill rakers	SRP		++	+			+		++					
gill raker area	FilAr		++	+			+		++					
Taste selection														
palatal taste buds density	TBD			0/+			++				++			
palatal organ area	POAr			0/+			++				++			
(closed) protrusion size	Prot						+				+			
Transport														
postlingual organ width	PLOW				0/+					0/+		+	0/+	++
(hooked-pointed phar. teeth)					0/+					0/+		+		++
Pharyngeal mastication														
pharyngeal jaw mass	PJM				0/++	+				0/+		0/+	++	
(type of teeth)		*grinding*		*grinding*	shearing lacerating cutting *grinding*	crushing splitting *grinding*	lacerating shearing cutting	*grinding*		splitting crushing lacerating	cutting lacerating	cutting lacerating	crushing splitting	piercing cutting lacerating
(occlusal contact area)*		++		++	--/++	0/++	--/0	++		-/+	-/0	-/0	0/+	-/0
interdigitation teeth	IntDig	-		-	+	-	0/+	-		-				
output lever tooth A2	A2OL/PJL	0/+		0/+	++	-/0	+	0/+		-/+	+	+		++
(impact angle teeth)*		--/0		--/0	--/0	0/++	--/0	--/0		-/++	-/0	-/0	++	-/0
symphyseal length pj	SymL/PJL				--/-	0/++	-			-/++	-	-	++	--
robustness phar. jaws	PJM/PJL3				--/0	0/++	-/0			-/+	-/0	-/0	++	-/0
tooth % hooked	A2Hook	--		--	-/++	--/0	-/++	--		-/++	-/++	-/++	-/0	-/++
A2 tooth base-width	A2W					+							+	
Digestion														
intestine length	GL	+		+	0/+		++							

large objects, like in some cichlids, but cyprinids as a group do not have oral teeth, and therefore will not develop biting jaws.

2) Too few food properties are taken into account. Food size is often the single parameter measured, whereas the fish has to cope with a large set of food properties. For example dragonfly larvae and bivalve molluscs can be very similar in size, but they differ widely in velocity, mechanical features and habitat, and fish require different adaptations to feed effectively on either of these food types.
3) Too few structural parameters critical in the total foraging and food processing of the fish are considered (e.g. Kotrschal 1989, Wainwright & Richard 1995, Webb 1984). Mouth size is often the single parameter (e.g. Norton 1995) and otherwise traditional external, taxonomic characters often predominate (e.g. Douglas & Matthews 1992). Fishes with similar mouth sizes can, however, have very different body shapes, resulting in different capabilities for e.g. pursuing prey.
4) Most studies focus on direct correlations between morphological and ecological parameters, rather than searching for functional explanations (e.g. Barel et al. 1989, Douglas & Matthews 1992, Felley 1984, Grossman 1986, Keast & Webb 1966, Motta et al. 1995, Wikramanayake 1990). Too little knowledge of the relation between form, function, behaviour (feeding performance) and ecology limits the understanding of functional links between structural and ecological diversity (Norton 1995). Large eyes, for example, may improve vision, but as long as it is not known which aspects of the eye contribute to which aspects of vision (e.g. resolution or sensitivity) it is impossible to predict what the effect of the larger eye will be on the organism's feeding performance.

This paper aims at predicting the feeding capabilities from proven functional relationships between the morphology of fish and their ability to cope with specific food properties. Such predictions have been rare until thus far (Wootton 1990), and have hardly ever been tested (Ricklefs & Miles 1994). The following section will explain how these predictions were made while handling or avoiding the above bottle-necks:

1) The *Barbus* species flock of Lake Tana (Ethiopia) is composed of 14 endemic species (Nagelkerke & Sibbing, submitted) which radiated into new ecological niches following the formation of the lake after preceding volcanic activity (Nagelkerke et al. 1994, 1995*b*). This 'natural laboratory' contains species with a recent common phylogenetic background, so their differences in form, functioning and behaviour will, in an adaptive view, primarily result from new ecological challenges (habitat, food resources). This lack of phylogenetic constraints offers immense opportunities for adaptation research.
2) Aquatic food types differ widely, not only in size, but also in shape, habitat (e.g. benthic versus pelagic), motility (e.g. sedentary versus swimming), mechanical (e.g. stiff-weak v. pliant-strong) and chemical properties (proteins v. carbohydrates, energetic value). The high diversity in feeding structures and their integrated performance in feeding is the evolutionary answer of fish

species to deal with cumulative sets of demands imposed by each of the food types (Sibbing 1991, Sibbing et al., 1994). Therefore we will take as many different aspects of the food into account as possible.

3) Feeding (i.e. foraging and food processing) in fish is composed of a chain of subactions (Holling 1966, Sibbing 1991*a*): search, detection (encounter), approach, intake (capture), size-selection, taste-selection (tests on palatability and food-texture), transport, mechanical breakdown (mastication), deglutition (swallowing) and chemical breakdown (digestion). To increase the effective utilization of particular food types animals have to specialize in specific subactions according to the cumulative challenges imposed by a specific food type. Pursuit and capture e.g. are required in piscivores, mechanical breakdown in molluscivores and phytophagous fish, and retention of small particles in planktivores. It is important to state, and an advantage of the present approach, that such demands are independent of the phylogenetic position of fish species, although meeting the demands is constrained by their evolutionary history. In our study structural parameters covering all subactions of feeding will be considered. The cumulative effect of subsequent limitations gradually narrows the food niche.
4) The selection of structural parameters for comparison of feeding abilities among species will be based as much as possible on form-function relationships tested in experimental studies, e.g. on branchial sieving (Hoogenboezem et al. 1991, Van den Berg et al. 1992, 1994) or pharyngeal mastication (Sibbing 1982). They provide evidence for the significance of structural parameters in (a) functioning of the subsystem, in (b) the total feeding performance and in (c) adjusting feeding behaviour to ecological parameters (food size, density, distribution, motility, habitat, mechanical and chemical properties) (Nagelkerke & Sibbing 1996*b*). Characters with unknown functional significance will obscure the predictions.

The barbs of Lake Tana

Lake Tana is a large (c. 3100 km^2), shallow lake (maximal depth 14 m) in the Ethiopian highlands (altitude of 1800 m) and the source of the Blue Nile. It is isolated from other fresh-water systems by 40 m high waterfalls in the Blue Nile, only 30 km from its outflow from the lake. Fisheries is developing in the lake since 1986 and the 1996 commercial catches (c. 1100 tons, GOPA-consultants 1996*a*) are mainly composed of catfish (*Clarias gariepinus*, c. 31% kg), tilapia (*Oreochromis niloticus*, c. 36% kg) and *Barbus* species (c. 32% kg). These barbs are mostly rather large fish (modus c. 32 cm, maximum 85 cm) showing a wide range of morphological and ecological diversity (Nagelkerke et al. 1994). Recently, evidence for the presence of 14 distinct species has been given, of which seven are new (Nagelkerke & Sibbing, accepted). Together they compose an unique species flock originating most probably from an ancestral riverine barb most similar to *Barbus intermedius* Rüppell, a polymorphous species, found in rivers all over the Ethiopian high plateau, including those tributing to Lake Tana. Probably, evolution can still be seen in action in the shore area where very variable barbs occur (Nagelkerke & Sibbing 1996*a*).

Before 1990, all large barbs were considered to be one polymorphic species (Banister 1973) and treated as one single fish stock in fisheries management. For a proper management towards sustainable fisheries the ecological role and interactions of the newly recognized fish stocks (i.e. the 14 *Barbus* species) should be investigated. Such knowledge is needed to explain and direct the changes in size and composition of fish species resulting from intensifying and selective fisheries exploitation (Sibbing et al. 1994, van Densen 1994 , Witte 1987), as well as for proper future management of the fisheries.

This study will elucidate the ecological position of the adult Lake Tana barbs (>15 cm fork length), focussing on food resources partitioning. Trophic abilities and inabilities are predicted from comparisons of food properties and morphological features of fish to cope with these properties. The predictions will be tested against field data (i.e. gut contents) in a following paper (Chapter 7). At a later stage of the project the relation between morphological and ecological diversity will be investigated in an evolutionary framework, unravelling the origin of the unique biodiversity of the Lake Tana barbs and the forces that drove its radiation.

The following section presents the subsequent steps taken to predict food resource partitioning among the barbs, from their diverse morphological designs.

METHODOLOGY

Feeding involves 1) the intake of animal or plant material by foraging and 2) absorption of its energy and nutrients by the intestine after mechanical and chemical breakdown. Feeding efficiency is defined as the ratio between energy gain and energy costs per unit of time and is bound to the properties of the food as well as to the properties of the forager (cf. Nagelkerke & Sibbing 1996*b*). This study is based on four assumptions: (a) specialisation in feeding increases the effectivity of an organism to cope with the properties of food items; this increase in effectivity is the drive behind specialization, because it will lead to increased fitness of the organism under its particular circumstances; (b) each food item is characterised by its cumulative properties and requires a cumulative set of specialisations from the animal; (c) each single food property challenges the animal for specialisation; (d) the cumulative set of specialisations at the same time narrows down the part of the available food spectrum that can be utilised by the animal.

The food-fish model (FFM)

The options for animals to cope with a particular set of demands from a food type are bound to their phylogenetic constraints and will be different in e.g. fish, birds and mammals. This paper focuses on cyprinid fish. The cyprinid 'bauplan' lacks oral teeth and a stomach, but is provided with highly developed pharyngeal jaws and teeth acting against a horny chewing pad fixed in the occipital base of the skull (Sibbing 1982, 1991*b*). Cyprinids also have protrusile upper jaws and a fleshy palatal organ, opposing the branchial sieve, which can be used for food sorting and transport (Sibbing 1988, 1991*a*, Sibbing et al. 1986). The success of this largest family of fresh water fish

(>2000 species, Nelson 1994) may well relate to the capability of these particular features to deal with highly demanding food. Cyprinid piscivores will however be constrained in catching prey by their lack of oral teeth (no biters or scale scrapers, such as in cichlids, are expected). In the next sections we will describe how the food-fish model (FFM), describing the relation between food properties and the structures of the cyprinid fish to deal with them, is developed (Fig. 6.1).

Food properties challenging animals

The first step is to define and assess for each food item feeding relevant properties such as its habitat, size, shape, velocity, mechanical and chemical properties (preferably in quantitative terms). Such an approach is common in food technology but rare in biology. If e.g. we take a fish as food, it can be regarded as a generally large and elongate, fast, pelagic food item, with a compliant-tough skin and a low C:N ratio. Each food sets its own cumulative demands to the feeding behaviour and mechanism of animals. For e.g. eating fish a first demand will be to search and detect the prey, secondly to reduce prey-predator distance rapidly by quickly approaching, thirdly to take in the fast and large prey, and finally to expose it to the digestive juices.

Options of animals to cope with food properties

Functional morphological analyses of the feeding apparatus, subdivided into functional components dealing with different feeding actions, provide the framework for linking food properties and feeding structures (Fig. 6.1*a*). The structural parameters that are critical in dealing with particular food properties are provided by previous studies on form, functioning and performance of the prey capture apparatus in fish (Muller and Osse 1984, van Leeuwen and Muller 1984, Lauder 1980 , Liem 1980). Quantitative relations of these parameters with their feeding performance have been predicted from models and were tested in experiments. Particularly in cyprinids such studies have extended to the intra-oral food processing (Sibbing 1982, 1991*a*, Sibbing et al. 1986, Hoogenboezem et al. 1991, Van den Berg et al. 1992, 1994): filter-feeding, food sorting, and pharyngeal mastication will specialise and thereby limit the use of food resources by fish.

For this study these previous results have been extrapolated to the Lake Tana *Barbus* situation. After the evaluation whether these extrapolations were tenable, structural parameters for the Lake Tana barbs could be selected (Fig. 6.1*b*). The cumulative set of measured structural parameters describes the feeding specializations and consequent limitations of the barbs, since the quantitative relations between the parameters and the feeding performance on particular food types are known.

Predicting food utilization by the barbs

Since the quantitative relations between structural parameters and feeding performance are now known, it is possible to derive a (hypothetical) structural character set or profile for the effective utilization of particular food types (Fig. 6.1*b*, Table 6.2). These profiles for each food type can be compared with the set of measured structural parameters for each of the 14 *Barbus* species. This

results in a prediction of food types that can be handled effectively by each measured fish species: the predicted food niche.

Trophic segregation and its final test

A comparison of predicted food niches will elucidate the potential trophic segregation and niche overlap among the Lake Tana *Barbus* species. These ultimate hypotheses will be tested by comparing them with field data, i.e. gut contents (actual food niches). Then an objective road from fish structures to the quantitative predictions of food utilization is constructed and its predictive value can be evaluated (Chapter 7).

The food-fish model (FFM)

The food-fish model is central to our whole approach. Since it has never been described before, we think it important to discuss it in detail, so every step can be evaluated thoroughly. The following sections will discuss the properties of food types and the structural options of fish to deal with them, in which all structural parameters that were used in our analysis and the studies from which they were derived will be addressed.

Properties of food types

Differences in habitat, size, shape, velocity, chemical and mechanical properties of fresh-water food types (Table 6.1, Fig. 6.2) impose widely different demands on the feeding of fish. Physical properties of food do not simply parallel commonly used (often taxonomic) categories (cf. Barel et al 1989). Within each category they may considerably diverge (e.g. fibrous and non-fibrous plants), whereas items from different categories may have similar physical properties (e.g. molluscs and seeds, both strong and stiff, with similar range of size, velocity and habitat). Even though the chemical and physical grouping of food items is of primary importance in the context of this paper, from a pragmatic point of view (comparison with other studies) the taxonomic categories are maintained, but their major properties are defined (Table 6.1). Food items which were physically extremely aberrant from the other members of their category were shifted to a category in which they fitted better (e.g. chironomid larvae are aberrant from other insects and are placed among the worms) or have been categorised separately (e.g. filamentous algae).

Biological categories

Plants foods, largely composed of carbohydrates, provided with strengthened cellulose walls:

1) Phytoplankton: minute, pelagic, floating algae and diatoms; non-fibrous
2) Sessile algae: epilithic and epiphytic algae and diatoms; non-fibrous
3) Filamentous algae: floating; non-fibrous; < 0.5 mm diameter
4) Macrophytes: large, mostly rooted plants; a wide variety of (often elongate) shapes; often fibrous, especially the larger species and those emerging from the water surface

5) Seeds: dispersed in benthic and littoral; strong and stiff capsules

6) Detritus: a mixture of decaying plant material, micro-organisms, bottom ooze (organic and inorganic) and small benthos (e.g. ostracods)

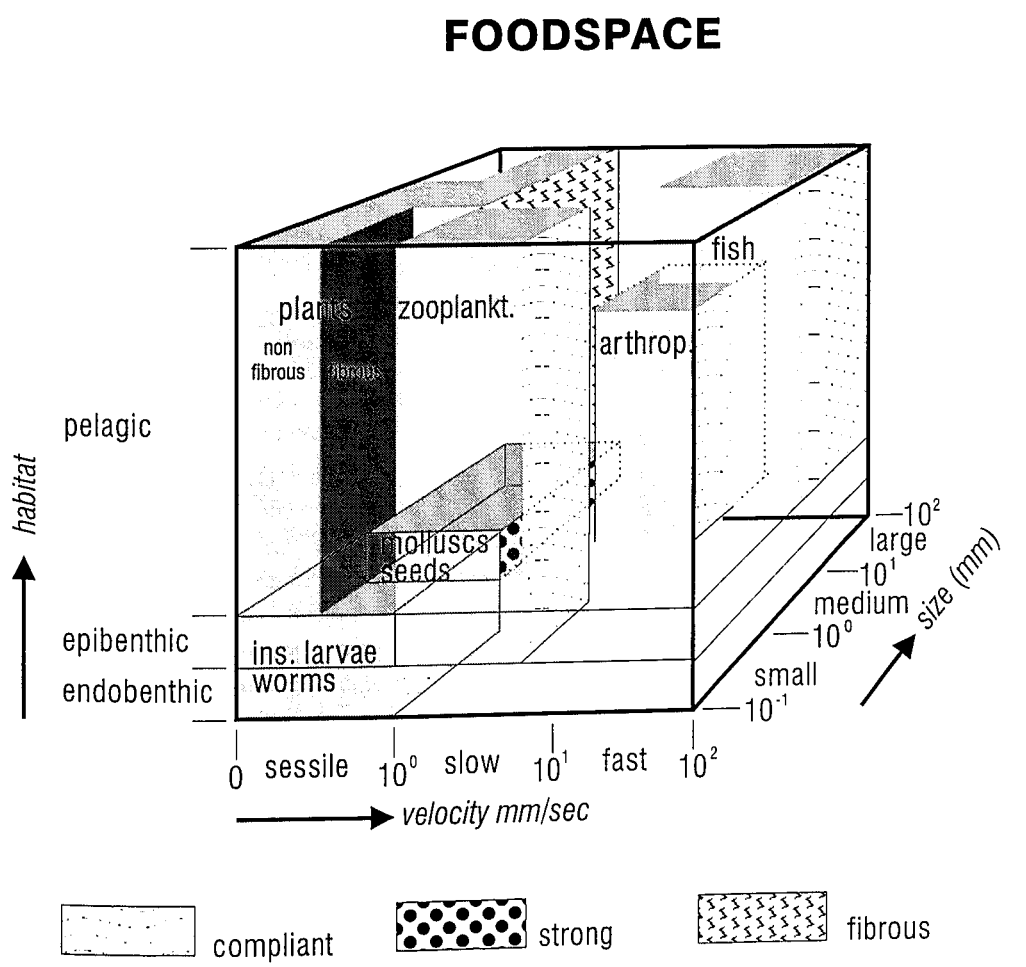


Fig. 6.2. Aquatic food types, arranged according to diverse properties which are relevant to animals feeding on them. Note that in addition to size, velocity, and habitat, also chemical (plants v. animals) and mechanical properties have been indicated (compliant, strong and fibrous). More details in Table 6.1.

Animal foods, largely composed of proteins, soft tissues, readily digestible:

7) Zooplankton: cladocerans and elusive copepods; mostly pelagic
8) Crustaceans: amphipods, isopods and stiff-skeleton decapods
9) Insects: chaoborid larvae, odonate, ephemeropteran and trichopteran nymphs, and beetles; elusive prey of varied size and shape; tough exoskeletons
10) Benthic insect larvae and worms: chironomid larvae and (tubificid) oligochaetes; sedentary, soft-skinned, compliant prey
11) Molluscs: strong and stiff shells, attached bivalves, or substrate dwelling gastropods; non-pelagic
12) Fish: fast, elusive prey with compliant fibrous skin; medium to large size

Physical categories

The following paragraphs deal with the above food categories, according to properties which are important for all feeding animals: habitat, size, shape, velocity, strength, compliance, fibrousness and chemical composition (Table 6.1). Such an evaluation of freshwater food items is visualized in a 'food space' with physical food types, each defined in its own range of properties (cf. Fig. 6.2). The challenges which these properties impose for effective utilization will be formulated. Solutions to meet these challenges by fish or other animals are discussed later.

Habitat

Four habitats have been distinguished: (a) endobenthic, (b) epibenthic, (c) complex (among rocks and vegetation) and (d) pelagic (Fig. 6.2). Specific habitats of food organisms imply different requirements for detection, pursuit and capture by fish. Each food type emits a spectrum of signals to foraging fish. The effectiveness of particular stimuli to alert and guide the fish depends on the physical conditions of the habitat (light conditions, turbidity, ion content, velocity of water flow).

Detection of detritus or endobenthic prey (a), hidden from predators in muddy or sandy substrates, is impossible by vision. Therefore, substrate feeders require chemosensory or electroreceptive, rather than visual specialisations, and they need to penetrate the substrate for probing. Epibenthos (b) imposes less strict demands on the forager although light conditions are poor at large depths and epibenthic prey are mostly inconspicuous sedentary animals. Complex and confined habitats among rocks and vegetation (c) offer shelter for prey and feeding techniques, and strategies may vary accordingly (e.g. ambush instead of pursuit hunting). In open pelagic areas (d) large and contrasting prey are especially vulnerable to prolonged, vision-guided pursuit in light and clear conditions.

Particle size

Prey size is widely accepted as a major factor in trophic segregation and resource partitioning (van Densen 1994, Wainwright and Richard 1995, Werner 1974). If we compare the above categories of aquatic food types, a large range of absolute sizes is apparent (Fig. 6.2). Food size relative to the oral gape is most important for fish, and the maximal diameter of a food item, rather

than its length, is limiting intake. Therefore, maximal diameter is taken as food size, and expressed as a percentage of the fish's oral gape (OG).

Qualifications as 'micro' and 'macro' in this paper never refer to the food's absolute size, but they are relative, referring to the fish's oral gape. They are defined as: pico (maximal diameter < 1% OG), micro (1-10% OG), meso (10-50% OG), macro (50-100% OG), mega (>100% OG). If, e.g. we take the oral gape as 10 % of FL, then for fish larvae <30 mm FL (and therefore with OG<3 mm) large zooplankters (e.g. 1.6 mm) may be macro-particles, whereas for adult fish (> 200 mm FL with OG > 20 mm) they are micro-food.

Particle-size is not only important for intake, but also for retention. Micro-particles easily pass into the mouth of fish but need to be retained from expulsion through the gill slits.

Particle shape

The maximal diameter of a particle is limiting intake. Its length may, however, impose special demands for internal transport (e.g. stems of aquatic weeds: grasscarp, Vincent & Sibbing 1992, or long worms). In filter-feeding the shape of zooplankton determines its retention probability (van den Berg et al. 1994).

Velocity

We divide aquatic organisms into arbitrary categories according to their absolute locomotion speed (Table 6.1, Fig. 6.2). Relative velocity as a food property refers to the ability of prey to escape pursuit and capture by the predator. It is evident that prey velocity should be compared with the swimming and suction abilities of foraging fish in order to evaluate prey refugia due to differences between prey and predator swimming capacity (cf. Christensen 1996). Both prey and predator swimming abilities are size dependent and expressed as body lengths per second in fish. Small organisms are usually limited to smaller areas.

Material properties

Strength, compliance and toughness of food types, and especially the fibrous texture of plants (Vincent 1991) require specific patterns of mechanical breakdown preparing chemical breakdown for efficient absorption of energy and nutrients. Depending on the material properties of the food item, different types of loading (compression, tension or shear stresses) are required for fracture (Gordon 1978). The total energy required for breaking a unit volume of food (its toughness [v. brittleness] in Joules/cm^3) is determined by its strength (amount of stress in N/m^2 required for breaking; strong v. weak), its compliance (% strain per unit of stress; compliant v. stiff), and its notch-resistance (capacity to absorb stresses that propagate cracks; notch-resistant v. notch-sensitive). The total energy for breaking a food item increases with each of these parameters (Fig. 6.3) and the food volume. Even if materials require equal amounts of energy for diminution, this may result primarily from different properties, such as strength (e.g. mollusc shells), compliance (e.g. worms), or notch-resistance (e.g. fibrous structure of plants).

Since fish have to cope with these properties using different masticatory operations and machinery (Sibbing, 1991*b*), aquatic food items are evaluated (Table 6.1, Fig. 6.2) for their strength, compliance and fibrousness (increasing the notch-resistance at breaking) per unit of volume. The most demanding components of usually heterogeneous biomaterials (e.g. shells in molluscs, exoskeletons in arthropods, skin in fish) are considered. Few data on the properties of complex biomaterials such as whole organisms are available from literature (cf. Jeronimidis 1991).

Chemical composition

The contrast between animal and plant foods is often strongest in the chemical composition. Plant materials have a high C:N ratio, a high content of structural polymers (fibres) and thick cell walls of cellulose, which impose high demands (low pH, ligninases, cellulases, time) on chemical breakdown by hydrolysis in digestion. Soft animal tissues, with low C:N ratio require mainly proteases, less aggressive conditions and less time.

Structural solutions of cyprinid fish to cope with food properties

This section discusses the structural optimizations by cyprinid fish to meet the challenges imposed on them by the different food types, as derived from quantitative functional morphological and performance studies. Table 6.2 lists the feeding related structural characters of cyprinids, arranged according to their role in the subsequent feeding actions (search and detection, approach, intake, size selection, taste selection, transport, mastication and digestion). The character values fitting the successive food types have been derived from mutual comparisons of the properties of the different food types, considering the role of each structural character in coping with these properties (cf. Table 6.1, Fig. 6.2). The values of each separate character are therefore comparative among different food types. The role of the structural parameters in coping with food properties are derived from model studies of particular functions, or from teleost literature, if no experimental studies were available and functional relations are nevertheless properly understood. Characters considered less significant or neutral for a particular food type, are coded zero and are not shown in the evaluation rows (ranging between -- and ++). The more detailed food properties are specified, the more accurate character values can be specified for the utilization of food types by fish. In the text, measured characters are indicated by their abbreviations (Tables 6.2 and 6.3).

The combined set of character values, rather than single characters, is instrumental in predicting the capacity of fish to utilize food types. These capacities are comparative among the studied barbs and do not reflect absolute abilities. Note that sometimes specialisations for one food property necessarily imply limitations for another. For example, a high kinematic efficiency of the lower jaw, for quickly closing the mouth will always decrease the force efficiency in grasping. All examples in the text are for cyprinid fish, although for a better understanding, sometimes examples from other groups are mentioned.

Search and detection

Food detection depends on signals alerting and guiding the fish, specific for both the food type and its habitat.

Pelagic prey of large size, conspicuous contrast and high velocity (e.g. macro-crustaceans, macro-insects and fish) will be detected and successfully pursued by vision during daytime. Visual sensitivity as well as visual acuity may increase with absolute eye size (Fernald 1991, van der Meer & Anker 1984). Therefore, fish foraging on small evasive preys at low light conditions, e.g. epibenthic zooplankters, will need large eyes (ED in Table 6.2). If food items are less conspicuous, or if the environment is turbid or dark, the labyrinth, neuromasts or electroreceptors may aid in detection at short distances, even sensing water turbulences by zooplankton (within 10 cm; cf. Kotrschal 1991). Chemosensory organs are inadequate for monitoring prey swimming and escape movements.

Searching the substrate surface for benthic food (e.g. detritus, insect larvae and worms) is directed by external taste buds, often densely packed on long barbels (ABL) acting as sensory

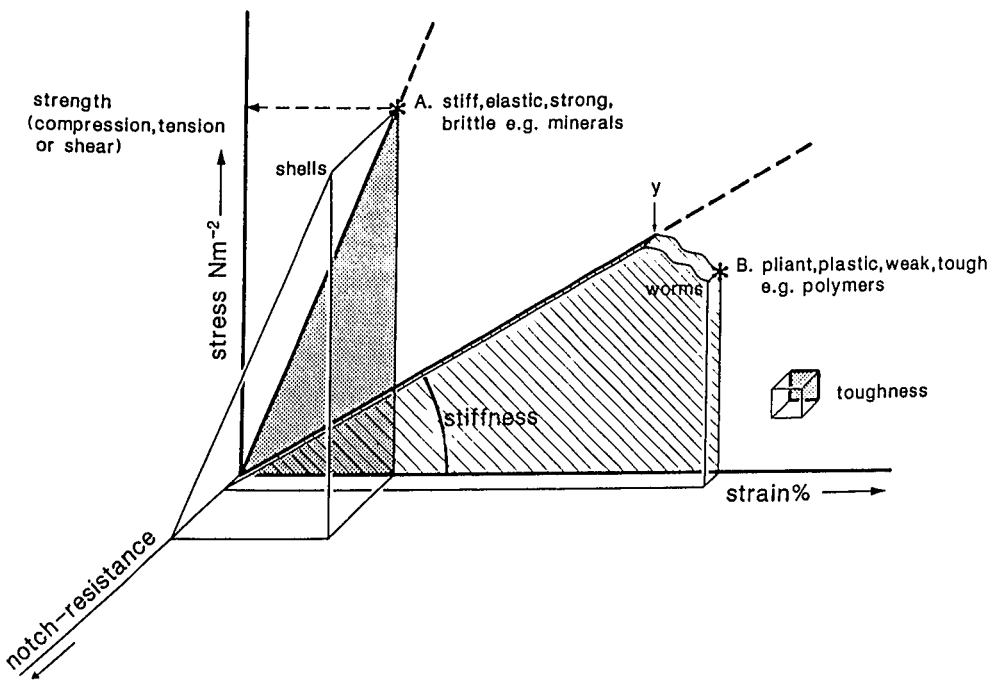


Fig. 6.3. Material properties of food, relevant to animals feeding on them. Each of the three properties (stress, strain and notch-resistance) increase the toughness (volume beneath the graph, indicated by a box) and therefore also the energy required for breaking a unit volume of food item. The type of loading determines the type of stress (compression, tension or shear). Note that similar toughness can be achieved through different combinations of food properties. See text for further explanation.

antennae (as in the catfish *Ictalurus nebulosus*, Atema 1971). Olfaction is of little use in localizing food but may have a signalling and guiding function over longer distances. Penetrating and sampling the substrate for buried benthic prey is triggered by external taste buds, but the selective sorting between food and non-food takes place in the pharyngeal cavity of cyprinids (see section on taste-selection).

Most other items in clear shallow water (micro-crustaceans) and those between rocks and littoral vegetation (molluscs, seeds) can be detected by vision during daytime. In murky waters and at low light intensities (e.g. large depths) external taste buds, electric sense organs and neuromasts (e.g. in roach larvae, Dabrowski 1982) may contribute in detection (Kotrschal 1991).

Barbel length (ABL) and eye diameter (ED) vary widely in cyprinid fish and are easy to measure, contrary to parameters of other sense organs. The relative volumes of the primary sensory centres in the brain are important structural characters reflecting the overall importance of sensory systems (cf. Kotrschal 1991). In fish provided with many external taste buds and large barbels the facial lobes are enlarged (Evans 1952). Such brain volumes are, however, difficult to measure accurately and are more indirectly related to the whole life style, making it unreliable predictors of feeding abilities.

Approach and food intake

Prey size, velocity and habitat are taken together in discussing foraging modes and their structural optimizations in cyprinids (Table 6.2). Predation (1), e.g. by pursuit or ambush, refers to hunting after large fast evasive prey, filter-feeding (2), e.g. by townet or pumping, refers to the collection of small non-evasive suspended particles, particulate feeding (3) refers to visually foraging on items of intermediate size and velocity, and biting, scraping, and gnathopulation (4) refers to browsing on often sessile mega-food objects.

1) Predation

Fish foraging on large and **fast, evasive prey** (e.g. fish, some macro-insects) have the following mechanisms for rapidly reducing the prey-predator distance (Muller & Osse 1984; van Leeuwen & Muller 1984): swimming (a), suction (b) and protrusion (c).

a) **Swimming** is effective to decrease large predator-prey distances and is dominant in pelagic cruisers and pursuit hunters, which basically overswim water and prey with open mouth (ramfeeding *sensu* Liem 1980) and open the opercular valves early, to avoid stagnation of water, which otherwise might push the prey forward.

Specialised cruisers which swim continuously, require a streamlined body with about equal depth and width (BD/BW) and a small depth/length ratio (BD/FL) to minimize drag in swimming, a low caudal peduncle (CPD), a small anal fin area (AFAr) and a high aspect ratio for their lunate caudal fin (Webb 1984, 1988). A large terminal gape area equalling the frontal area of the fish (GAr/BAr) avoids the pushing effect of the approaching predator on the prey at short distance. A minimal inclination of the head and body profile serves the same goal. Cruisers search a larger area than ambush hunters (see below) and require red rather than white muscle fibres for prolonged

swimming (Boddeke et al. 1959). Note, that if prey are small and non-elusive (e.g. phytoplankton) swimming speed can be low and a large gape size increases the volume of suspension taken per second (cf. tow-net filter-feeding).
b) Voluminous and fast **suction**, opening the opercular valves only late to maximize the sucked volume, is another technique for taking large evasive prey. Suction is only effective at short predator-prey distance and dominates in ambush- and 'sit and wait' predators, commonly found in structurally complex habitats which prevent fast swimming.

Volume expansion in the head is crucial in suction and the size of the hyoid bar (HyL/FL) reflects abilities for volume increase (Muller & Osse 1984, Barel & de Visser 1996). For maximizing the internal head volume by lateral expansion Muller (1989,1995) calculates the ratio between the hyoid bar and the lower jaw-suspensorium-interhyal bar (HyL/LJL is used as an estimate) to be optimal at 0.71. The length of the branchiostegal rays, the opercula and the opercular valve (OpMW) together determine their maximal contribution in volume increase with still closed opercular valves (OpVV). It has been calculated that a high ratio between length and depth of the opercula (POrL/OpD) increases the volume properties of the opercula (Elshoud 1986). A long head relative to body size (HL/FL) will generally increase the suction volume per unit of fish volume, which is of advantage in volume sucking predators and filterfeeders. The smaller the oral gape (OG/FL), the higher the suction velocity into the gape with equal expansion velocity. A small oral gape will however limit maximal prey size.
c) **Protrusion** of the upper jaws towards the prey (Osse 1985; Motta 1984) rapidly decreases the prey-predator distance at low energetic costs and directs the suction flow to the prey (Prot).

Predatory fish combine the three above mechanisms (van Leeuwen 1984) according to the habitat of their prey (Table 6.2).
In **clear open water**, large evasive prey (mostly fish) will notice predators at a long distance. Predators need to pursue these prey by prolonged swimming (periodic propulsion, Webb 1984) eventually sucking the prey at short distance, opening the opercular valves early to avoid stagnation of the inflowing water (**cruisers** and especially **pursuit hunters**). Pursuit hunters add substantial suction to swimming and search smaller areas than cruisers.
Environments of **complex** structure (restricted, among vegetation and rocks) hardly allow prolonged pursuit of fast evasive prey (e.g. fish, some macro-insects) and prey can easily hide. Predators lie in **ambush** and wait for approaching prey. They suddenly lunge at high acceleration to the prey (transient propulsion, Webb 1984) and suck it by fast and voluminous expansion, aided by protrusion of the upper jaws (Prot) which directs the suction flow. A large caudal fin area, with low aspect ratio and a high caudal peduncle (CPD) increases the thrust of the tail in the initial strike (Webb 1984). **Sit and wait** predators (not known in cyprinids) do not swim at all but merely suck after the prey by fast and voluminous expansion.

All the above predators require a streamlined internal head profile in line with the direction of water flow and short and widely spaced gill rakers (RL, IR, SRP), since also internal drag should be reduced and stagnation avoided. A small oral or pharyngeal gape (PhG) excludes feeding on large

prey. Megaphagous predatory fish (prey > oral gape) such as sharks and piranha's bite pieces off the prey. In cyprinid fish megaphagous predation is impossible due to the lack of oral teeth.

Capturing fast prey requires fast jaw movements to prevent the prey's escape. A small ratio between input (ILJ) and output lever (OLJ) of the lower jaw in closing the oral gape is preferable for this (Anker 1974, Wainwright and Richard 1995), since it optimizes the kinematic efficiency. If the ratio is large, force, rather than kinematic transmission is optimized; this is expected in biters (not in cyprinids), scrapers, and graspers (such as grass carp, Vincent & Sibbing 1992).

2) Filter-feeding

Foraging on **small suspended particles** with little velocity and escape abilities (e.g. phytoplankton and micro-crustaceans) requires processing large volumes rather than fast feeding actions. Acceleration of water, which is energetically costly, is not required. Fast swimming with open mouth will even cause stagnation in the pharynx due to the high branchial sieve resistance (RL/IR). Suspensions are most efficiently taken by slowly overswimming large volumes with a large terminal gape (OG) (specialised townet filter-feeding, cf. Lazzaro 1987). Prolonged swimming in tow-net filterfeeders requires similar adaptations as in cruising predators (streamline, large gape compared to frontal area, high aspect ratio, horizontal head profile, high proportion of red muscles). If prey distribution is patchy, pump-filter-feeding, or - if fish are less specialised - gulping small volumes is employed (Janssen 1976, Lammens and Hoogenboezem 1991, Sibbing 1991). A long head (HL) is of advantage in volume sucking predators as well as in pump-filterfeeders because of its large volume. If overall particle densities become low, fish may switch from filter-feeding (several particles taken at the same time) to particulate feeding (on single particles) to increase their net energy gain (Hoogenboezem et al. 1991). In all filterfeeders the mesh size of the branchial sieve should be small to retain the small particles (cf. size-selection). Note that zooplankters will be meso- or even macro-prey for small fish, resulting in a different set of demands.

3) Particulate feeding

Intermediate size and velocity (**meso-particles**) of prey impose less extreme demands on swimming and suction of the fish. Such prey (seeds, detritus, worms, crustaceans, insects (larvae) and molluscs) allow a smaller oral gape (OG) in order to direct and increase suction flow velocity, but this may limit prey size. Combined with protrusion (Prot) this 'particulate feeding' allows predators to suck dense sedentary and even loosely attached (snails), or deeply hidden prey (mussels, buried insect larvae) from inaccessible places between plants, crevices and from the substratum with a highly directed suction flow. A deep and short body (BD) with flexible fins around its centre of gravity increases manoeuvring capacity among rocks and weeds (Webb 1984). Anal and dorsal fins are extended caudally. Such browsers and grazers should remain close to a shelter against predation, unless they have other anti-predator devices (e.g. large size or spines).

Common carp sucks pellets with velocities up to 0.6 m sec^{-1} from a head length distance (Sibbing et al., 1986) and can penetrate 12 cm into the substrate (further than other fish can,

Nikolsky 1963). Food properties other than size and velocity may differ tremendously and impose high demands (shape, habitat, mechanical and chemical) on other systems.

4) Scraping , biting and gnathopulation

Mega-food types and food **attached** to rocks, plants, or animals cannot be taken by suction or swimming. Fish feeding on such food require specific specialisations for detachment, like strong horny lower jaws for scraping sedentary prey or algae (e.g. *Varicorhinus beso*, Matthes 1963), or robust and firmly suspended jaws with high force efficiency in jaw closure (and therefore low kinematic efficiency: OLJ/ILJ) for biting macrophytes (e.g. *Ctenopharyngodon idella*, grasscarp). Grasping and tearing off small pieces from mega-food objects (e.g. scales) is impossible for cyprinids due to their lack of oral teeth.

Whatever the feeding mode applied, adjusting the direction of the oral axis (PrA) especially if protruded (terminal, supra-terminal or inferior), aims the suction flow to the position of the food item, whether benthic, pelagic, floating or among weeds and rocks.

Size selection

Both upper and lower limits of prey size impose specific demands on feeding mechanisms. The size of **large** prey is chosen by vision and limited by the diameter of the oral gape. Many fish in this sense are 'oral gape limited' in feeding (Zaret 1980, Werner 1974). Especially cyprinid fish are 'pharyngeal gape limited', since food items must pass their chewing cavity between pharyngeal jaws and chewing pad prior to entering the esophagus for digestion (Nagelkerke & Sibbing 1996*b*). Here the principle of cumulative structural limitations narrowing down the utilisable food spectrum is apparent. Pharyngeal jaw limitations also occur in cichlids with their hypertrophied pharyngeal jaws (Witte 1987, Wainwright & Richard 1995). So feeding on voluminous prey (fish, macro-arthropods, some molluscs and seeds) requires both large oral (OG) and pharyngeal gapes (PhG).

Feeding on **small** particles (phytoplankton, micro-crustaceans) is size-limited by the mesh size of the branchial sieve, modelled for filter-feeding in cyprinids by Hoogenboezem et al. (1989) and by van den Berg et al. (1993). Length of the gill rakers (RL), inter-raker distance (IR), channel width and filter area (FilAr) are critical parameters. Fragments of scraped algae and detritus smaller than the mesh size may also be lost through the opercular slits together with expelled water, and could be retained by other mechanisms, such as sticky mucus or a vomero-palatal organ which aggregates small particles by mucus into boluses (e.g. in *Labeo*, Matthes 1963). Feeding on suspensions requires a large filtering area (FilAr) to allow for filtering of large volumes.

Taste selection

Foraging on invisible items, such as benthos buried in the substrate (detritus, insect larvae, worms) requires sensors for e.g. electrical or chemical prey signals. Cyprinid fish feeding on these food types (e.g. common carp, bream and goldfish) repetitively penetrate and probe the substrate, ingest food and substrate and retain the palatable components, while expelling the waste. In

cyprinids this intra-oral sorting is performed by the large internal muscular palatal organ (POAr), studded with high densities of taste buds (TBD)(up to 820 per mm^{-2} in common carp, Sibbing and Uribe 1985). Sorting is a repetitive process, gradually purifying the mixture (Sibbing, 1988). It requires protrusion of the upper jaw (Prot) with a closed mouth. This functions as a mechanism to wash the substrate mixture back into the oral cavity for resuspension, after which it will be pressed into the pharyngeal slit again for another sorting action. A high sorting capacity requires a large palatal surface (POAr) and a small distance between roof and floor of the mouth. Specialisations of the actual selective retention are reflected in the brain centres processing sensory information from the pharyngeal lining into motor patterns stimulating the palatal organ (Finger 1988, Sibbing 1987).

Transport towards chewing cavity and esophagus

In fish, toothed bony elements lining the oro-pharyngeal cavity serve transport of food towards the esophagus. In cyprinid fish such elements have been largely lost during evolution (Sibbing 1991*a*). The muscular lining of the pharynx (dorsal palatal organ and ventral postlingual organ) propulses food items by peristalsis to the hypertrophied pharyngeal jaws (Sibbing et al. 1986). Transport of wide struggling food objects (e.g. macro-insects and fish) requires wide postlingual organs (PLOW) for grip and power, thus competing in space with the branchial sieve area. X-ray movies show that especially elongate food items (e.g. macrophytes, macro-insects, fish, earthworms) require repetitive propulsive actions to pass them into the esophagus step by step. Pointed, or hooked anterior pharyngeal teeth provide grip for the transport of large, struggling prey (e.g. earthworms and fish). Piercing of these easily digestible, fleshy prey items at the same time facilitates entrance of digestive enzymes (as in asp, cf. Sibbing 1991*b*).

Pharyngeal mastication

The lack of oral teeth, a stomach, and acid conditions in the alimentary tract of cyprinids poses high demands on mechanical breakdown in their pharynx. This especially applies to herbivorous fish, since cellulases are also absent in cyprinids (Hofer 1988, 1991). Pharyngeal mastication between pharyngeal jaws and the chewing pad, an anvil fixed in the base of the skull (cf. Fig. 6.4*g*), is therefore crucial in cyprinid feeding (Sibbing 1982, 1991). Two types of mechanical breakdown are distinguished: macro- and microdiminution. Large food items, especially those with strong capsules (e.g. shells and seeds) or fibrous texture (e.g. plants), need **'macro-diminution'** to break them into fragments (Table 6.1). **'Micro-diminution'** should further increase the exposure area to digestive enzymes, especially by breaking down indigestible barriers at the tissue and cell level (e.g. plant cell walls). Some large food items, due to their easily digestible contents, merely need macrodiminution (e.g. fish); others, due to their small size, merely require micro-diminution (e.g. phytoplankton, sessile algae and micro-crustaceans). For breakdown of such food items homodont dentitions are sufficient. Many food types need both macro- and micro-diminution for effective digestion (Table 6.1). Therefore many cyprinids have heterodont dentitions gradually changing from anterior teeth, built for macrodiminution (e.g. crushing), to posterior teeth, built for

microdiminution (e.g. grinding). Since material properties differ among both large and small food items, different masticatory operations are required for the effective breakdown of either.

Mechanical breakdown of food in fish has been reviewed by Sibbing (1991*b*). Strength, compliance and notch-sensitivity are the major food properties for fish to cope with (Table 6.1, Figs 6.2, 6.3). Tooth profiles and their movements determine the type of loading they can exert (Sibbing 1991*b*). Accordingly, masticatory operations in cyprinid fish have been modelled into crushing, splitting, piercing (compression between the occlusal surfaces dominates) and grinding, cutting, tearing and shearing (adding a second movement component, parallel to the occlusal surfaces, causing tension and/or shear; Sibbing 1991*b*). The masticatory modes required for specific food types and sizes are listed in Table 6.2 together with the structural requirements for their operation in fish.

Strong v. weak materials

Maximal stresses (Nm^{-2}) increase with reduction of the contact area between food, teeth and chewing pad (occlusal surfaces) at constant muscular power. Strong materials (mollusc shells, seeds, some macrophytes and macro-arthropods) require high masticatory stresses, and hence small contact areas in occlusion (e.g. in piercing, shearing and lacerating). Crushing serves diminution of large, strong and stiff materials, which by their shape and orientation determine the contact area. Hence, the tooth crown for crushing is generally large and rounded, absorbing high reactive stresses. The closer the teeth are to the rotational centre of the jaws (small output lever teeth, A2OL), the higher their force output and the smaller their amplitudes (e.g. nut cracker). At the same time high stresses on strong food items require strong, and therefore heavy, pharyngeal jaws (PJM) in order to absorb reaction stresses.

The implantation of the pharyngeal teeth, measured as their impact angle (between their length-axis and the occluding chewing pad surface), should be in line with the direction of loading thus avoiding large bending moments on the teeth which might cause them to break. Crushing shells and seeds on the chewing pad therefore requires an impact angle approaching 90°, i.e. perpendicular to the chewing pad. If horizontal movements of the teeth, parallel to the chewing pad, dominate (as in grinding phytoplankton, algae and plant fragments), their impact angle should approach zero. Hence, the impact angle of teeth predicts the type of loading they usually exert, and so their role in mastication (cf. Nagelkerke and Sibbing 1996*b*). The width of the tooth base (A2W) reflects the amount of stress it can maximally resist.

A long tight symphysis (SymL) and strong muscles between left and right pharyngeal jaw will at the same time stabilise and severely restrict their intrinsic movements. In high-loading operations, that require only small amplitudes (crushing and splitting strong-stiff non-fibrous materials such as mollusc shells, seeds and some macro-crustaceans) this is an advantage, but it is disadvantageous when large amplitudes are required.

Compliant v. stiff materials.

Large movements are required for breaking compliant materials. The excursion range of the pharyngeal teeth increases with the absolute angle of jaw rotation and their relative distance from the centre of rotation. The latter is measured as their output levers (A2OL). Interdigitation of teeth (IntDig) almost doubles the amplitudes of tooth movements and is a precondition for shearing. Long output levers for large deformation of the food result in slender pharyngeal jaws (low PJM/PJL). Diminution of extremely tough materials, combining high strength and high compliance, require the most heavy pharyngeal jaws with long output levers for the teeth.

Long symphyses (SymL) stabilising high-stress compression between pharyngeal jaws and chewing pad restrict intrinsic pharyngeal jaw and teeth movements for tension and shear. Thus the set of requirements for strong-stiff materials (shells, seeds) and pliant-fibrous food types (macrophytes) are incompatible. Such conflicting demands allow clear distinctions in food types that can be utilised.

Notch-resistant v. notch-sensitive materials.

Fibrous materials are notch-resistant and most effectively diminuted by lacerating and shearing, combining high tensile stresses and large strain. Non-fibrous and especially brittle (non-yielding) materials are notch-sensitive and readily diminuted by cutting if they are compliant and by crushing or splitting if they are stiff. After macro-diminution, micro-diminution of many small particles of brittle or fibrous nature (especially plant fragments), is accomplished by grinding.

Digestion

Plant cell walls can be broken down by cellulases in e.g. cichlid fish species with stomach pH<2 (Moriarty 1973, Hofer 1988, 1991). Cyprinids, however, lack both a stomach and cellulases. Contributions of ingested prey or symbiotic micro-organisms in digesting plant cell walls are also negligible. Therefore, they only rely on mechanical breakdown for utilization of plants. The large proportion of indigestible structural polymers and long digestion time result in the need for voluminous and long intestines. In cyprinid fish intestinal length ranges from 2.5 SL (Standard body Length) in macro-herbivores to 17 SL for micro-herbivores (e.g. diatom feeders, Hofer 1991). The largest gut length found among cyprinids is 15-21 SL in the detritivorous *Labeo horie* (Bond 1979) feeding on detritus, which is largely composed of micro-organisms and decaying plant material, and contains a large indigestible fraction. In general, the relative gut length (GL) will increase with decreasing quality of the diet (Wootton 1990). A large body cavity is needed to accommodate such voluminous intestines and increases the length, width and/or depth of such fish. This may well result in relatively long bodies and thus short heads (HL/FL), especially in riverine species which need to be streamlined.

For teleost fish in general (>10 cm body length), gut lengths range from 0.7-0.9 SL for specialised carnivores via 1.2-2.2 SL in omnivores to 5-29 SL in specialised herbivores (Kramer and Bryant 1995).

The lack of a stomach in cyprinid fish may also reduce storage capacity for large animal prey such as fish, even though the anterior part of the gut is extended and partly compensates for this.

All above elaborations (summarized in Table 6.2) form a solid base, composed of widely different characters which together underly the predictions about expected food types in the 14 *Barbus* species.

MATERIAL AND TECHNIQUES

Measurements

Measurements were taken on a total of 1307 barbs (fork length > 15 cm), caught by trawl and gill-nets in October 1992 until November 1995 in Lake Tana, Ethiopia. Most measurements were taken on fresh fish. Branchial sieve parameters were measured on material, preserved in a 4% formaldehyde solution. Pharyngeal jaw measurements were made on macerated pharyngeals, preserved in water. The measured parameters are summarized in table 6.3, and most of them are shown in Fig. 6.4. All measurements are in millimeters (mm) and grammes (g), unless otherwise stated.

The following parameters need further explanation:

-Filter area (FilAr) of the complete branchial sieve was calculated according to the formula: $14.4 \times \sum_{i=1}^{5} RLm \times CWm$,

in which RLm is the medial raker length and CWm is the medial channel width. These have been measured for 5 rakers and channels. The factor 14.4 (an average value for three Dutch cyprinids from the work of van den Berg et al. 1992) is a value to estimate the total filtering area, since we did not measure whole branchial sieves in this study.

-Opercular valve volume (OpVV) is the extra volume that can be sucked into the head with closed opercula, due to the width of the opercular membrane. The OpVV can be approximated as the rectangle of postorbital length (POrL) times opercular membrane width (OpMW). The POrL is taken as a measure of operculum length.

-Output lever of tooth A2 (A2OL) was taken as the distance from the anterior tip of the pharyngeal jaw to the basis of the A2 tooth, the second tooth of the medial row. This tooth is usually the largest tooth, responsible for the initial contact with the food.

-Palatal organ area (POAr) was calculated taking the left and right first and fourth gill-arches as the points of a trapezium.

- Pharyngeal gape diameter (PhG) was measured by inserting a marked cone-shaped wooden probe into the chewing cavity of fresh decapitated fish, until resistance was felt. The diameter of the stick was measured at the mark that was visible at the posterior side of the chewing cavity.

-Pharyngeal symphysis length (SymL) is the length of the symphysis between the left and right pharyngeal jaws, measured in macerated condition.

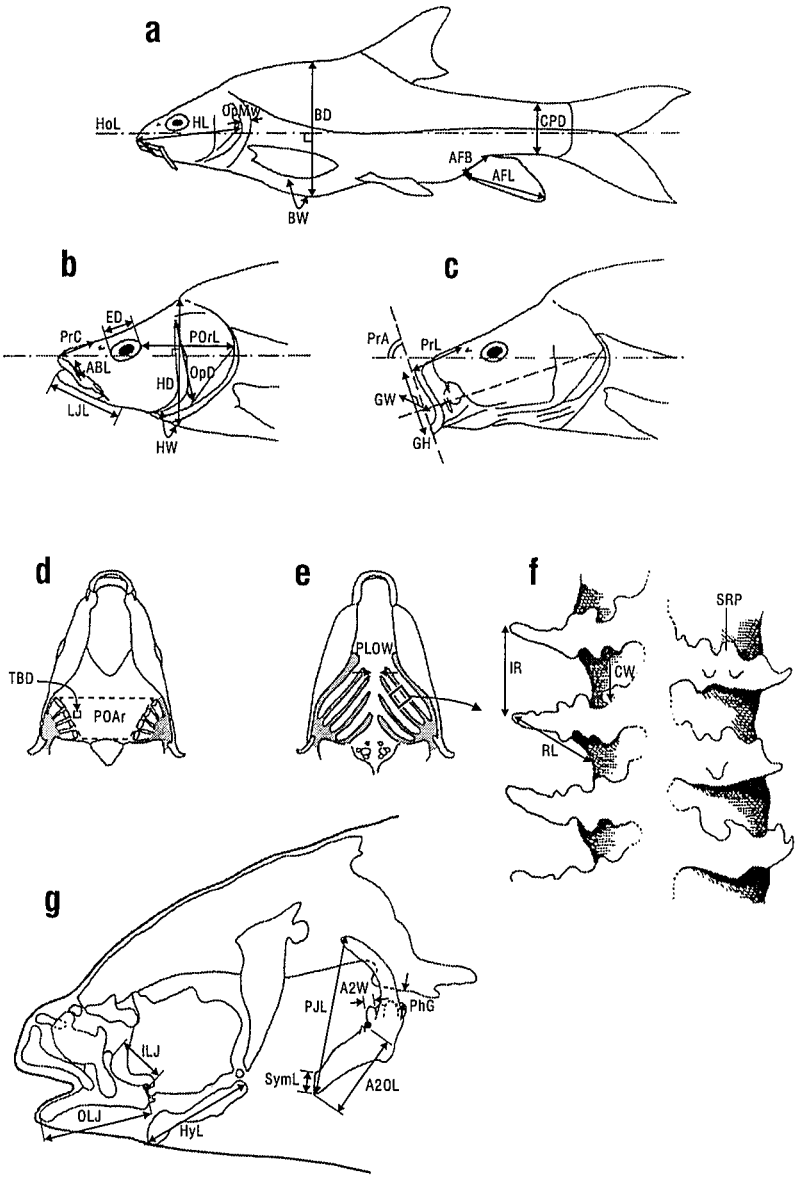


Fig. 6.4. Measurements taken on the *Barbus* species (cf. Table 6.3 for abbreviations and descriptions): (**a**) entire fish, lateral (HoL=horizontal line, the reference for angular measurements); (**b**) head, lateral, mouth closed; (**c**) head, lateral, mouth protruded; (**d**) pharynx roof seen from the interior of the mouth cavity, gill-arches are removed; (**e**) pharynx floor seen from the interior of the mouth cavity, gill-arches are removed; (**f**) gill-arch, dorsal side, the secondary raker profile (SRP) in the drawing has value 3 (on a scale from 1 to 5); (**g**) skeletal elements of the head, lateral.

- Postlingual organ width (PLOW) was measured as the distance between the left and right second gill-arches in the pharyngeal floor.
-Secondary raker profile (SRP) is our name for the outgrowths of the raker cushions (van den Berg et al. 1992, Zander 1906). SRP was categorized from 1 (hardly any outgrowths) to 5 (elaborate outgrowths).
-Taste bud density laterally on the palatal organ (TBD) was measured close to the second gill-arch in the pharyngeal roof. The taste buds were coloured *in situ* in freshly deep-frozen fish, modifying the method by Kiyohara et al. (1984). TBD decreases with body size, and therefore it was multiplied by fork length (FL), as this yielded a more constant value for each species.

Analysis

The predictions of potential food niches from structural parameters were made by comparing the hypothetical parameter values for effectively utilizing particular food types according to the food-fish model (Fig. 6.1*a*) (Table 6.2) with the actual measurements of the same parameters in the 14 *Barbus* species (Fig. 6.1*b*). This is the basis of the analysis. However, first the raw data had to be processed to allow for useful comparisons. All analysis steps are shown in Figure 6.5.

Processing of the data

The hypothetical profiles for the effective utilization of particular food types (Table 6.2, the predicted data sets), as well as the measurements on the barbs (the measured data sets), had to be separately prepared for analysis.

Predicted data set

The hypothetical profiles for the effective utilization of particular food types (Table 6.2) were translated into numbers ('--'=-2; '-'=-1; '0' =0; '+'=1; '++'=2), resulting in the predicted data set (Table 6.4) that can be compared to the measured values of the same parameters in the *Barbus* species.

Measured data set

The raw data-matrix of the 1307 specimens is a compilation of measurements that have been performed on the Lake Tana barbs over 1992-1995. Different character-sets have been measured on different specimens (e.g. branchial sieve characters were measured on one series of specimens, external head parameters were measured on another series), resulting in a compiled raw data-matrix with many missing values. As a consequence, a multivariate dimension-reduction technique, such as principal component analysis (PCA), cannot be performed meaningfully on the whole data-matrix. Therefore, we searched for a method which gives one numerical value for each parameter for each species, because despite the fact that not all measurements were taken on all specimens, they were taken on (almost) all species. The absolute numerical value was not important, since it was only used as a comparative value among the species, but it did need to reflect the variation

Table 6.3. Parameters, measured in 1307 *Barbus* specimens larger than 15 cm FL, their abbreviations, source or description (cf. Fig. 6.4), and derived ratios. B,S,O & H: Van den Berg et al. (1992); C: Chu (1935); H,B&E: Holčik et al. (1989); H&L: Hubbs & Lagler (1947); M: Muller (1987) ; N&S: Nagelkerke & Sibbing (1997); N,S,B,L&O: Nagelkerke et al. (1994); N,S&O: Nagelkerke et al. (1995); W&R: Wainwright & Richard (1995); Z: Zander (1906).

Parameter	Abbreviation	Source or description	Ratios
Anal fin area	AFAr	Anal fin length * Anal fin base length	$(100*AFL*AFB)/(FL^2)$
Anal fin base length	AFB	H&L	
Anal fin length	AFL	H&L	
Anterior barbel length	ABL	N,S,B,L&O	ABL/FL
Body area	BAr	Body width * Body depth	(GH*GW)/(BD*BW)
Body depth	BD	H&L	BD/FL, BD/BW
Body width	BW	H,B&E	BD/BW
Caudal peduncle depth	CPD	H,B & E	CPD/FL
Eye diameter	ED	N&S	ED/FL
Filter area	FilAr	B,S,O&H (see formula in text)	$1000*FilAr/FL^2$
Fork length	FL	H,B & E	
Gape area	GAr	Gape height*Gape width (N,S & O)	(GH*GW)/(BD*BW)
Gape height	GH	N,S & O	
Gape width	GW	N,S & O	
Gut length	GL	N,S,B,L&O	GL/FL
Head depth	HD	H,B &E	
Head length	HL	H,B&E (excluding the opercular membrane)	HL/FL
Head width	HW	H,B &E	
Hyoid length	HyL	M	HyL/FL, HyL/LJL
In-lever lower jaw	ILJ	W&R	
Interdigitation pharyngeal teeth	IntDig	Presence or absence of interdigitation between left and right pharyngeal teeth	
Inter-raker distance, lateral	IRl	B,S,O&H	IRl/FL
Inter-raker distance, medial	IRm	B,S,O&H	IRm/FL
Kinematic efficiency closing lower jaw	OLJ/ILJ	W&R	OLJ/ILJ
Lower jaw length	LJL	N,S,&O	LJL/FL
Opercular depth	OpD	N&S	POrL/OpD
Opercular membrane width	OpMW	H,B &E	
Opercular valve volume	OpVV	Opercular membrane width * Postorbital length	$1000*(OpMW*POrL)/ FL^2$
Oral gape diameter	OG	Average of oral gape width and gape height (N,S&O)	(GH+GW)/(2*FL)
Out-lever lower jaw	OLJ	W&R	
Output lever tooth A2	A2OL	Distance between tip of pharyngeal and basis of tooth A2 (second tooth of medial row)	A2OL/PJL

Table 6.3. (continued).

Parameter	Abbreviation	Source or description	Ratios
Palatal organ area	POAr	Surface area of the pharynx roof, calculated as a trapezium using the left and right, first and fourth gill-arches as points	$100*POAr/FL^2$
Pharyngeal gape diameter	PhG	As measured by inserting a marked conical stick between pharyngeal teeth and chewing pad	PhG/FL
Pharyngeal jaw length	PJL	C	$10^5*PJM/PJL^3$
Pharyngeal jaw mass	PJM	Wet mass of cleaned pharyngeal (average of left and right jaw)	$(10^8*PJM)/FL^3$
Pharyngeal symphysis length	SymL	Length of the symphysis between left and right pharyngeal jaw	SymL/PJL
Pharyngeal tooth A2 hooks	A2Hook	Presence or absence of a hook on the A2 tooth (second tooth of medial row)	
Pharyngeal tooth A2 width	A2W	Width of base of A2 tooth (second tooth of medial row);C	100*A2W/FL
Pharyngo-opercular volume	PhOpV	Volume of the cone with the Postorbital length as length, the ellips with radii Head depth and Head width as basis, and the ellips with radii *Operculum depth and Head width as top*	$\{100*\pi/2*([OpD*HW]+[HD*HW])*POrL\}/FL^3$
Postlingual organ width	PLOW	Width of the pharynx floor between the left and right second gill-arches	PLOW/FL
Postorbital length	POrL	*H,B &E (estimate for Operculum length)*	
Protrusion angle	PrA	N&S	PrA
Protrusion chain length, closed	PrC	N,S,&O	
Protrusion chain length, open	PrL	N,S,B,L&O	
Protrusion length increase	Prot	Protrusion chain length, open - Protrusion chain length, closed	(PrL-PrC)/FL
Raker length, lateral	RLl	B,S,O&H	RLl/FL
Secondary raker profile	SRP	Outgrowths of the raker cushions, ranging from 1 (almost absent) to 5 (very elaborate ourgrowths); Z	
Taste bud density on lateral palatal organ	TBD	Taste bud density of the palatal organ at basis of second gill arch	TBD*FL

within each species. Therefore, a simple arithmetic mean of each parameter did not suffice. Thus we chose a method that provided us with relative numerical values for each parameter for each species, which only differed among species when there was a statistically significant difference between them: the generalized gap-coding procedure (Archie 1985).

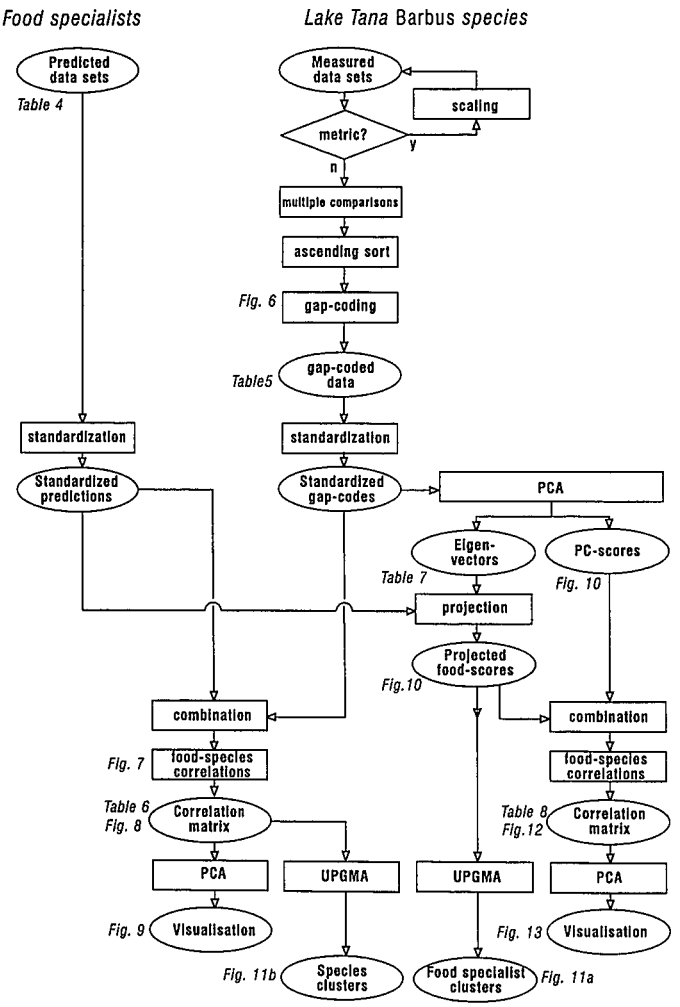


Fig. 6.5. Flow chart presenting the successive and alternative steps in the construction of quantitative diet predictions from morphometric data sets measured from the *Barbus* species. Ellipses are data sets, rectangles are operations on data sets, diamonds represent choices (y=yes, n=no). The figures and tables in which the data-sets and operations can be found are indicated.

Table 6.4. Predicted relative values of fish parameters, meeting the demands imposed by the properties of different food types, according to the food-fish model. Only those characters from Table 6.2 that were actually measured in the barbs have been translated numerically: -2=--, very low value demanded; -1=-, low value demanded; 1=+, high value demanded; 2=++, very high value demanded; 0=no specific demands, neutral parameter. If food categories have varying properties the relative values have been averaged (e.g. '-' and '++' becomes '0.5'). For abbreviations see Tables 6.2 and 6.3.

	Phyto-plankton (t)	Phyto-plankton (p)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (t)	Micro-crustaceans (p)	Macro-crustaceans	Larvae/ worms
ABL/FL	0	0	0	0	0	2	0	0	0	2
ED/FL	0	0	0	0	0	0	0	1	0	0
BD/FL	-1	0	0	1	1	1	-1	0	0	1
BD/BW	0.5	0	0	0	0	0	0.5	0	0	0
GAr/BAr	1	0	0	0	0	0	1	0	0	0
CPD/FL	-1	0	0	0	0	0	-1	0	0	0
AFAr	-1	0	0	0	0.5	0.5	-1	0	0	0.5
PrA	0	0	0	0	0	-1	0	0	0	-1
Prot	0	0	0	-2	1	2	0	0	1	2
LJL/FL	0	0	-1	-2	0	0	0	0	0	0
OLJ/ILJ	0	0	-1	-2	0	0	0	0	0	0
PhOpV/FL[3]	0	1	0	0	0	0	0	1	0	0
HL/FL	1	1	-1	-1	0	0	1	1	0	0
HyL/FL	0	0	0	0	0	0	0	0	0	0
HyL/LJL	0	0	0	0	0	0	0	0	0	0
POrL/OpD	0	1	0	0	0	0	0	1	0	0
OpVV	0	0	0	0	0	0	0	0	0	0
RLI/IRI	2	2	0	0	0	0	2	2	0	0
OG/FL	2	0	0	0	0	-1	2	0	0	-1
PhG/FL	0	0	0	0	0.5	0	0	0	1	0
RLI/FL	2	2	1	0	0	1	2	2	0	0
IRm/FL	-2	-2	-1	0	0	-1	-2	-2	0	0
SRP	2	2	1	0	0	1	2	2	0	0
FilAr/FL[2]	2	2	1	0	0	1	2	2	0	0
TBD*FL	0	0	0.5	0	0	2	0	0	0	2
POAr/FL[2]	0	0	0.5	0	0	2	0	0	0	2
PLOW/FL	0	0	0	0.5	0	0	0	0	0.5	0
PJM/FL[3]	0	0	0	1	1	0	0	0	0.5	0
IntDig	-1	-1	-1	1	-1	0.5	-1	-1	-1	0
A2OL/PJL	0.5	0.5	0.5	2	-0.5	1	0.5	0.5	0	1
SymL/PJL	0	0	0	-1.5	1	-1	0	0	0.5	-1
PJM/PJL[3]	0	0	0	-1	1	-0.5	0	0	0	-0.5
A2Hook	-2	-2	-2	0.5	-1	0.5	-2	-2	0.5	0.5
A2W/FL	0	0	0	0	1	0	0	0	0	0
GL/FL	1	1	1	0.5	0	2	0	0	0	0

The detailed steps of the procedure were as follows (cf. Fig. 6.5).

1) In the case of metric distance measures individual parameters were scaled to compare shape-differences between species separately from size-differences (the size-range of specimens was already limited to >15 cm fork length). Scaling was done by the use of ratios. Ratios can cause statistical problems because of the underlying correlations between numerator and denominator (Albrecht, 1978; Reist, 1984), especially in a multivariate context. Other authors (James & McCulloch, 1990) maintain that the problems with ratios are not necessarily greater than those with raw data.

Since the calculated ratios were almost always normally distributed (even without ln-transformation), and were only used for univariate comparisons we considered their use justified.

2) Differences in the means of normally distributed ratios, codes and angles among species were tested using the Tukey-Kramer method for multiple, unplanned comparisons, as this method is well suited for unequal sample sizes (Sokal & Rohlf, 1995). The significance level was set at $p<0.05$.

Non-normally distributed parameters were tested nonparametrically using a Mann-Whitney U-test for two samples (Sokal & Rohlf, 1995: p.427). To adjust for the number of comparisons among all 14 species (i.e. 14*(14-1)/2=91), the significance level was adjusted to $1-(1-0.05)^{1/91}=0.00055$ (Dunn-Šidák method: Sokal & Rohlf, 1995: p. 239).

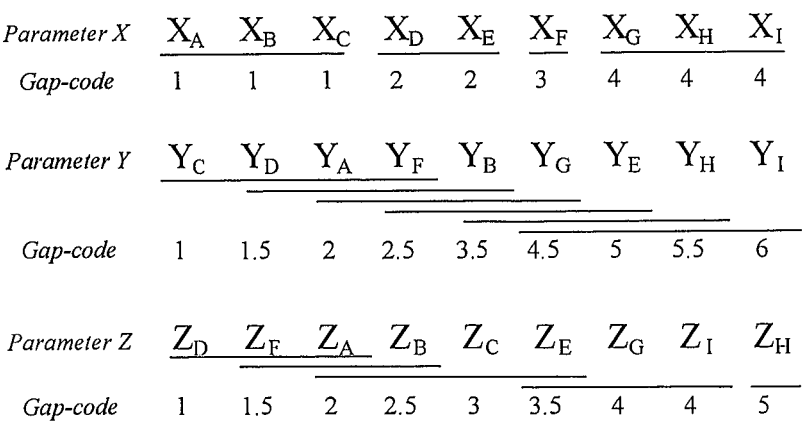


Fig. 6.6. An example of the gap-coding procedure for morphometric data (adapted from Simon, 1983). X, Y, and Z are different parameters. The suffixes A, B, C...I indicate the species. The mean parameter values for individual species are sorted in ascending order. Lines connect mean values of a parameter that are not significantly different, following the generalized gap-coding method of Archie (1985). Each start or stop of a line adds 0.5 to the gap-code. Lines can be non-overlapping (top), regularly overlapping (middle), or a complex situation can occur (bottom).

3) For each parameter separately the means for all the species were sorted in ascending order (Fig. 6.6). Means that are not significantly different are joined by a line, according to the generalized

gap-coding procedure (Archie, 1985). Gap-coding procedures are used to (graphically) summarize statistically significant differences among species means of measured parameters. Each species is coded numerically, according to the method of Simon (1983) and Archie (1985). The first species (i.e. the one with the lowest mean value) receives code 1 and every line that appears or disappears in consecutive species results in an addition of 0.5 for the code. If a line stops at one species and a new one begins at the next species, this should be read as the disappearance of the first and the appearance of the next line, resulting in an addition of 0.5+0.5=1. An example is shown in Fig. 6.6.

This procedure results in a measurement matrix containing for each species a code for each parameter: the measured data set (Table 6.5; note that also the average values of each parameter are listed in this table for comparison with other studies and/or fish groups; they are not used in the further analysis however).

Comparison of predicted and measured data sets to predict potential food niches

At this stage we have a predicted (Table 6.4) and a measured (Table 6.5) data set which can be compared with each other to predict potential food niches. The ranges of the predicted and measured parameter values are different (from -2 to 2 for the predicted values; from 1 to maximally 8 for the measured values). Therefore we standardized both data sets separately by subtracting from each value for a particular parameter the parameter-mean and dividing it by the standard deviation of the parameter. This results in a standardized predicted data set, and a standardized measured data set which can be compared.

This comparison is performed by taking the standardized measured parameter set of a species and the standardized predicted parameter set of a particular food type specialist and calculating the correlation coefficient between them. A graphical example is given in Figure 6.7. The standardized measured value of each parameter is taken as the X-coordinate, and the standardized predicted value of the same parameter as the Y-coordinate. This is done with all parameters, resulting in a cloud of points, each representing a different parameter. A linear regression is performed through these points. The resulting correlation coefficient is regarded as the summary of the total fit between the predicted and measured values of all parameters. If high predicted values of a food type match with high measured parameter values of a species this means that the overall fit of that species with that food type is high. This is expressed in a high correlation coefficient. High correlations are interpreted as high capability to eat a particular food type. All species-food type correlations are listed in Table 6.6. The size and direction of the correlations form a quantitative prediction as to how important a certain food type will be in the diet of a fish species.

Table 6.5. Gap-codes (see text) assigned to measured fish parameters (abbreviations in Table 6.3). Average values of the original parameters are listed below the gap-codes. Italics indicate for which species parameters show extreme (minimum or maximum) values. The range of specimen numbers for individual characters is indicated below the species names. The bottom of the table lists the number of parameters analyzed for each species (note that OLJ/ILJ and IntDig do not differ among the barb species; they are not used in the further analysis, making the maximum number of parameters 33), and the number of extreme values per species.

		B acutirostris	*B brevicephalus*	*B crassibarbis*	*B dainellii*	*B gorgorensis*	*B gorguan*	*B longissimus*	*B macrophtalmus*	*B megastoma*	*B nedgia*	*B platydorsus*	*B surkis*	*B truttiformis*	*B tsanensis*
	# specimens	10-45	9-26	8-21	7-35	7-15	10-26	9-16	10-29	10-39	8-52	10-47	9-45	10-28	8-47
Search and detection	ABL/FL	*1*	3	7	3.5	6	2.5	*1*	1.5	*1*	6	4.5	3	1.5	5.5
		0.028	0.037	0.058	0.038	0.050	0.035	*0.023*	0.029	*0.029*	0.051	0.043	0.038	0.029	0.047
	ED/FL	6.5	7	4.5	3	1.5	4.5	*1*	*8*	4	4.5	5.5	5.5	2	5.5
		0.048	0.049	0.041	0.039	0.036	0.043	0.035	0.059	0.041	0.042	0.044	0.045	0.037	0.044
Approach	BD/FL	*1*	4	4.5	*1*	6.5	2	1.5	4.5	*1*	3	4.5	*7*	4.5	5.5
		0.219	0.238	0.243	0.215	0.269	0.224	0.221	0.239	0.215	0.236	0.243	0.270	0.242	0.253
	BD/BW	2.5	*3*	2	1.5	2.5	*1*	1.5	2.5	1.5	1.5	1.5	*3*	1.5	2.5
		1.99	2.14	1.93	1.87	1.99	1.71	1.82	2.00	1.90	1.91	1.88	2.14	1.83	1.99
	GAr/BAr	5.5	1.5	3.5	*6*	2.5	5.5	4.5	3.5	5.5	2	4	*1*	5	2.5
		0.272	0.111	0.218	0.358	0.115	0.282	0.241	0.209	0.285	0.112	0.231	0.083	0.248	0.145
	CPD/FL	*1*	6.5	7.5	1.5	7	2.5	5.5	4.5	2	6.5	3.5	6	*8*	7
		0.085	0.099	0.103	0.088	0.102	0.091	0.098	0.095	0.090	0.100	0.093	0.098	0.106	0.102
	100*AFAr/FL^2	*1*	2.5	3	2.5	*4*	2.5	1.5	3.5	2	3	3	3	*4*	2.5
		1.07	1.21	1.24	1.19	1.32	1.19	1.12	1.28	1.13	1.25	1.24	1.23	1.30	1.19
Intake	PrA	3	*1*	*1*	*1*	1.5	2.5	*4*	3	*4*	*1*	3	2	3	*1*
		65.8	50.6	46.9	46.2	52.7	63.5	77.6	68.0	79.6	47.5	65.8	58.7	67.1	49.6
	Prot/FL	1.5	2	*4*	3.5	2.5	3	1.5	3	1.5	3.5	1.5	1.5	*1*	3.5
		0.041	0.040	0.066	0.051	0.047	0.047	0.038	0.048	0.039	0.051	0.040	0.037	0.031	0.051
	LJL/FL	*5*	1.5	*5*	*5*	2	*5*	*5*	4.5	*5*	3	4	*1*	3	3
		0.109	0.077	0.108	0.110	0.082	0.107	0.109	0.104	0.110	0.092	0.100	0.075	0.095	0.090
	(OLJ/ILJ)	1		1	1		1	1	1	1		1		1	1
		0.355		0.340	0.343		0.354	0.330	0.357	0.362		0.345		0.330	0.347
	100*PhOPV/FL^3	2.5	*1*	6.5	4	5.5	7	4	4	3	4.5	6.5	1.5	5.5	5.5
		0.487	0.354	0.710	0.576	0.605	0.774	0.588	0.569	0.488	0.595	0.710	0.413	0.631	0.619

Table 6.5 (continued).

		B acutirostris	*B brevicephalus*	*B crassibarbis*	*B dainellii*	*B gorgorensis*	*B gorguari*	*B longissimus*	*B macrophtalmus*	*B megastoma*	*B nedgia*	*B platydorsus*	*B surkis*	*B truttiformis*	*B tsanensis*
Intake (continued)	HL/FL	*5*	*1*	4	*5*	2	*5*	4	4	4	4	4	*1*	3	3
		0.271	0.206	0.250	0.274	0.222	0.267	0.250	0.251	0.248	0.247	0.253	0.205	0.238	0.237
	HyL/FL	2.5	.	1.5	*3*	.	2.5	3	2.5	2	.	*3*	.	2.5	*1*
		0.105		0.096	0.110		0.105	0.110	0.103	0.100	.	0.111	.	0.102	0.092
	HyL/LJL	2	.	*1*	3	.	3.5	*4*	2	1.5	.	*4*	.	3.5	3.5
		0.964		0.920	0.994		1.014	1.053	0.966	0.942	.	1.054	.	1.024	1.008
	POrL/OpD	*7*	1.5	3	6	2	5.5	5.5	3.5	5.5	2	4.5	*1*	5.5	3
		1.657	1.149	1.237	1.490	1.201	1.449	1.431	1.260	1.449	1.177	1.333	1.114	1.409	1.230
	1000*OpVV/FL^2	*4*		*1*	3	.	*4*	*1*	2	2	.	3.5	.	2	1.5
		1.24		0.76	1.15		1.27	0.79	0.95	0.91	.	1.19	.	0.90	0.89
	RLl/IRl	*1*	4.5	*1*	*1*	2.5	2	*1*	3	*1*	3.5	1.5	*5*	1.5	4
		1.09	1.61	1.00	0.98	1.29	1.22	1.01	1.39	1.06	1.43	1.19	1.64	1.13	1.45
Size selection	OG/FL	4	*1*	3	6.5	1.5	*7*	6	4.5	4.5	2.5	5.5	*1*	4.5	2.5
		0.082	0.060	0.076	0.090	0.065	0.090	0.086	0.084	0.083	0.073	0.086	0.057	0.084	0.071
	PhG/FL	2		1.5	1.5	1.5	1.5	1.5	1.5	1.5	*1*	1.5	.	1.5	*1*
		0.052		0.043	0.049	0.043	0.052	0.045	0.050	0.048	0.043	0.051	.	0.050	0.043
	RLl/FL	2	3	*1*	*1*	2	*3*	1.5	*3*	*1*	*3*	2.5	2.5	*3*	3
		0.0061	0.0068	0.0054	0.0053	0.0060	0.0070	0.0056	0.0075	0.0056	0.0066	0.0066	0.0065	0.0071	0.0070
	IRm/FL	2	*1*	2	2.5	1.5	2.5	2	2	.	2	2.5	*1*	*3*	2
		0.0053	0.0039	0.0052	0.0054	0.0046	0.0055	0.0051	0.0052	.	0.0047	0.0053	0.0039	0.0061	0.0049
	SRP	1.5	5	1	1.5	3	1.5	1	3.5	2.5	3.5	2	4	3	4
		1.89	4.75	1.20	1.50	2.67	1.40	1.22	3.25	2.46	3.10	2.30	3.93	2.50	3.57
	1000*FlAr/FL^2	2.5	1.5	1.5	1.5	2	2.5	1.5	3	.	2.5	3	*1*	3	*3*
		1.47	1.18	1.20	1.16	1.25	1.46	1.24	1.76	0.00	1.49	1.86	1.05	1.72	1.65

Table 6.5 (continued).

		B.acutirostris	*B.brevicephalus*	*B.crassibarbis*	*B.dainellii*	*B.gorgorensis*	*B.gorguari*	*B.longissimus*	*B.macrophtalmus*	*B.megastoma*	*B.nedgia*	*B.platydorsus*	*B.surkis*	*B.truttiformis*	*B.tsanensis*
Taste selection	TBD*FL	*1*	2.5	.	.	.	.	.	1.5	.	*4*	.	3.5	.	*4*
		48485	76421	.	.	.	.	.	62011	.	110077	.	91863	.	110974
	100*POAr/FL^2	*3*	*1*	.	.	.	.	.	2	.	3	.	*3*	.	*3*
		0.309	0.266	.	.	.	.	.	0.307	.	0.314	.	0.321	.	0.338
Transport	PLOW/FL	3.5	1.5	3	*1*	2.5	*4*	*4*	1.5	.	2	2.5	1.5	3.5	*1*
		0.01216	0.00972	0.012062	0.007716	0.011952	0.015083	0.013396	0.009801	.	0.01033 8	0.011094	0.00956 8	0.012329	0.009175
Pharyngeal mastication	10^6*PJM/FL^3	*1*	.	3	2	*4*	2	2	2	2	2.5	2	3	1.5	2
		1.00284	.	1.49812	1.12078	5.49074	1.39434	1.1503	1.09734	1.08821	1.40157	1.33178	1.49649	1.02263	1.38958
	(IntDig)	1	.	1	1	1	1	1	1	1	1	1	1	1	1
		0	.	0	0	0	0	0	0	0	0	0	0	0	0
	A2OL/PJL	6.5	.	4	5	*1*	3.5	*7*	4	*6*	3.5	4	1.5	5.5	2.5
		0.51226	.	0.45606	0.47658	0.39235	0.4548	0.52711	0.46149	0.49304	0.45378	0.46162	0.42087	0.48362	0.43279
	SymL/PJL	*1*	.	2	*1*	*4*	1.5	2	1.5	2	2.5	1.5	3	*1*	2.5
		0.17535	.	0.19763	0.17622	0.27065	0.19184	0.19414	0.19005	0.19434	0.2184	0.1914	0.22303	0.18025	0.21536
	10^5*PJM/PJL^3	1.5	.	*1*	*1*	*3*	1.5	1.5	*1*	*1*	1.5	*1*	2	*1*	1.5
		2.6207	.	2.1831	2.1654	6.6448	2.7733	2.6455	2.357	2.3596	2.7315	2.5785	3.3234	2.3703	2.5884
	A2Hook	*2*	.	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*
		1	.	0.77778	1	0.2	0.91667	1	1	1	0.96429	1	1	1	0.85714
	100*A2W/FL	*1*	.	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
		0.93049	.	0.99657	0.98372	1.9348	0.92635	0.95651	0.91558	0.92189	1.02621	0.99501	1.0425	0.9513	0.96942
Digestion	GL/FL	1.5	4	5	*1*	*7*	1.5	2	2.5	3	6	2.5	*7*	3	5.5
		1.698	2.054	2.273	1.516	3.399	1.655	1.708	1.821	1.908	2.412	1.831	2.898	1.916	2.277
	# parameters	*33*	*23*	31	31	*28*	31	31	*33*	*28*	30	31	29	31	*33*
	# extremes (%)	*45*	35	32	*42*	25	29	35	*15*	29	20	*16*	*45*	29	27

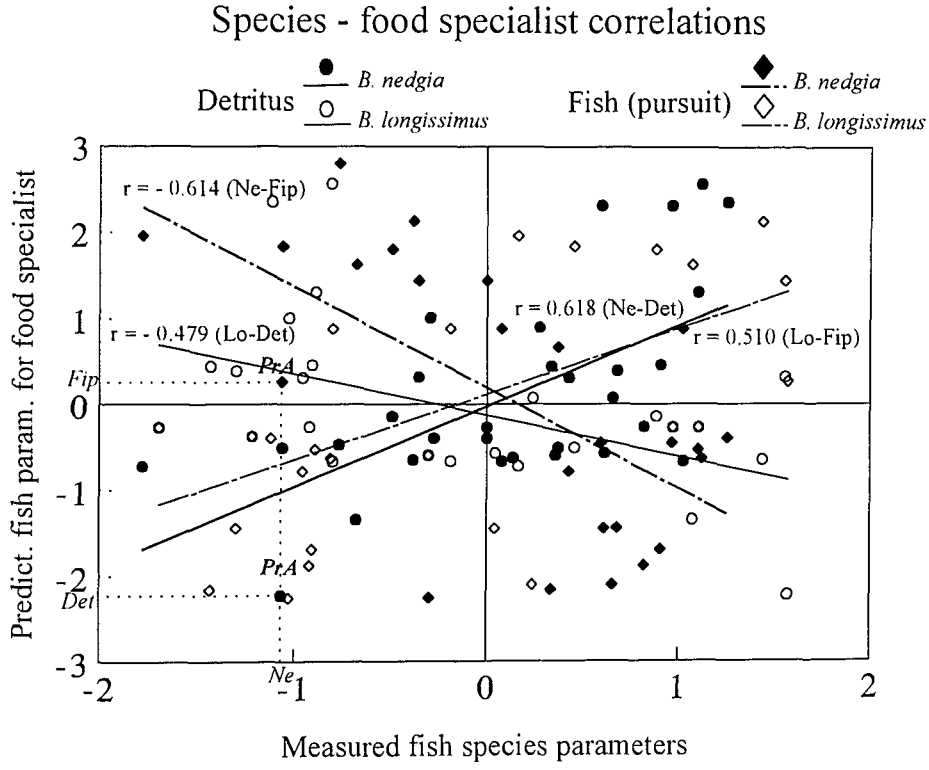


Fig. 6.7. An example of correlations between the fish parameter values derived from food properties (detritus/substratum and fish [pursuit]; standardized values on the Y-axis) and the parameter values, measured in the *Barbus* species (*B. nedgia* and *B. longissimus*; standardized values on the X-axis). Every data-point represents one fish parameter (e.g. protrusion angle, PrA). In the graph two data-points are explained. On the X-axis the standardized value for the PrA of *B. nedgia* is indicated (-1.07). On the Y-axis the standardized value for PrA for detritus (-2.23) and fish (0.267) are indicated. This results in the data-points (-1.07 , -2.23) for PrA in the regression of *B. nedgia* with detritus, and (-1.07 , 0.267) for PrA in the regression of *B. nedgia* with fish. The whole cloud represents the complete character set, and the regression line gives the total fit of a fish to a food type. The larger the positive correlation is, the larger the predicted ability of a fish species to utilize this food type successfully. Negative correlations suggest serious limitations of a fish species to feed on a certain food type. This example suggests that *B. longissimus* is an able piscivore, but performs poorly on detritus, while *B. nedgia* is a poor fish-eater and is better at eating detritus. It is important to note that correlation values are mainly interesting in a comparative way among the measured *Barbus* species. Such correlation factors of all fish species versus all food type specialists are given in Table 6.6 and Fig. 6.8.

Intercorrelation among the measured parameters and its complications

An alternative comparison between predicted and measured data sets is performed, by first performing a principal components analysis (PCA) on the measured data sets before calculating correlations between the two. The reason for this is the (sometimes strong) correlations of the measured parameters with each other (e.g. large heads and long lower jaws are strongly correlated). This could lead to artifacts in the construction of diet predictions: it is e.g. possible that the strong correlation between head length and lower jaw length causes disproportionate mutual enhancement

of their influence in the diet predictions. Principal components (PCs) are linear combinations of the original parameters (the factors of the linear combinations are described by eigenvectors), but they are by definition uncorrelated. By first performing a PCA on the measured parameter values, resulting in a new parameter data set (consisting of uncorrelated PC-scores) we expect to avoid the problem of intercorrelations among original parameters.

The PCA is performed on the standardized measured data-set, resulting in a data set of PC-scores (cf. Fig. 6.10). The standardized predicted values for effective utilization of food types are projected in PC-space, using the eigenvectors of the PCA. This means that food specialists are projected into the measured morphological species space: the matching between food specialists and our barb species. These projections have their own PC-scores. PC-scores of measured and predicted data-sets, as well as the original parameters can be graphically represented in a biplot (cf. Fig. 6.10).

Now we have a data set with PC-scores of measured data and a data set consisting of PC-scores of the predicted data set. The correlations between these two data sets can be calculated in the same way as for the original measured and predicted data sets (Fig. 6.7, Table 6.8), and can be used as alternative quantitative diet predictions.

Visualization of diet predictions

In order to visualize the diet predictions a PCA can be performed on the correlation matrix between food types and species (Table 6.6 or 6.8). In this case the PCA is only performed to summarize the diet predictions in a single plot, saving as much of the original variation as possible (dimension reduction). In these plots (Figs. 6.9, 6.13) the proximity of species reflects their similarity in diet predictions.

This can also be shown differently by performing an UPGMA-clustering (unweighted pair-group method clustering, using the arithmetic average, Rohlf 1993) on the same data, resulting in a tree of species (Fig. 6.11*b*), in which clusters can be interpreted as trophic groups (since they have similar predicted diets). UPGMA-clustering was also used to make a tree of the food types, based on their PC-scores that were projected in morphological fish space. This tree (Fig. 6.11*a*) shows the similarity of food types as 'perceived' by the fish.

Results

The morphometric data sets of Lake Tana *Barbus* feeding structures

The actually measured values of fish parameters are listed in Table 6.5. Both the mean values and the assigned codes, according to the generalized gap-coding procedure (Archie, 1985), are listed. For all species together, a total of 1307 specimens have been measured (ranging from 7 to 47 measurements per parameter per species). Whereas for many characters a wide and significant

Table 6.6. Correlations coefficients between the fish parameter set predicted for feeding on a particular food type (Table 6.4) and the actual sets measured in the *Barbus* species (gap-codes, Table 6.5). Both data-sets were first standardized. Italics indicate minimum and maximum values per species (rows); minimum and maximum values per food type are underlined (columns). Note that only bold correlation coefficients are significant. However, our purpose is describing the pattern of correlations, not to test: therefore we also use non-significant correlations in our further analysis (see text). This table is visualized in Figures 6.8 and 6.9.

	Phyto-plankton (townet)	Phyto-plankton (pump)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (townet)	Micro-crustaceans (pump)	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish (pursuit)	Fish (ambush)
B.acutirostris	0.196	-0.281	*-0.339*	-0.113	-0.288	-0.326	0.246	-0.042	-0.001	-0.260	0.119	-0.245	***0.643***	0.155
B.brevicephalus	0.151	0.367	0.347	0.204	-0.033	0.106	0.128	***0.446***	-0.140	-0.036	-0.318	-0.066	*-0.406*	-0.394
B.crassibarbis	**-0.443**	-0.273	**-0.363**	-0.100	0.055	**0.372**	***-0.491***	-0.247	0.168	***0.482***	0.328	0.092	0.150	0.100
B.dainellii	-0.019	**-0.504**	***-0.595***	-0.254	-0.126	-0.094	0.049	**-0.394**	0.027	0.191	0.169	-0.171	***0.473***	**0.422**
B.gorgorensis	-0.103	0.172	0.380	-0.091	**0.647**	0.084	-0.158	-0.081	-0.051	-0.025	-0.272	***0.649***	***-0.441***	-0.267
B.gorguari	0.050	-0.177	***-0.398***	-0.266	-0.179	-0.349	0.134	-0.080	0.040	-0.180	0.229	-0.137	0.351	***0.362***
B.longissimus	-0.033	-0.319	-0.257	0.112	-0.106	***-0.479***	0.008	**-0.420**	0.169	-0.350	0.267	-0.051	***0.510***	**0.385**
B.macrophtalmus	0.241	0.287	-0.070	-0.097	-0.110	-0.262	0.301	***0.586***	-0.029	*-0.294*	0.044	-0.208	-0.068	-0.112
B.megastoma	0.245	-0.216	-0.234	0.025	-0.166	**-0.414**	0.251	-0.142	0.079	***-0.443***	0.285	-0.138	***0.566***	-0.014
B.nedgia	-0.049	**0.398**	0.306	-0.121	-0.069	***0.618***	-0.126	0.206	-0.174	**0.467**	-0.264	-0.076	***-0.614***	-0.237
B.platydorsus	-0.122	-0.102	-0.153	0.158	-0.270	-0.196	-0.057	0.055	-0.150	-0.070	0.197	*-0.320*	0.144	***0.423***
B.surkis	-0.038	0.217	***0.447***	0.236	0.237	0.237	-0.116	0.144	0.104	0.090	-0.293	0.290	***-0.518***	**-0.455**
B.truttiformis	-0.100	-0.022	0.178	***0.419***	-0.204	-0.120	-0.074	-0.187	-0.034	-0.096	0.216	*-0.276*	0.010	0.259
B.tsanensis	0.132	**0.422**	**0.370**	-0.116	-0.003	***0.527***	0.086	0.331	-0.175	**0.393**	**-0.412**	-0.064	***-0.507***	**-0.491**

differentiation has been measured (gap-codes ranging up to 7), some other characters were uniform (e.g. no barb had interdigitating pharyngeal teeth). Note that the percentage of extreme gap-code values for the whole set of characters differs considerably among species, ranging from 15% in *B. macrophtalmus* to 45% in *B. acutirostris* and *B. surkis*, suggesting that the first species has a generally much more average morphology than the other two. The predicted data set for effective utilization of a particular food type, derived from the food-fish model (see Methodology) have also been coded numerically (Table 6.4).

Predicted and measured data sets are compared to construct quantitative diet predictions, using two alternative methods (cf. Fig. 6.5): 1) by directly calculating correlations between predicted and actual data sets, and 2) by calculating correlations between PC-scores of predicted and actual data sets (see Material & Techniques for the reason of these two alternatives).

Predicting diets from the original measured fish parameter set

To investigate the matching between the measured data set of each barb (Table 6.5) and each predicted data set for effective utilization of a food type (Table 6.4), correlation coefficients were calculated for each combination, using the full set (from 23 to 33, depending on the number of missing values) of characters. This resulted in correlations for all food-species combinations (Table 6.6, Fig. 6.8), which are considered measures of the overall fit, and therefore of the overall capability of a species to utilize a particular food type. This does not mean that this fit has to be corroborated by each individual parameter. This can be seen in Figure 6.7, which shows that even though *B. longissimus*'s overall fit with piscivory (open diamonds) is good, some characters deviate strongly from the general regression trend. It should be clear that this is a relative scale as it is exclusively based on mutual comparisons of the Lake Tana barbs.

The correlation matrix of all food type specialists - species combinations is listed in Table 6.6 and shown in Figure 6.8. Of the 378 possible (also among species and among food types) correlations that were calculated, 52 were significant, meaning that the matrix contains useful information, and that the significant correlation coefficients in the matrix are meaningful (it can be estimated that at least 30 significant correlations should occur for this, using a Poisson distribution: Rohlf & Sokal 1995: p.87). We are mainly interested in describing the comparative pattern of correlations among food types and species to predict the potential diet differences among the *Barbus* species, and not in testing individual values. Therefore we used all correlations in the matrix, and not only the significant ones, to develop quantitative diet predictions.

For each species (rows in Table 6.6) its highest and lowest predicted feeding abilities are given in italics, whereas the highest and lowest ranking in utilizing a particular food type among the barbs (columns in Table 6.6) are underlined. For some barb species individual peak abilities coincide with peak abilities among all the barbs (e.g. r =0.643 for fish pursuit in *B. acutirostris*). However,often peak performances within a particular species (Fig. 6.8) are beaten by other species (e.g. detritus feeding in *B. tsanensis:* r=0.527, which is highest for this species, compared to *B. nedgia* r=0.618), or sub-peak performance of one species appears to be yet the highest for that food

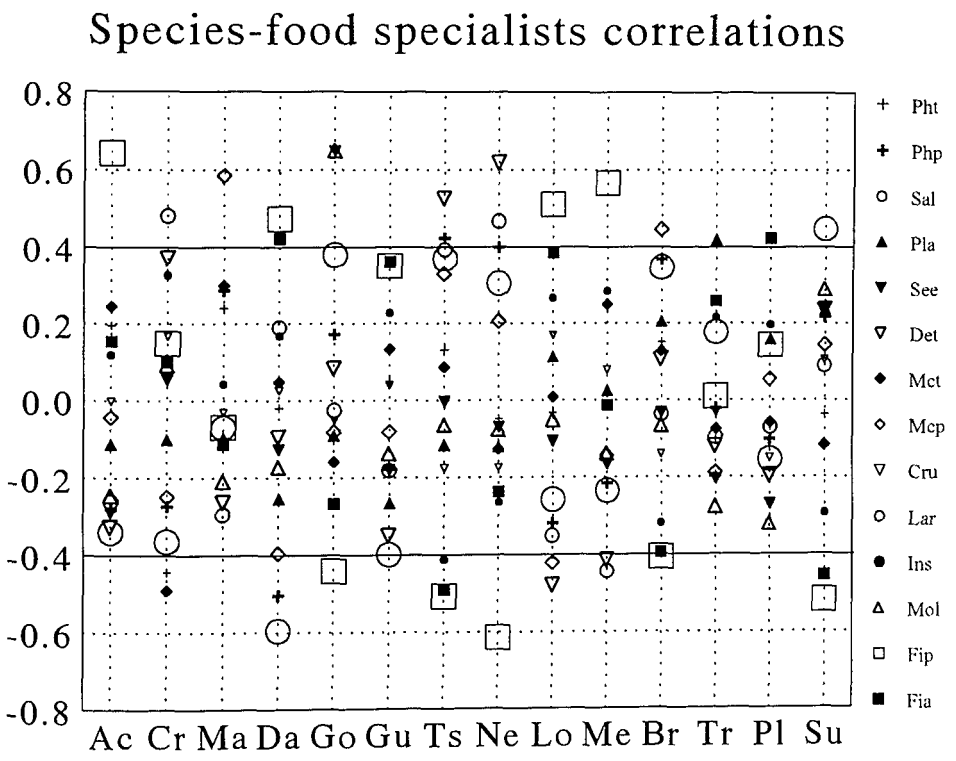


Fig. 6.8. Correlations between species and specialists for particular food types, based on the gap-coded measured and predicted values of the original 33 parameters (Table 6.6). Depending on the number of missing values in the data-set the significant correlation-level ranges from 0.355 (e.g. *B.acutirostris*: 33 parameters) to 0.434 (e.g. *B.brevicephalus*: 22 parameters). An average significance-level of 0.4 is indicated in the graph (horizontal lines). The larger the positive correlation values, the larger the capability of that species to utilize a certain food type (only compared with the other species in the analysis!), the larger the negative correlations, the larger the difficulties of a species to utilize a food type. Note the differences in correlation-ranges among the species; e.g. the large range in *B. nedgia* suggests marked specializations and limitations in food utilization, while the small range in *B. truttiformis* suggests generalized capabilities. Abbreviations: Ac = *B.acutirostris*, Cr = *B.crassibarbis*, Ma = *B.macrophtalmus*, Da = *B.dainellii*, Go = *B.gorgorensis*, Gu = *B.gorguari*, Ts = *B.tsanensis*, Ne = *B.nedgia*, Lo =*B.longissimus*, Me = *B.megastoma*, Br = *B.brevicephalus*, Tr = *B.truttiformis*, Pl = *B.platydorsus*, Su = *B.surkis*, Pht = phytoplankton (townet), Php = phytoplankton (pump), Sal = sessile algae, Pla = macrophytes, see = seeds, det = detritus/substratum, Mct = micro-crustaceans (townet), Mcp = micro-crustaceans (pump), Cru = macro-crustaceans, Lar = insect larvae/worms, Ins = macro-insects, Mol = molluscs, Fip = fish (pursuit), Fia = fish (ambush).

type among all the barbs (e.g. phytoplankton feeding in *B. megastoma*, r=0.245). The correlations have been plotted in Figure 6.8, which facilitates the drawing of conclusions about the presumed trophic differences among the Lake Tana barbs.

Potential trophic segregation was further visualized by performing a PCA on the data from Table 6.6 (Fig. 6.9). In this way most of the variation can be summarized in a single plot. The correlations of a species with all food types (columns) were taken as new parameters. A plot of the

first two principal component scores of the *Barbus* species (explaining 72.3% of the variance) and the factor loadings of the food types on these axes are shown. There are roughly five major groups of food type specialists, based on the supposed solutions cyprinid fish developed, to meet the challenges imposed by the food properties: 1) phytoplankton and micro-crustaceans, taken by townet filter-feeding; 2) phytoplankton and micro-crustaceans taken by pump filter-feeding, sessile algae and plants; 3) detritus/substratum, larvae/worms, seeds, and molluscs; 4) macro-insects and fish taken by pursuit and ambush; 5) macro-crustaceans. The PCA also shows (as expected) that structural demands for efficiently feeding on fish and macro-insects are predicted to be incompatible with those for feeding on plants, sessile algae and detritus (vectors have opposing directions). Also, feeding on micro-crustaceans will be incompatible with feeding on macro-crustaceans.

The fish species cluster in five groups: 1) *B. dainellii*, *B. longissimus*, *B. gorguari*, *B. megastoma*, and *B. acutirostris*; 2) *B. platydorsus* and *B. truttiformis*, all associated with food group 4: macro-insects and fish; 3) *B. crassibarbis*, not clearly associated with any food group, but most to 3 and 5; 4) *B. macrophtalmus*, associated with filter-feeding (food group 1); 5) *B. gorgorensis*, *B. surkis*, *B. nedgia*, *B. tsanensis*, and *B. brevicephalus*, which are associated with food type groups 2 and 3: benthic organisms and pump filter-feeding. Note, however, that grouping of food types and barbs is based on the first two PCs only and that more accurate and detailed data are available in the original correlation matrix (Table 6.6 and Fig. 6.8).

Predicting diets from PC-scores, derived from the original fish parameter set

Calculating the correlations between food types and species from the original (gap-coded) parameter values may cause artefacts, because these parameters themselves can be highly correlated, e.g. if two parameters of the same feeding structure are highly correlated. This can result in too much weight of this structure in the total parameter set. However, if we calculate the correlations between food types and species from the PC-scores, these are per definition uncorrelated (see Material & Techniques).

Therefore a PCA was performed on the standardized gap-coded measurement matrix (Table 6.5). The eigenvectors (containing the factors that describe the relation of the original parameters with the PC-scores) and eigenvalues (expressing the percentage of the total variance that is explained by each PC) of the first three principal components are listed in Table 6.7. The food type specialists were projected in the same space as the species (Fig. 6.10), using the same eigenvectors that were calculated from the standardized measurement matrix! To compare food specialists with species, only the position of the species along the vector through the origin and the projected food type specialist is interesting (see example in Fig. 6.10), not the absolute proximity between food type specialist and species projection. However, the absolute mutual proximities of the food specialist projections in the PC space are interesting to compare among them. The closer food specialists are, the more similar the demands food types impose on fish structures. Figure 6.10 also shows the parameters that have the highest factor loadings on the principal axes. If these parameter

vectors have similar directions, they are highly positively correlated. The fact that there are vectors that are very similar in size and direction and are therefore strongly correlated (e.g. between pharyngo-opercular volume [PhOpV] and palatal organ surface) justifies this method of calculating correlations between species and food types based on PC-scores.

The procedure for quantifying food-species correlations using PC-scores is similar to using the original parameter values. We used the first 20 PCs as they describe 100% of the total variance. The correlations between species and food type specialists are listed in Table 6.8 and shown in Fig 6.12. These predictions were further visualized by performing a PCA on the data from Table 6.8 (Fig. 6.13). This method gives a similar pattern of food-species correlations as the previous, using the original gap-coded fish parameter set. This confirms the robustness of the method. Note that the five major groups of food types from Figure 6.9 are also present in this graph, although plants and sessile algae appear to form additional groups now.

Table 6.7. Eigenvectors and eigenvalues of the first three principal components of the correlation matrix of the gap-coded parameters (cf. Fig 6.10). The factor loadings with the five highest absolute values are bold. If such large values did not occur for a parameter in the first three principal components the parameters are not shown.

	PC1	PC2	PC3
Eigenvalue	14.6	5.1	4.0
% (cumulative)	40.1	54.0	64.9
POrL/OpD	**-0.252**	0.050	-0.034
GAr/BAr	**-0.247**	0.080	-0.058
OG/FL	**-0.234**	0.127	0.058
PhG/FL	-0.161	-0.154	**-0.298**
A2Hook	-0.122	-0.092	**0.345**
PhOpV/FL^3	-0.035	**0.378**	0.091
POAr/FL^2	-0.022	**0.356**	-0.106
ED/FL	0.017	**-0.337**	0.215
RLl/FL	0.092	-0.069	**0.297**
A2W/FL	0.122	0.092	**-0.345**
BD/BW	0.162	**-0.296**	-0.102
PJM/PJL^3	0.163	0.098	**-0.305**
TBD*FL	0.222	**0.309**	0.208
SymL/PJL	**0.230**	0.100	-0.186
GL/FL	**0.245**	0.071	-0.045

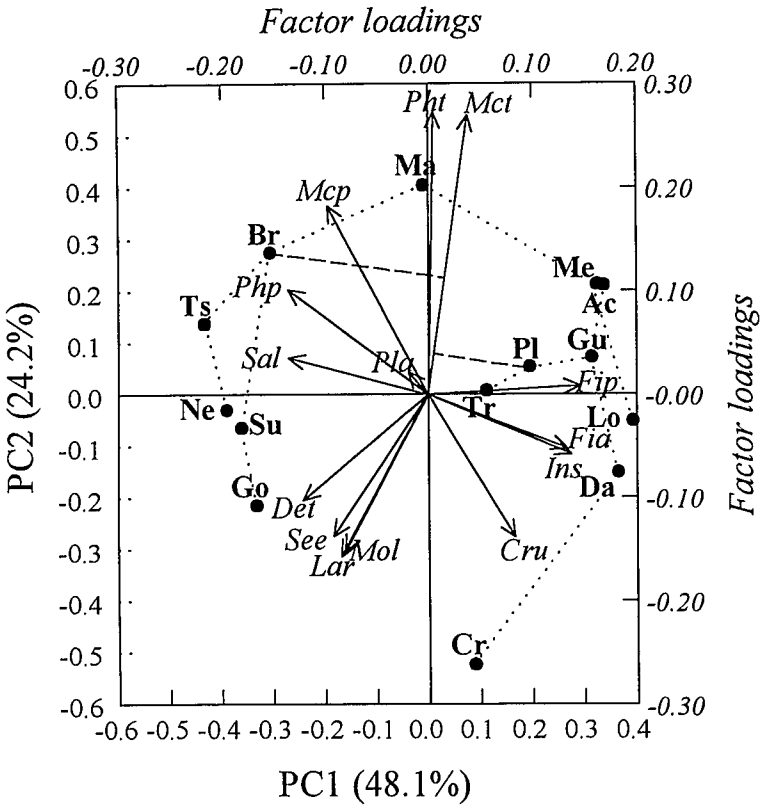


Fig. 6.9. PCA of all correlation-values from Table 6.6 or Fig. 6.8. The PC-scores of the species on the first two principal components and the factor loadings of the food specialists are plotted (note the different scale for the food types [italics]). A first impression of the ability of a species to utilize a food type can be derived by comparing their relative position along the food specialist vector. As an example the relative positions of *B. brevicephalus* and *B. platydorsus* along the micro-crustaceans (townet) vector have been indicated by perpendicular lines, suggesting that the former species is better at townetting micro-crustaceans. Note however, that not all variance (72.3%) is explained by PC1 and PC2, so for detailed predictions of the capabilities of species Table 6.6 and/or Fig. 6.8 should be read. A minimum spanning tree (dashed line), connecting species with most similar predicted diets, based on all PCs is superimposed. Abbreviations in Fig. 6.8.

A UPGMA clustering of the food type specialists (Fig. 6.11*a*), based on the correlation matrix of scores on the first 20 PCs (the cophenetic value of the tree is 0.79, meaning that it fits the correlation matrix on which it was based well) shows the relations among food types, based on their properties relevant to feeding fish (i.e. as 'perceived' by the fish). The clustering shows three large food-type groups, each with several subdivisions: 1) phytoplankton and micro-crustaceans, both taken by townet (1a) and pump (1b) filter-feeding, 2) sessile algae and macrophytes (2a), detritus/substratum and larvae/worms (2b), and seeds and molluscs (2c), and 3) macro-crustaceans (3a), macro-insects and fish taken by ambush hunting (3b), and fish taken by pursuit hunting (3c).

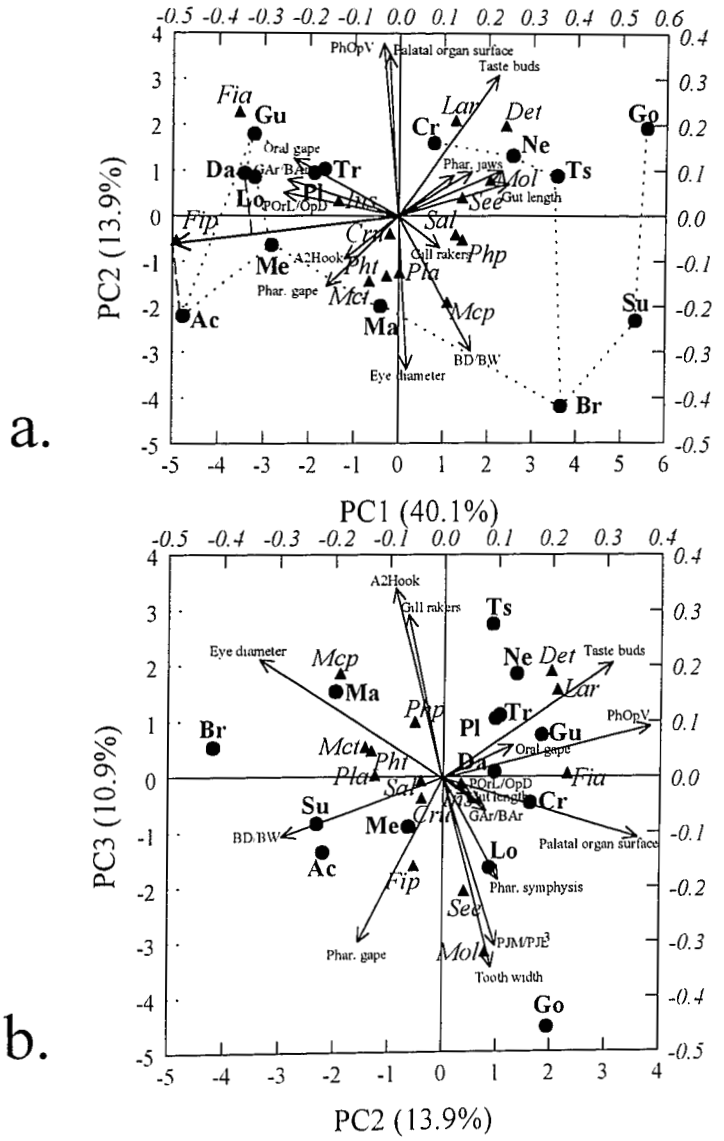


Fig. 6.10. PCA of the standardized gap-coded values. The scores of the species (bold) along the PC1 and PC2 axes (**a**) and along the PC2 and PC3 axes (**b**) are shown, as well as the projection of the food specialists (italics) along these axes. The PC-scores of the food specialists were calculated with the eigenvectors of the PCA on the measured species, of which the 15 most important are listed in Table 6.7 and shown in the figure (note the different scale for the food types [italics]). To compare the food specialists with the species, the symbol of a food type should be interpreted as the end of a vector through the origin (e.g. the vector to Fish [pursuit]). These vectors form axes along which the species are positioned. The farther from the origin a species is placed in the direction of the vector, the more it is able to utilize this food type (e.g. *B. acutirostris* is positioned farther along the Fip vector than *B. dainellii* [perpendicular lines], suggesting that the former is a better pursuit hunter for fish). Note that not all variance is explained by these three PC-axes (64.9%), so the comparison of species and food types from these plots is only approximate! A minimum spanning tree (dashed lines), based on the total variance connects species that are closest in total PC-space (the same in both plots). Abbreviations in Fig. 6.8. Abbreviations of the measured parameters in Table 6.3.

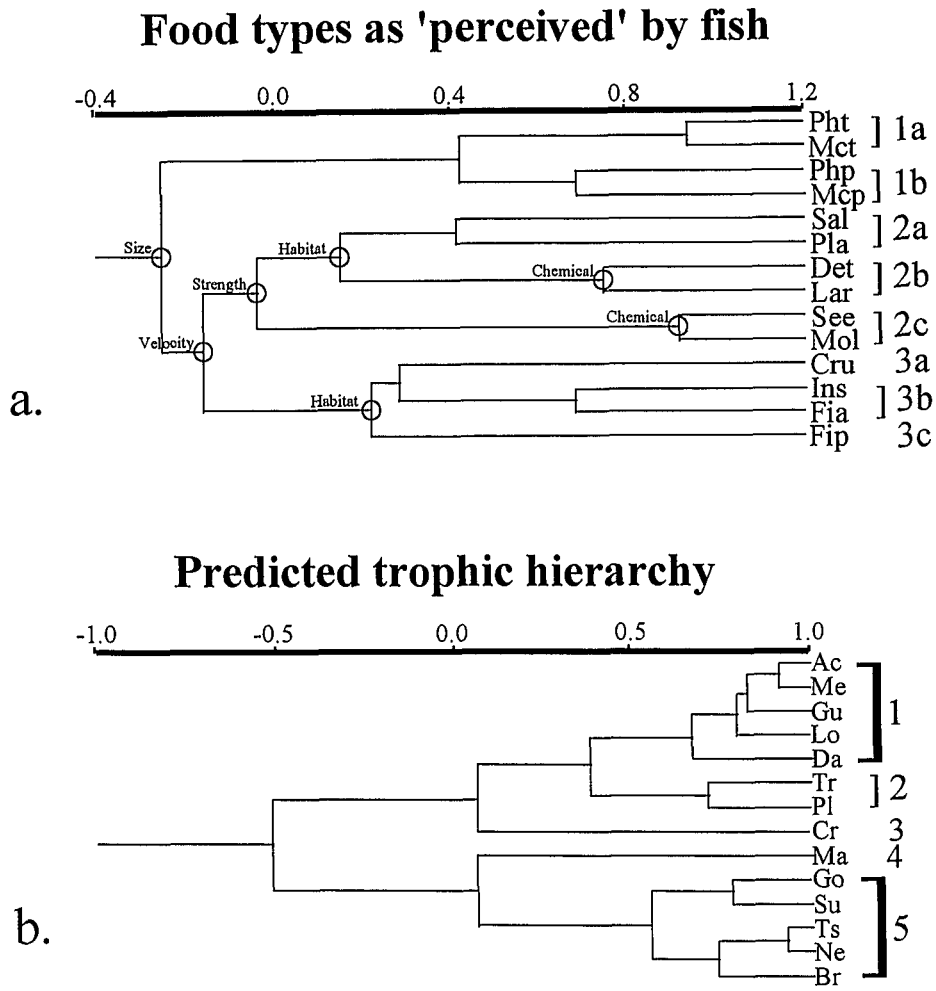


Fig. 6.11. UPGMA-tree of food specialists (**a**), based on the correlation matrices of their PC-scores, calculated with the eigenvectors of the species (cf. Table 6.7; 20 PCs were used, explaining 100% of the variance); this tree therefore shows the relatedness of different food types, as 'perceived' by our 14 *Barbus* species (and cyprinids in general). If there were food properties that were dominant in explaining splits in the tree they are indicated. Groups and subgroups are indicated (see text). UPGMA-tree of species (**b**), based on the prediction matrix (Table 6.6); the tree therefore reflects the relatedness among the species in predicted food utilization, based on their morphology. Groups are indicated (see text). The cophenetic value of the food type tree is 0.79, that of the species tree is 0.82, meaning that both trees fit well to the correlation matrices on which the clustering was based. Abbreviations in Fig. 6.8.

The UPGMA tree shows the similarity in food types according to the predicted structural demands they impose on the fish. It is evident that in this tree the chemical distinction between animal and plant materials (so between herbi- and carnivores) is far subordinate to the distinction between small suspended and large, evasive and benthic food types.

The UPGMA clustering of the barb species (Fig. 6.11*b*, cophenetic value is 0.86 indicating a good fit with the data from which it is derived) is based on the quantitative diet predictions from Table 6.6 and is basically an alternative graphic representation of the mutual proximities of the species in Figure 6.9. It shows a predicted trophic hierarchy of two major groups, each with several subgroups. This is fully supported by the grouping in both PCA diagrams (Figs 6.9, 6.13).

DISCUSSION

It is probable that selective pressure on the abilities of the Lake Tana barbs to utilize different food types, played an important role in their speciation, when considering the wide structural differentiation in feeding related characters, and the short diverging history of this species flock. The varied challenges from different food types and their associated habitat are not covered by the common distinction between herbivores and carnivores (Fig. 6.11*a*). Based on the food-fish model (Fig. 6.1) and its underlying functional morphology, the distinction among food types according to their demands to fish is primarily one between 1) fine suspended particles (phyto- and zooplankton), 2) large evasive prey (fish, macro-arthropods), 3) a spectrum of benthic organisms including sessile algae and plants and 4) strong and stiff encapsulated food (seeds, molluscs).

Adaptive behaviour as a first response to changing environmental food conditions

Adaptive behaviour enables animals to switch feeding modes according to environmental changes, and is guided by the relative abundances of predator and prey. Each feeding strategy, however, is constrained by the performing constructions.

A first example is filter-feeding on plankton, either by townetting or by pumping. Ultimately, both modes of filter-feeding are constrained by the mesh width and retention capacity of the branchial sieve. If fish size and the mesh size of its branchial sieve increase isometrically (such as in some widespread cyprinids: van den Berg et al. 1992), growing fish need to shift diets towards larger prey or, like in common bream, develop a unique gill-raker system that by instantaneous action reduces the mesh size (van den Berg et al. 1994, Hoogenboezem et al. 1991).

A second example are piscivores, which can switch from ambush hunting in complex environments to pursuit hunting in open water, depending on their visibility for prey and the prey's hiding capacity. The option for switching, however, is in this case constrained by the incompatibility of structural demands if the organism is optimized for either of these behavioural specialisms (cf. Table 2).

Table 6.8. Correlation coefficients between food type specialists and *Barbus* species, derived from the first 20 PC-scores of the gap-coded measurements of the fish species and the projected predicted parameter values for the food types (see text). Italics indicate minimum and maximum values per species; minimum and maximum values per food type are underlined. Note that only bold correlation coefficients are significant. However, our purpose is the describing the pattern of correlations, not to test: therefore we also use non-significant correlations in our further analysis (see text). These data are visualised in Figures 6.12 and 6.13.

	Phyto-plankton (townet)	Phyto-plankton (pump)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (townet)	Micro-crustaceans (pump)	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish (pursuit)	Fish (ambush)
B.acutirostris	0.164	-0.428	-0.381	-0.087	*-0.429*	-0.284	0.233	-0.128	0.014	-0.161	0.123	-0.400	***0.720***	0.205
B.brevicephalus	0.174	0.343	***0.464***	0.263	0.112	0.015	0.174	0.435	0.090	-0.110	-0.393	0.079	-0.396	***-0.468***
B.crassibarbis	**-0.469**	-0.259	-0.331	-0.043	0.159	0.208	***-0.534***	-0.258	0.397	0.306	***0.446***	0.216	0.190	-0.005
B.dainellii	-0.016	***-0.558***	**-0.472**	-0.148	-0.143	-0.133	0.077	**-0.463**	0.182	0.201	0.165	-0.233	***0.499***	0.350
B.gorgorensis	-0.081	0.240	0.344	-0.145	**0.829**	0.042	-0.154	-0.034	-0.145	-0.117	-0.266	***0.830***	***-0.466***	-0.234
B.gorguari	0.009	-0.242	***-0.603***	-0.389	-0.341	-0.237	0.092	-0.086	-0.147	-0.090	0.298	-0.240	0.383	***0.610***
B.longissimus	-0.130	**-0.486**	-0.250	0.149	-0.228	-0.312	-0.075	***-0.563***	0.176	-0.085	0.249	-0.193	***0.573***	**0.458**
B.macrophtalmus	0.256	0.316	-0.159	-0.155	-0.162	-0.296	0.317	***0.616***	-0.072	*-0.398*	0.121	-0.243	-0.082	-0.014
B.megastoma	0.150	-0.329	-0.110	0.121	-0.332	-0.152	0.175	-0.289	0.185	-0.058	0.183	*-0.370*	***0.608***	-0.097
B.nedgia	0.039	**0.592**	0.295	-0.170	-0.014	***0.618***	-0.056	0.343	-0.275	0.396	-0.235	0.024	***-0.682***	-0.288
B.plarydorsus	-0.086	-0.071	-0.291	0.088	-0.288	*-0.303*	-0.007	0.116	-0.225	-0.201	0.246	-0.291	0.137	***0.511***
B.surkis	-0.035	0.246	***0.477***	0.238	0.346	0.281	-0.129	0.172	0.119	0.112	-0.339	0.392	***-0.543***	**-0.449**
B.truttiformis	-0.138	-0.046	0.092	0.360	-0.287	-0.125	-0.136	-0.208	-0.121	-0.143	0.306	*-0.336*	0.031	*0.426*
B.tsanensis	0.207	***0.591***	0.424	-0.147	0.000	**0.559**	0.150	**0.452**	-0.259	0.352	-0.436	-0.039	**-0.560**	***-0.567***

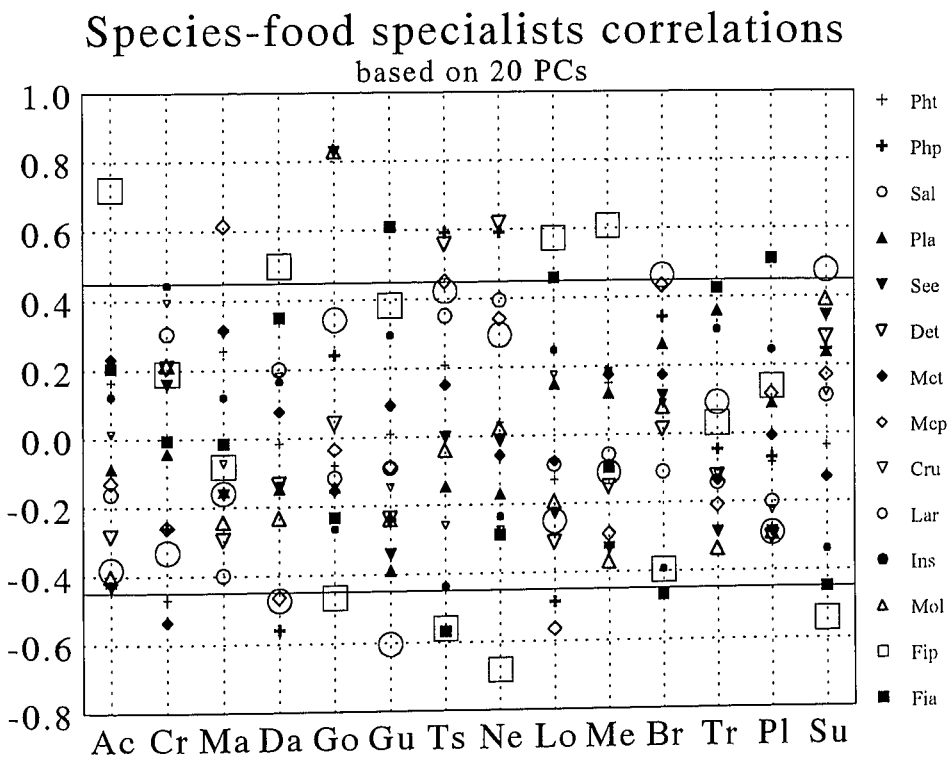


Fig.6.12. Correlations between species and food specialists, based on the first 20 PC-scores (100% of variation) of the measured parameter values and the projection of the parameter values predicted to be effective for feeding on particular food types, using the eigenvectors from Table 6.7. Values of the correlations are listed in Table 6.8. Correlations larger than 0.444 are significant (horizontal line). The larger the positive correlation values, the larger the capability of that species to utilize a certain food type (only compared with the other species in the analysis!), the larger the negative correlations, the larger the difficulties of a species to utilize a food type. Abbreviations in Fig. 6.8.

Even when food has already been taken in, switching in intra-oral masticatory operations occurs (e.g. crushing versus grinding in carp, cf. Sibbing 1982), but these options, activated by different motor patterns are integrated in the design and so constructionally compatible. Modulation of feeding actions, e.g. adjusting it to the exact position of the prey (Sibbing 1991*a*), is a common and compatible feature, even in highly specialized action patterns.

In conclusion, adaptive behaviour provides animals with flexibility to adjust to environmental changes, but the feeding construction limits this behaviour and hence the utilization of food resources.

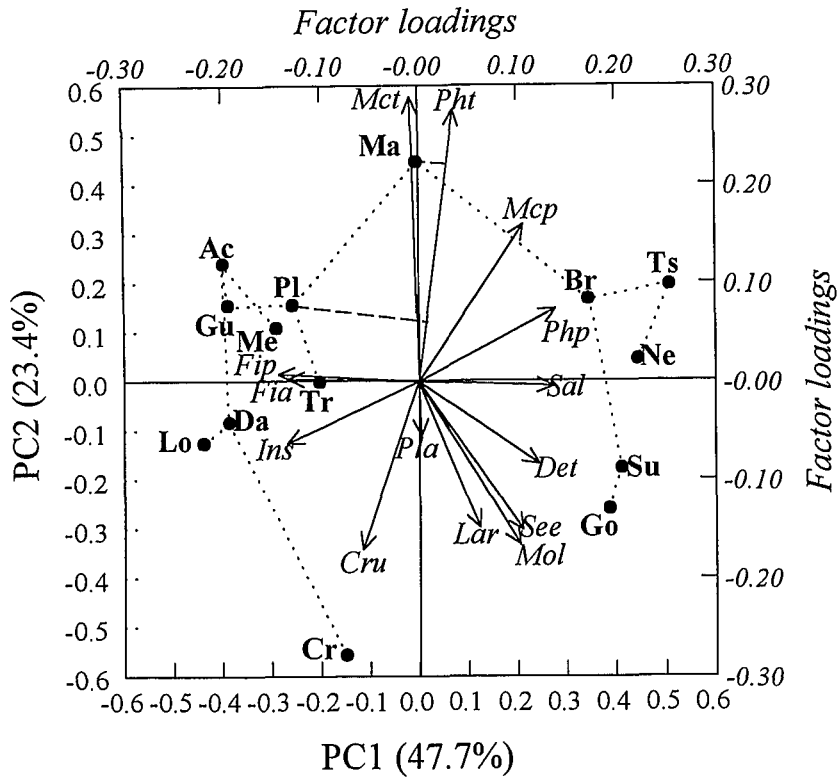


Fig. 6.13. PCA of all correlation-values from Table 6.8 and Fig. 6.12. The PC-scores of the species on the first two principal components and the factor loadings of the food specialists are plotted (note the different scale for the food types [italics]). A first impression of the ability of a species to utilize a food type can be derived by considering its position along the food type vector. As an example the relative positions of *B. macrophtalmus* and *B. platydorsus* along the phytoplankton (townet) vector have been indicated by perpendicular lines, suggesting that the former species is better at townetting phytoplankton. Note however, that not all variance is explained by PC1 and PC2 (71.1%), so for detailed predictions of the capabilities of species Table 6.8 and/or Fig. 6.12 should be read. A minimum spanning tree, connecting species with most similar predicted diets, based on all PCs is superimposed. Abbreviations in Fig. 6.8.

Does structural specialisation imply narrowing of trophic niches?

Generally spoken, the answer may be 'yes'. The extent of structural specialisation may be derived from the number of extreme structural parameter values that were measured. *B. acutirostris* and *B. surkis* have 45% extreme values and *B. dainellii* 42%, (Table 6.5). They are considered structural specialists, contrasting with structural generalists like *B. macrophtalmus* (15% extremes) and *B. platydorsus* (16%). This structural specialisation, however, does not necessarily result in the prediction of a further trophic narrowing (cf. Fig. 6.8). For example, for *B. nedgia* some extreme specialisations (for detritus/substratum) and limitations (for pursuing fish) are predicted, but it has

only 20% structural extremes, while there are no such specialisations and limitations for *B. truttiformis* which has 29% structural extremes! This means that the whole set of morphological extremities of *B. truttiformis* does not fit very well or very bad with any of the food types which we took into account. This might be a signal to reconsider or extend our hypotheses on the structural demands some of the food types impose on the feeding structures of the fish. The unequal distribution of the number of measured characters over different feeding components may also contribute to such discrepancies.

Potential diets predicted for the Lake Tana barbs

The actual measurements on the barbs were transformed into predicted diets, using the food-fish model (Fig. 6.1) based on the functional morphology of feeding in cyprinid fish. Two methods were applied: 1) direct use of the gap-coded data-set (Table 6.6), and 2) PC-scores of the gap-coded data-set (Table 6.8). The results of both methods were very similar. We therefore decided to develop the predicted diets based on the first method, using the gap-coded data set without performing a subsequent PCA (without PCA: Table 6.6, Figs 6.8 and 6.9; with PCA: Table 6.8, Figs 6.12 and 6.13), since we prefer to limit the number of steps in the (already complex) analysis. The similarity of the two methods is probably increased by the fact that the gap-codes were already derived from scaled original measurements and ratios, and that there is only one value for each parameter per species, thereby limiting the variance. If a data-set without missing values can be obtained, values of each individual fish can be used directly without the need for gap-coding. We believe that in such a case it is worthwhile to examine the data set both before and after PCA, because the variance of all individuals is then included.

In the next section diet predictions will be presented for each individual species (synopsis in Table 6.9). The relative abilities to utilize food types within the species as well as the relative abilities among the species will be discussed. Values between brackets refer to correlation coefficients.

B. acutirostris will perform very well in feeding on fish, exclusively by pursuit hunting. This barb species has the highest number of extreme characters (45%, Table 6.5) and the highest matching between fish and food (r=0.643, Table 6.6, Fig. 6.8). Lowest abilities are predicted for utilising sessile algae (r =-0.339), whereas it will perform poorest of the species in feeding on seeds (r=-0.288).

B. brevicephalus will be a good pump filter-feeder of micro-crustaceans (r=0.446), a bit less on phytoplankton (r=0.367) and may utilize sessile algae (r=0.347). It has its lowest abilities as piscivore (r=-0.406 for pursuit; r=-0.394 for ambush).

Table 6.9. Synopsis of the predicted diets per species based on Table 6.6. Correlation values between -0.2 and 0.2 are not shown. Correlation values smaller than -0.2 or larger than 0.2 that are not significant are placed between brackets. Significant correlation values between -0.4 and -0.6 are coded as '-', values between 0.4 and 0.6 as '+'. Values smaller than -0.6 or larger than 0.6 are coded as '--' and '++' respectively. The scale from '--' to '++' can be interpreted as ranging from 'very restricted utilizing capability' to 'very good utilizing capability'.

	Phyto-plankton (townet)	Phyto-plankton (pump)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (townet)	Micro-crustaceans (pump)	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish (pursuit)	Fish (ambush)
B.acutirostris		(-)	(-)		(-)	(-)	(+)			(-)		(-)	++	
B.brevicephalus		(+)	(+)	(+)				+			(-)		-	(-)
B.crassibarbis	-	(-)	(-)			(+)	-	(-)		+	(+)			
B.dainellii		-	-	(-)				(-)					+	+
B.gorgorensis			(+)		++						(-)	++	-	(-)
B.gorguari			(-)	(-)		(-)					(+)		(+)	(+)
B.longissimus		(-)	(-)			-		-		(-)	(+)		+	(+)
B.macrophtalmus	(+)	(+)				(-)	(+)	+		(-)		(-)		
B.megastoma	(+)	(-)	(-)			-	(+)			-	(+)		+	
B.nedgia		(+)	(+)			++		(+)		+	(-)		--	(-)
B.platydorsus					(-)							(-)		+
B.surkis		(+)	+	(+)	(+)	(+)					(-)	(+)	-	-
B.truttiformis				+	(-)						(+)	(-)		(+)
B.tsanensis		+	(+)			+		(+)		(+)	-		-	-

B. crassibarbis is predicted to be good at feeding on detritus/substratum (r=0.372) and especially on benthic insect larvae/worms (r=0.482). It has lowest abilities for townet filter-feeding on micro-crustaceans (r=-0.491). Among the barb species it is the presumed best in feeding on larvae/worms (r=0.482) and macro-insects (r=0.328) and the worst townet filter-feeder for both phytoplankton (r=-0.443) and for micro-crustaceans (r= -0491).

B. dainellii is predicted to be a very good piscivore, both by ambush (r=0.422) and pursuit hunting (r=0.473). Sessile algae will be utilised very poorly (r=-0.595), and it will be a poor pump filter-feeder (r=-0.504 for phytoplankton, r=-0.394 for micro-crustaceans). For these food types it has even the lowest abilities among all barbs. Although it is not the best piscivore in either ambush or pursuit hunting, *B. dainellii* most probably can employ both strategies approaching (benthic) prey from above (large inferior protrusion upper jaw). It is extreme in 42% of its feeding related characters (Table 6.5).

B. gorgorensis has a very high matching with feeding on seeds (r=0.647) and molluscs (r=0.649) and has by far the highest abilities for utilising these among the barbs. Its equipment for piscivory, however, is very poor (r=-0.441 for pursuit, and r=-0.267 for ambush hunting).

B. gorguari has rather good abilities for piscivory, employing both ambush (r=0.362) and pursuit (r=0.351) hunting. Sessile algae (r=-0.398) and detritus substrate (r=-0.349) can hardly be utilised. Feeding abilities on macrophytes will be the lowest (r=-0.266) among all barbs.

B. longissimus has high abilities for piscivory (r=0.510 for pursuit, r=0.385 for ambush hunting), whereas benthos can hardly be utilized (r=-0.479 for detritus/substratum, r=-0.350 for larvae/worms) and its pump filter-feeding performance is poor (r=-0.420 for micro-crustaceans, r=-0.319 for phytoplankton). Among the barbs it is expected to be the best macro-crustacean feeder and the worst at detritus and pumping micro-crustaceans.

B. macrophtalmus will be a very good pump filter feeder on micro-crustaceans (r=0.586) but rather poor in utilising larvae/worms (r=-0.294). Among the barb species it is predicted to be the best filterer of micro-crustaceans, even by townetting (r=0.301). It is the least extreme barb in its feeding structures (15%, Table 6.5) and it is therefore expected to be a generalized feeder with few inabilities in competing for food resources.

B. megastoma will be a very good pursuing piscivore (r=0.566), and a much poorer ambush hunter (r=-0.014). It will be bad at feeding on detritus (r=-0.414) and larvae/worms (r=-0.443). On a relative scale it is the best townet filter-feeder of phytoplankton (r=0.245) among all barbs.

B. nedgia is predicted to be the best detritivore (r=0.618), also utilizing larvae/worms (r=0.467) and phytoplankton (r=0.398), and is by far the poorest piscivore by pursuit hunting (r=-0.614). This species shows the largest range of (in)abilities (cf. Fig. 6.8) and therefore appears to be rather specialized. This implies that adaptation that excludes *B. nedgia* from some food types, is strongest of all barb species: specialisations for detritivory, such as a narrow downward mouth, appear incompatible with those for pursuit hunting on fish.

B. platydorsus is expected to be a good ambush hunter on fish (r=0.423) with lowest abilities for molluscs (r=-0.320). Also in comparison with the other barbs it has extreme values for these food types. Still this species (like *B. truttiformis*) has few conspicuous specialisations and limitations, which corroborates with the small number of structural extremes (16%, Table 6.5).

B. surkis is well equipped for feeding on sessile algae (r=0.447), more than any other barb and second best in utilizing macrophytes (r=0.236) and seeds (r=0.237). It has severe limitations in feeding on fish (r=-0.518 for pursuit and r=-0.455 for ambush hunting). This barb, together with *B. acutirostris*, has the largest percentage of structural extremes (45%, Table 6.5) but specialisations and limitations are completely opposite among these two barbs.

B. truttiformis's predicted specialisations and limitations are less extreme than in many other species (smallest range in Fig. 6.8). It suggests less efficient feeding on specific types but utilizing a wide spectrum of food resources. It is best at feeding on macrophytes (r=0.419), and worst at eating molluscs (r=-0.276). Among the present barbs its abilities to utilize plants are the highest (r=0.419).

B. tsanensis will be a very good detritivore (r=0.527) and an able benthivore. It has its lowest abilities for fish (r=-0.491 for ambush, and r=-0.507 for pursuit hunting) and macro-insects (r=-0.412). Compared to the other barbs it has the highest ability to feed on phytoplankton by pumping (r=0.422), and the lowest for large evasive prey like fish and macro-arthropods.

Which structural characters are determinants for resource utilization?

It is important to state once more, that a comparison of the Lake Tana barbs has the enormous advantage of their common ancestry, which makes it probable that their current diversity is adaptive. However, their recent evolutionary divergence also implies that time may have been too short for extreme adaptations in an absolute sense (i.e. the Lake Tana barbs are not extreme if compared to the whole cyprinid family). So what we call structural extremes in Table 6.5, is strictly comparative and only applies to the current spectrum of Lake Tana barbs. Moreover, it seems that different feeding actions and their underlying structures are under unequal selective pressures. This is suggested by the large differences in the apparatus for approach and intake, whereas the pharyngeal jaws are more similar and do not show many of the features expected in trophic specialists (Sibbing 1991*a*, 1991*b*).

Yet, if we consider 1) the range of structural differences measured, 2) the functional significance of these differences and 3) the interrelations of the characters explaining the total morphological variance (as shown in the PCA, cf. Fig. 6.10, Table 6.7), then we may have traced key structures or complexes that determine adaptation in the major trophic groups among cyprinids.

Incompatible feeding modes and food types

We predicted that the major "dilemma" in specialisation is between feeding on suspensions of small particles (such as phytoplankton and micro-crustaceans) and large evasive prey (such as fish and macro-insects) (Figs. 6.10, 6.11). These two food categories both impose high demands on fish, and are mutually incompatible (cf. Barel et al. 1989). This is apparent from the PCA (Fig. 6.10) in which they are clearly separated, especially along the first and third PC (fish in the far left in Fig. 6.10*a*, and in the bottom in Fig. 6.10*b*; phytoplankton and micro-crustaceans below and right of the middle in Fig. 6.10*a*, and in the left top quadrant in Fig. 6.10*b*). The highest loadings along the first and third PC-axes (Table 6.7) are for characters that strongly influence the (in)abilities for piscivory and suspension-feeding (cf. Table 6.2). The characters that are congruent with piscivory (along PC1) are 1) a large oral gape (OG/FL), 2) a short symphysis of the pharyngeal jaws, allowing for tearing compliant material with large amplitudes (SymL/PJL), 3) a short gut length (GL/FL), 4) large volume properties of the operculum to increase the volume with still closed opercular valves (POrL/OpD), and 5) a gape area approaching the cross body area to prevent pushing away the prey in pursuit (GAr/BAr). The highest loadings congruent with piscivory along PC3 are 6) a large pharyngeal gape (PhG/FL), 7) hooked pharyngeal teeth (A2Hook), 8) slender pharyngeal jaws (low PJM/PJL^3) and 9) short gill-rakers (RLl/FL). The relation of these characters with suspension-feeding is almost completely conflicting, although suspension-feeders do not need very strong pharyngeal jaws. Pump filter-feeders would profit from a large suction volume and townet filter-feeders from a large oral gape, just like piscivores. However, they both need a fine branchial sieve which yield a high flow resistance, which is incompatible with rapidly passing accelerated water through the gill-slits in piscivores.

A second important incompatibility is that between large, evasive, compliant prey (such as fish and macro-insects) and slow, sedentary, fibrous (plants) and stiff food types (such as seeds and molluscs) (Fig. 6.11*a*). The latter occupy the right top quadrant in Fig. 6.10*a*. The incompatibility between these two food categories is already partly explained in the preceding section. Note that now pharyngeal jaw characters are dominant in the abilities to feed on seeds, molluscs and detritus. This is apparent from the high factor loadings on the first, and especially the third principal component (Table 6.7): 1) a long symphysis stabilizing the pharyngeal jaws during heavy duty crushing and splitting (Sym/PJL), 2) a large pharyngeal gape (PhG/FL), 3) robust pharyngeal jaws (PJM/PJL^3), 4) a small percentage of hooked teeth (A2Hook), and 5) a wide base of the A2 tooth (A2W/FL).

Another specialisation is apparent from high factor loadings on the second principal component (Table 6.7) implying specialisation for feeding on benthic organisms: 1) a large surface area of the

palatal organ ($POAr/FL^2$), and 2) a high density of taste buds on this organ to sort between food and non-food (TBD*FL).

CONCLUSIONS

1) A food-fish model based on functional morphological experiments provides us with a large character set which, due to its manyfold and cumulative effects on feeding abilities enables us to predict diets and trophic hierarchy among the extant Lake Tana barbs.
2) Basic to the food-fish model is the structural differentiation of fish underlying adaptive feeding strategies, but also a firm quantification of food types in size, shape, habitat, velocity, mechanical and chemical properties.
3) The predictions of the food-fish model have promising resolving power and are robust.
4) Most major structural specialisations for feeding on different resources are incompatible and therefore fish which specialize have to 'choose' between feeding on: a) suspended micro-particles, b) evasive macro-prey, c) benthic organisms, d) stiff and strong encapsulated items.
5) The above predictions must be tested by comparing gut contents of the Lake Tana barbs with diet predictions from the food-fish model (Chapter 7).

Significance and perspective of the approach

Diets predicted with the food-fish model reflect the feeding options of a particular species and its potential competitive abilities in comparison with the other present barbs. This provides a solid base for predicting resource partitioning among them. The major advantage of this approach is its relative independence of the precise actual circumstances in the aquatic ecosystem, providing universal predictions. In this way insight into food webs is not wholly restricted anymore to extensive sampling programmes over time (year, seasonal, diurnal) and areas, which only have little predictive value and demand much more investment than measurements on a relatively small number of fishes.

However, precondition for the evaluation of the approach presented here (cf. Fig. 6.1) is a test of our predictions against field data (the actual gut contents, preferably in comparison with the environmental availability of the different food types). This test is the major aim of the following paper. If the test proves successful, the method can be applied in studies on the cascading effects in aquatic ecosystems of e.g. overfishing, or the introduction of species to fill up unoccupied niches (cf. Lammens et al. 1987, Mills et al. 1987, Pet et al. 1996). These studies have to start from the level of interacting organisms and their trophic hierarchy as this is the only way to explain the role of biodiversity in the (short term) stability and (long term) resilience of the ecosystem (Levêque 1995).

ACKNOWLEDGEMENTS

We thank the Ministry of Agriculture in Addis Ababa for its cooperation, as well as the Amhara National Regional State Bureau of Agriculture in Bahar Dar for cooperation in the local implementation of our work. We also acknowledge all the people that helped collecting in the field, Geert van Snik, Michiel Helmes, Hans van Oostenbrugge, Sander Kranenbarg, Arnold van den Burg, and Suzanne van Gaans. Furthermore, we thank Albert Otten for his help with the statistics. Jan Osse is acknowledged for his very useful suggestions on improving the manuscript. This study was financed by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W88-176, the Interchurch Foundation Ethiopia/Eritrea (ISE, Urk, The Netherlands), and the Interchurch Coordination Commission for Development Projects (ICCO, Zeist, The Netherlands).

Chapter 7

Trophic segregation within the *Barbus* species flock of Lake Tana, Ethiopia: 2. Test of diet predictions and food partitioning

Leo A.J. Nagelkerke[1] & Ferdinand A. Sibbing[1]

[1] *Agricultural University, Wageningen Institute of Animal Sciences (WIAS), Experimental Zoology Group, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*

ABSTRACT

Previously developed quantitative predictions of diets and food partitioning among the Lake Tana *Barbus* species are tested against actual gut contents data. Frequency of occurrence and volume-percentages of the gut contents give a similar picture of resource partitioning, consistent with the five large trophic groups that were predicted: 1) *B. gorgorensis*, *B. surkis*, *B. nedgia*, *B. tsanensis*, and *B. brevicephalus*: (mostly benthic) non-piscivores; 2) *B. dainellii*, *B. longissimus*, *B. gorguari*, *B. megastoma*, and *B. acutirostris*: the almost exclusive piscivores. 3) *B. platydorsus* and *B. truttiformis*: facultative piscivores that also utilize considerable amounts of other foods; 4) *B. macrophtalmus*, which is intermediate, feeding on micro-crustaceans, benthos, and fish; and 5) *B. crassibarbis*, of which the position is less consistent (feeding mainly on benthic food types). Within the non-piscivorous group, the mainly benthivorous *B. tsanensis* and *B. nedgia*, and the macrophyti-/molluscivorous *B. gorgorensis* and *B. surkis* were accurately predicted. The peripheral position of *B. platydorsus* in the piscivorous group was also predicted well. It was more difficult to predict the diets of individual species accurately, e.g. because of uneven distribution of food types. Abundant food types, that usually set high demands on the fish, and are of high quality (viz. fish, micro-crustaceans (if taken by pump filter-feeding), molluscs, detritus/substratum, macro-crustaceans, and larvae/worms) can be predicted most accurately. In conclusion, we believe that the ecomorphological method is a useful tool in predicting the trophic niches of a group of fish species, in a comparative context. Food partitioning is better predictable than the absolute diets of single species. The method performs best with closely related species, but the underlying principles of challenges of food types that have to be met by the predator are universal and most probably cross phylogenetic boundaries. Feeding guilds should be based on feeding modes and not on food category taxonomy. True specialists are often characterised by a high number of extreme structural parameters, generalists by a low number. This relates to the mutual incompatibility of constructions for specialised performances. However, morphological specialisation does not necessarily imply ecological specialisation and vice versa. The insights in the Lake Tana food web suggest that the diversification in the number of piscivores is driven by a 'zooplankton bottle-neck'. Most of the primary production is converted to zooplankton and is only available to the large barbs through the intermediate level of small zooplanktivorous fish, which are the most abundant food source in the otherwise poor Lake Tana. The ecomorphological method is also of practical use in evaluating the role of (morphological) biodiversity in the ecosystem and predicting the effects of environmental changes in ecosystem, which can be instrumental in the development of a strategy towards sustainable fisheries.

INTRODUCTION

In order to study the trophic interrelations of the 14 large Lake Tana *Barbus* species, we have used an ecomorphological methodology (Chapter 6, Sibbing et al. 1994, Wainwright & Richard 1995). In the preceding paper (Chapter 6) quantitative hypotheses have been developed for the *Barbus* species which predict their relative abilities to utilize specific food resources.

These hypotheses were based on a model linking specific properties of 14 food types to feeding structures of a cyprinid fish (the food-fish model: FFM). This provided a cumulative set of parameter values that cyprinid fish were expected to have in order to cope with properties of particular food types (food-fish demands: FFD). The same set of parameters was measured in the different *Barbus* species and by comparison with the hypothesized values for food specialists, potential diets and food partitioning were predicted. This paper aims at testing the predicted diets and food partitioning (Table 7.1) against the actual dietary data of the species in the field, derived from gut contents analysis.

Dietary differences were approached from two different angles. Firstly, the predicted differences among the food types within each particular species were tested (species are analysed independently). In this way the predicted diet spectra were tested, i.e. the relative importance of food types for a particular species, as compared with other food types. Secondly, predicted differences among species were tested for each food type separately (food types are analysed independently). In this way, predicted food partitioning (i.e. the differential use of a particular food type by all the species) was tested. Some factors complicating the effective prediction of diets and food partitioning will be treated in the Discussion.

We have chosen an ecomorphological approach because we expect that (and want to test whether) 1) it will give rapid insights into potential diets of fish species without the need for an extensive ecological sampling programme, and 2) it will allow for dynamic predictions of food partitioning among species, i.e. it will predict dynamic trophic interrelations accurately under different (given) circumstances. If environmental changes occur (e.g. the overfishing of a particular species, the introduction of a new species, or the increased abundance of a particular prey type) the method will enable us to predict the shifts in trophic interactions among the compared species, because it is based on their structural (in)abilities. This makes it a potentially practical tool in the development of sustainable fisheries, which, by its selectivity, always invokes some environmental changes.

We use the same set of quantitative predictions expressing the relative (in)ability of each species to utilize particular food types (Chapter 6) for testing the accuracy of the predicted diet spectra as well as the predicted food partitioning. We use two approaches for testing the predictions: 1) calculations of the correlations between predicted and actual diet spectra and food partitioning, and 2) multivariate techniques in which differences in diet spectra and food partitioning are summarized in few dimensions; the accuracy of the predictions is evaluated graphically. Details of these approaches are described in Material and Methods.

Table 7.1. Predicted potential diets and food partitioning. Values are correlations between food type specialists and *Barbus* species, derived from the required parameter values for effectively utilizing particular food types and the actually measured parameters in the fish species (see Chapter 6). Italics indicate minimum and maximum values per species (rows); minimum and maximum values per food type are underlined (columns). Note that only bold correlation coefficients are significant. However, our purpose is the description of the pattern of correlations, not to test: therefore we also use non-significant correlations in our further analysis.

	Phyto-plankton (townet)	Phyto-plankton (pump)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (townet)	Micro-crustaceans (pump)	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish (pursuit)	Fish (ambush)
B.acutirostris	0.196	-0.281	*-0.339*	-0.113	-0.288	-0.326	0.246	-0.042	-0.001	-0.260	0.119	-0.245	***0.643***	0.155
B.brevicephalus	0.151	0.367	0.347	0.204	-0.033	0.106	0.128	***0.446***	-0.140	-0.036	-0.318	-0.066	*-0.406*	-0.394
B.crassibarbis	**-0.443**	-0.273	**-0.363**	-0.100	0.055	**0.372**	***-0.491***	-0.247	0.168	***0.482***	0.328	0.092	0.150	0.100
B.dainellii	-0.019	**-0.504**	***-0.595***	-0.254	-0.126	-0.094	0.049	**-0.394**	0.027	0.191	0.169	-0.171	***0.473***	**0.422**
B.gorgorensis	-0.103	0.172	0.380	-0.091	**0.647**	0.084	-0.158	-0.081	-0.051	-0.025	-0.272	***0.649***	***-0.441***	-0.267
B.gorguari	0.050	-0.177	***-0.398***	-0.266	-0.179	-0.349	0.134	-0.080	0.040	-0.180	0.229	-0.137	0.351	***0.362***
B.longissimus	-0.033	-0.319	-0.257	0.112	-0.106	***-0.479***	0.008	**-0.420**	0.169	-0.350	0.267	-0.051	***0.510***	**0.385**
B.macrophtalmus	0.241	0.287	-0.070	-0.097	-0.110	-0.262	0.301	***0.586***	-0.029	*-0.294*	0.044	-0.208	-0.068	-0.112
B.megastoma	0.245	-0.216	-0.234	0.025	-0.166	**-0.414**	0.251	-0.142	0.079	***-0.443***	0.285	-0.138	***0.566***	-0.014
B.nedgia	-0.049	**0.398**	0.306	-0.121	-0.069	***0.618***	-0.126	0.206	-0.174	**0.467**	-0.264	-0.076	***-0.614***	-0.237
B.platydorsus	-0.122	-0.102	-0.153	0.158	-0.270	-0.196	-0.057	0.055	-0.150	-0.070	0.197	*-0.320*	0.144	***0.423***
B.surkis	-0.038	0.217	***0.447***	0.236	0.237	0.237	-0.116	0.144	0.104	0.090	-0.293	0.290	***-0.518***	**-0.455**
B.truttiformis	-0.100	-0.022	0.178	***0.419***	-0.204	-0.120	-0.074	-0.187	-0.034	-0.096	0.216	*-0.276*	0.010	0.259
B.tsanensis	0.132	0.422	**0.370**	-0.116	-0.003	***0.527***	0.086	0.331	-0.175	**0.393**	**-0.412**	-0.064	***-0.507***	-0.491

MATERIAL AND METHODS

Gut contents

Of the 14 species of large Lake Tana barbs: *B.acutirostris*, *B.brevicephalus*, *B.crassibarbis*, *B.dainellii*, *B.gorgorensis*, *B.gorguari*, *B.longissimus*, *B.macrophtalmus*, *B.megastoma*, *B.nedgia*, *B.platydorsus*, *B.surkis*, *B.truttiformis*, and *B.tsanensis*, a total of 1247 gut contents samples from 4711 specimens (maximally 10 specimens were pooled per sample) larger than 15 cm fork length (FL) were collected. The number of samples varied from 27 (from 33 specimens) for *B. gorgorensis* to 195 (from 1555 specimens) for *B. tsanensis*.

Fish were caught from January 1993 until January 1995, in the southern Bahar Dar Gulf of Lake Tana, Ethiopia (covering around 300 km^2, c. 10% of the lake's surface). Samplings were done regularly over time (seasonal, diurnal) and covered five habitat types: 1) littoral between or very close to papyrus beds, 2) shallow (depth < 3m), rocky substratum, 3) shallow, muddy/sandy substratum, 4) deep (depth > 3m), rocky substratum, and 5) deep, muddy/sandy substratum. All habitats were fished with bottom gill-nets (stretched mesh sizes: 16, 25, 32, 44, 60, 80, 100 mm), the muddy/sandy stations also by bottom trawling (stretched mesh size of the cod-end 20 or 40 mm).

The samples were preserved in a 4% formaldehyde solution within three hours after the catch was collected, and analysed by microscopy. An estimate of the volume-percentage of each particular food type was made. These data were either used directly, or were transformed to frequency of occurrence (f.o.o.) data: if a food type constituted 10% or more of the gut contents it was considered present, otherwise it was recorded as absent.

The reason for also using f.o.o. data is that we wanted to account for the possibility that the relative volume in the gut is not necessarily an indication of the importance of a food type. It is possible that e.g. a barb has large volumes of detritus in its gut, but that the insect larvae that live between it, and only make up a fraction of the total gut volume, are the food items that are really important for the fish. When taking f.o.o. data the absence or presence of a food item is considered to be more important than its actual volume. We recorded food items with volume-percentages of less than 10% as absent because we wanted to prevent food items that were taken incidentally (e.g. attached to other foods) to play too great a role in the analysis. Our f.o.o. method is therefore rather hybrid.

F.o.o. data can have somewhat contra-intuitive results as the total percentage of presence or absence of food types in a species usually exceeds 100%. For each food type the percentage of specimens that have that food type in their gut is calculated separately. Therefore, if there are specimens that have eaten more than one food category, the total percentage of f.o.o. of a species will be larger than 100% (e.g. if 50% of the total number of specimens had insect larvae, and 70% of them had molluscs this automatically means that some of the insect larvae eaters also had molluscs; the total percentage will be 120% in this case).

Food categories were Phytoplankton (Phy), Sessile algae (Sal), Macrophytes (Pla), Seeds (See), Detritus/substratum (Det), Micro-crustaceans (Mcr), Macro-crustaceans (Cru), Insect larvae/worms (Lar), Macro-insects (Ins), Molluscs (Mol), and Fish (Fis).

Availability of food resources

The availability of food resources was sampled regularly (on average every two months) at all stations. Plankton samples were taken at least every month with a plankton-net (diameter of 15 cm, and mesh-size of 80 μm). At the muddy/sandy stations series of 5 bottom-grabs were made, the substratum was sieved (0.1 mm mesh) and organisms collected. At rocky stations, rocks were scraped incidentally , and organisms collected. When plants were present, a sample of it was taken and organisms living on it were collected. All samples were stored in a 4% formaldehyde solution. Food organisms were identified to the lowest possible taxonomic level (i.e. genus or species for zooplankton; order or family for most other organisms) and later pooled into the food categories described above. Results of food resource collections are described in Chapter 1.

Analysis

Before the comparisons between predicted and actual diet spectra and food partitioning can be made, first we have to prepare the data, as is described in the next section. Next, the methods of comparison are discussed.

Getting the data in shape

1) Frequency of occurrence (f.o.o.) data

Frequency of occurrence data (Table 7.2) can be compared directly (without transformation) with the quantitative predictions, since they consist of a single frequency number for each food type-species combination. These numbers can be used for testing both the predicted diet spectra and the predicted food partitioning.

2) Volume percentage data

Volume-percentages, however, were taken for each individual fish (or batch of pooled fish) separately, and therefore averages had to be calculated for comparison with the predictions.

Average volume-percentages of all food types within each particular species were tested for statistical differences to compare diet spectra. As the volume-percentages were distributed non-normally, they were tested by ranking the volume-percentages of all food types in the samples of each species separately. Subsequently these ranks were transformed according to van der Waerden's method (SAS Institute Inc. 1989, p. 1198), resulting in an approximately normal distribution. The differences among the average volume-percentages of the food types were now tested using these transformed ranks according to the Tukey-Kramer method for multiple, unplanned comparisons (which is well suited for unequal sample sizes: Sokal & Rohlf 1995). The

Table 7.2. Frequency of occurrence of food types in gut contents of barbs larger than 15 cm fork length, expressed as the percentage of samples in which the food types were present. If a food type constituted 10% or more of the volume of the gut contents it was considered present. The number of samples and specimens per species vary from 27 to 195 and from 33 to 1555 respectively. Italics indicate minimum and maximum values per species (rows); minimum and maximum values per food type are underlined (columns). The average values per food type (lower row) also vary considerably (from 0.4% seeds to 44.1% fish). The sum of the percentages (right column) gives an impression whether a species is a specialized or generalized feeder (sum close to 100%: very specialized; the larger the sum, the more generalized) (see Discussion).

	# samples	# specimens	Phyto-plankton	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish	Other	sum
B.acutirostris	121	238	5.0	*0.0*	4.1	*0.0*	10.7	3.3	*0.0*	14.0	7.4	1.7	*82.6*	14.0	143
B.brevicephalus	107	972	15.0	*0.0*	31.8	*0.0*	18.7	*58.9*	*0.0*	30.8	48.6	14.0	0.9	5.6	224
B.crassibarbis	51	84	13.7	*0.0*	2.0	*0.0*	*64.7*	33.3	*0.0*	58.8	19.6	29.4	3.9	5.9	231
B.dainellii	58	81	3.4	*0.0*	13.8	*0.0*	5.2	*0.0*	3.4	10.3	8.6	1.7	*75.9*	6.9	129
B.gorgorensis	27	33	11.1	*0.0*	*37.0*	*0.0*	29.6	*0.0*	3.7	11.1	*0.0*	*37.0*	14.8	7.4	152
B.gorguari	123	310	13.0	1.6	30.1	*0.8*	9.8	4.1	3.3	15.4	5.7	9.8	*66.7*	8.9	169
B.longissimus	38	74	5.3	*0.0*	21.1	2.6	5.3	*0.0*	2.6	5.3	*0.0*	2.6	*76.3*	10.5	132
B.macrophtalmus	87	356	12.6	3.4	16.1	*0.0*	10.3	25.3	1.1	31.0	17.2	*0.0*	*56.3*	3.4	177
B.megastoma	76	130	1.3	*0.0*	28.9	*0.0*	1.3	1.3	1.3	14.5	13.2	1.3	*82.9*	10.5	157
B.nedgia	152	417	7.9	1.3	13.2	*0.7*	56.6	16.4	2.6	*73.0*	27.6	48.0	13.8	4.6	266
B.platydorsus	84	141	10.7	*0.0*	23.8	*0.0*	10.7	2.4	*0.0*	29.8	15.5	10.7	*59.5*	8.3	171
B.surkis	90	268	14.4	*1.1*	*82.2*	*1.1*	3.3	6.7	*1.1*	10.0	12.2	2.2	2.2	*1.1*	138
B.truttiformis	38	52	5.3	*0.0*	5.3	*0.0*	5.3	5.3	5.3	5.3	*0.0*	5.3	*78.9*	15.8	132
B.tsanensis	195	1555	10.8	*0.0*	13.8	0.5	64.1	24.6	*0.0*	*90.3*	17.9	49.7	3.1	4.6	279
average	89	337	9.3	0.5	23.1	*0.4*	21.1	13.0	1.8	28.5	13.8	15.3	*44.1*	7.7	178.6

Table 7.3. Average volume-percentages of food types in gut contents of fish larger than 15 cm fork length (%, top line) and the gap-codes within (diet spectra, GC_d, middle line) and among (food partitioning, GC_p, bottom line) species. For further explanation see text. The number of samples and specimens per species vary from 27 to 195 and from 33 to 1555 respectively. Italics indicate minimum and maximum values within species; minimum and maximum values among species are underlined. The sum of the percentages is not always equal to 100%, because there are some minor food categories (e.g. fish eggs) that are not included in the table.

	# samples	# spec.		Phyto-plankton	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish
B.acutirostris	121	238	%	3.2	0.1	2.0	*0.0*	2.6	0.6	*0.0*	7.9	3.5	0.7	*76.0*
			GC_d	1.5	*1*	1.5	*1*	2.5	1.5	*1*	3	2	*1*	*4*
			GC_p	1.5	1	1	1	1.5	1	1	1.5	1.5	1	4
B.brevicephalus	107	972	%	7.4	0.2	14.6	*0.0*	3.9	*34.0*	*0.0*	9.4	23.2	5.2	0.2
			GC_d	4	2	6	1.5	4.5	7	*1*	5.5	7	3	1.5
			GC_p	1.5	1	3.5	1	1.5	4	1	1.5	4	1	1
B.crassibarbis	51	84	%	10.4	0.3	0.7	0.3	28.2	8.8	*0.0*	*28.8*	7.3	11.8	2.1
			GC_d	2.5	2	2	2	*5*	3.5	*1*	*5*	3	4	1.5
			GC_p	1.5	1	1.5	1.5	5	3	1	3	2	2	1
B.dainellii	58	81	%	2.1	*0.0*	8.5	*0.0*	1.0	*0.0*	2.4	5.7	7.3	1.6	*69.2*
			GC_d	2	*1*	3	*1*	2	*1*	2	2.5	2	1.5	*4*
			GC_p	1.5	1	2.5	1	1	1	1	1.5	2	1	3.5
B.gorgorensis	27	33	%	8.5	0.1	*31.6*	0.1	14.6	*0.0*	3.3	1.6	*0.0*	27.0	11.5
			GC_d	2	1.5	*4*	*1*	3	*1*	1.5	2.5	*1*	3.5	2.5
			GC_p	1.5	1	4	1.5	2.5	1	1	1.5	1.5	2	1
B.gorguari	123	310	%	6.9	*0.2*	15.8	0.7	3.4	1.4	2.4	6.5	1.2	3.6	*55.4*
			GC_d	3.5	1.5	5	*1*	3	2	2	4.5	2.5	2.5	*6*
			GC_p	1.5	1	3.5	1	1.5	1	1	1.5	1.5	1	2.5
B.longissimus	38	74	%	3.8	0.1	12.9	0.7	2.9	*0.0*	2.6	2.5	0.1	0.8	*71.0*
			GC_d	1.5	*1*	2	*1*	1.5	*1*	*1*	1.5	*1*	*1*	*3*
			GC_p	1.5	1	3	1.5	1	1	1	1	1	1	3.5
B.macrophtalmus	87	356	%	9.6	1.8	8.4	*0.3*	3.2	6.5	0.5	13.0	10.4	*0.3*	*45.3*
			GC_d	2	1.5	3	2	3.5	3.5	*1*	4	3	1.5	*5*
			GC_p	1.5	1	2.5	1.5	1.5	2.5	1	1.5	2	1	2
B.megastoma	76	130	%	1.3	0.1	13.9	*0.0*	0.7	1.3	0.3	6.8	6.9	0.3	*66.8*
			GC_d	1.5	1.5	3	*1*	1.5	1.5	1.5	1.5	2	1.5	*4*
			GC_p	1	1	3	1	1	1	1	1.5	2	1	3.5
B.nedgia	152	417	%	5.0	*0.3*	4.7	*0.3*	18.9	3.2	1.1	*32.5*	10.8	16.3	5.6
			GC_d	*1*	*1*	*1*	*1*	4	*1*	*1*	*5*	2	3	*1*
			GC_p	1.5	1	2	1.5	4.5	2	1	3	3	2	1
B.platydorsus	84	141	%	9.4	*0.0*	10.3	*0.0*	3.2	1.2	0.1	17.6	3.6	4.0	*49.0*
			GC_d	1.5	*1*	2.5	*1*	1.5	*1*	*1*	3	1.5	1.5	*4*
			GC_p	1.5	1	3	1	1.5	1.5	1	2	2	1	2.5
B.surkis	90	268	%	7.9	0.3	*70.9*	0.6	2.8	5.2	*0.2*	4.9	4.3	0.4	2.1
			GC_d	2.5	1.5	*4*	*1*	1.5	2	*1*	2.5	3	*1*	*1*
			GC_p	2	1	5	1	1	1.5	1	1.5	2	1	1
B.truttiformis	38	52	%	4.2	*0.0*	3.3	*0.0*	3.7	2.8	5.1	1.3	*0.0*	1.6	*72.3*
			GC_d	1	1	1	1	1	1	1	1	1	1	2
			GC_p	1.5	1	2	1	1.5	1.5	1	1	1	1	4
B.tsanensis	195	1555	%	6.3	0.2	4.6	0.8	14.2	6.2	*0.0*	*42.6*	4.9	17.7	1.3
			GC_d	4	2	4.5	3	6	5	*1*	7	5	6	1.5
			GC_p	1.5	1	2	2	3.5	2.5	1	4	2.5	2	1
average %				6.1	0.3	14.4	0.3	7.4	5.1	1.3	12.9	6.0	6.5	37.7

significance level was set at $p<0.05$. Subsequently, the mean volume-percentages of the food types were sorted in ascending order and coded numerically (GC_d in Table 7.3), according to the generalized gap-coding method of Simon (1983) and Archie (1985) (see Chapter 6 for a detailed description of this method).

The volume-percentages were also tested for significant differences among the species (food partitioning). In this case the volume-percentages of a particular food type in the samples of all species were ranked, transformed and tested. This results in different gap-codes (GC_p in Table 7.3).

The described procedure resulted in a matrix containing the average volume-percentages and the two different gap-codes for each food type-species combination (Table 7.3). Note that GC_p values are always used for the analysis of food partitioning, and that GC_d values are exclusively used for the analysis of diet spectra.

Comparison of predicted and actual diet spectra and food partitioning

Method 1: Correlations between predictions and gut contents data

Before correlations were calculated, gut contents data (gap-codes or f.o.o. data) and quantitative predictions were separately standardized by subtracting from each value the mean value of that particular variable and dividing it by the standard deviation of that variable. This was done to make the ranges of all variables similar (before standardization the values of predictions range from c. -0.8 to 0.8, those of the f.o.o. data range from 0 to 100, after standardization all ranges are between -3 and 3).

Gut contents data (either gap-codes of volume-percentages or frequency of occurrence data) and the quantitative predictions were compared by calculating correlations between them in two different ways.

a) The correlations between the predicted use of all food types within species separately versus the actual, measured use of food types: diet spectra (Fig. 7.1*a*).

b) The correlations between the predicted use per food type separately among all species versus the actual, measured use of that food type: food partitioning (Fig. 7.1*b*).

The resulting correlation coefficients give a summary as to how well a predicted and actual diet spectrum (or predicted and actual food partitioning) match: the higher the correlation coefficient, the better the prediction was (examples in Fig. 7.1).

Summarizing the fit between quantitative predictions and gut data

For both types of correlations (between predicted and actual diet spectra and between predicted and actual food partitioning; Tables 7.4 and 7.6 respectively) the absolute correlation values between hypotheses and gut data are interesting, but their relative values are more interesting for the fit of predictions and actual gut data in a strictly comparative way among the different *Barbus* species, or among the food types.

In order to express the absolute correlation coefficients as a relative fit measure we took the following steps:

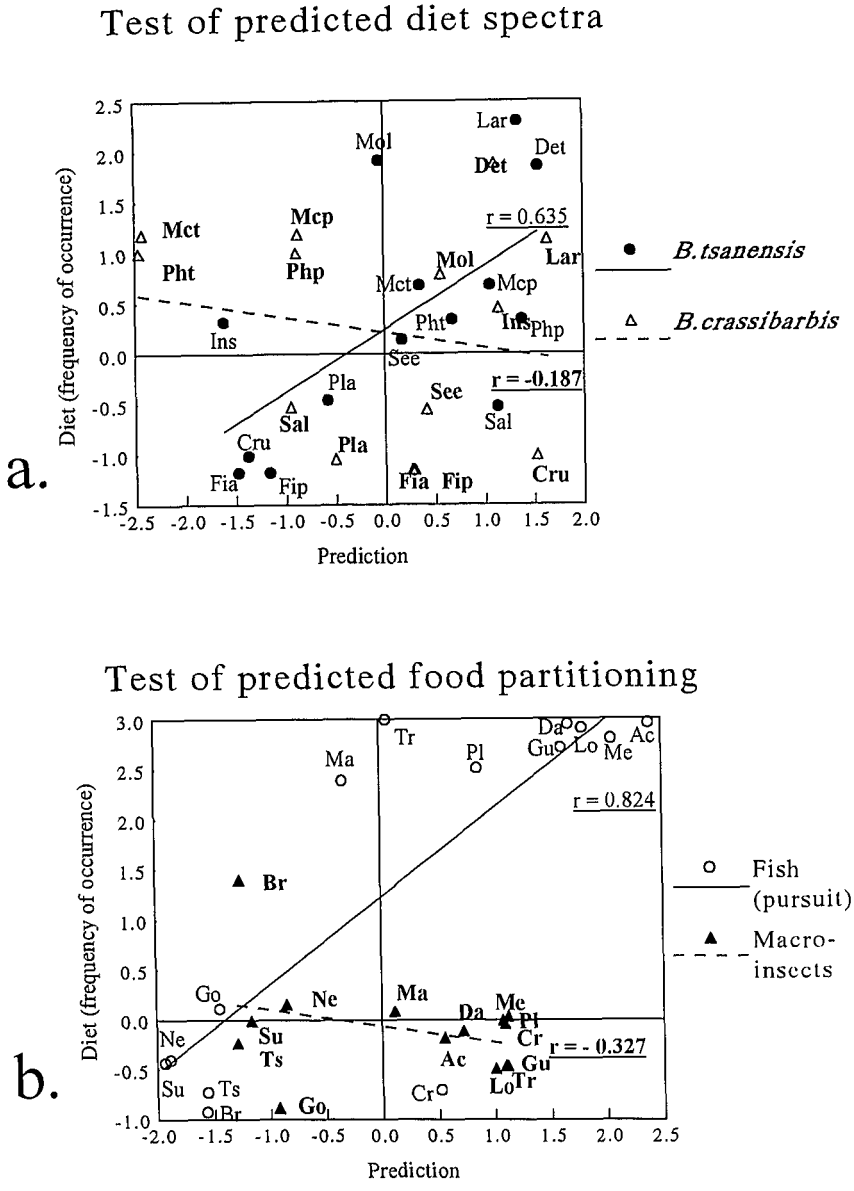


Fig. 7.1. An example of correlations between the predicted and actual diet spectra within species (Table 7.4) (**a**), and between the predicted and actual food partitioning among species (Table 7.6)(**b**). All data-sets were first standardised (see text), which causes the X- and Y-axes to range from -3 to 3. Every data-point represents a different food type (**a**), or species (**b**). Therefore, the regression lines give the accuracy of the prediction: a large positive correlation means that the hypothesis predicts the diet well. This example shows that the diet of *B. tsanensis* was well predicted, that of *B. crassibarbis* was not (**a**). The occurrence of fish (pursuit) in the diets of the *Barbus* species was predicted well, while the occurrence of macro-insects was poorly predicted (**b**). Abbreviations: Ac = *B.acutirostris*, Cr = *B.crassibarbis*, Ma = *B.macrophtalmus*, Da = *B.dainellii*, Go = *B.gorgorensis*, Gu = *B.gorguari*, Ts = *B.tsanensis*, Ne = *B.nedgia*, Lo =*B.longissimus*, Me = *B.megastoma*, Br = *B.brevicephalus*, Tr = *B.truttiformis*, Pl = *B.platydorsus*, Su = *B.surkis*, Phy = phytoplankton, Sal = sessile algae, Pla = macrophytes, See = seeds, Det = detritus/ substratum, Mcr = micro-crustaceans, Cru = macro-crustaceans, Lar = larvae/worms, Ins = macro-insects, Mol = molluscs, Fis = fish.

First we sorted the correlations and gave them rank numbers (separately for frequency of occurrence and volume-percentage data). The lowest correlation is given rank value 1, the highest 11 or 14, depending on the total number of categories. Ranks were assigned both per column and per row. Now each prediction-gut data combination has two rank values: 1) a rank value expressing the relative fit of a particular prediction to the gut data (column, $rank_1$), and 2) a rank expressing the relative fit of the gut data to the predictions (row, $rank_2$). As an example, consider the volume-percentage data of *B. longissimus* (Table 7.4). The predicted and actual diets of this species have a correlation of 0.574. This value has $rank_1$ value 12 (maximum is 14), because the gut data of *B. dainellii* (r=0.748) and *B. megastoma* (r=0.772, the highest value, and therefore printed in italics in the table) have higher correlations with the hypothesis for *B. longissimus* than the latter species itself. $Rank_2$ however, has value 14, since the gut data of *B. longissimus* fit best with the hypothesis for the same species (therefore this value is underlined in the table; note that *B. dainellii* and *B. megastoma* have correlation values of 0.434 and 0.417 in this case).

Since we have now two rank numbers for each prediction-gut data combination, we want to combine these into a single, overall fit value, ranging from 0 (no fit) to 1 (perfect fit). We also wanted to take into account whether the absolute correlation value was statistically significant, because even in a comparative way, to our view a significant correlation value should weigh heavier than a non-significant value. To arrive at this overall fit value we divided each rank value by the largest rank number in its column or row. If the correlation between prediction and actual gut data was significantly negative, a prediction-gut data combination was assigned a 'significance number' of minus one (-1), if it was significantly positive, a value of one (1) is assigned, non-significant correlations get a zero value (0). The mean of the two ranks and the significance number is calculated for each prediction-gut data combination and scaled so that the possible values range from 0 to 1, according to the formula:

$$\frac{([(rank_1/\max[rank_1])+(rank_2/\max[rank_2])+significance]/3)-c}{(1-c)}$$

, in which 'c' is a constant, viz. the minimum value of the mean of the relative ranks and the significance number ([1/14+1/14-1]/3=-0.286). The resulting values for prediction-gut data combinations were qualitatively interpreted as: 0 to 0.6: poor fit; 0.6 to 0.8: fair fit; 0.8 to 1: good fit (Tables 7.5 and 7.7).

In our example of *B. longissimus*, the correlation is positively significant (>0.532), and therefore gets the significance number 1. The total fit of predicted and actual diet of *B. longissimus* can now be calculated as: ({[(12/14)+(14/14)+1]/3}+0.286)/(1+0.286)= 0.963, which is interpreted as a good fit (Table 7.5).

The above fit-values can be assigned both for the frequency of occurrence data and for the volume-percentage data. When taking their average a summarized conclusion about the predictability of diet spectra or food partitioning can be made. This predictability will be evaluated

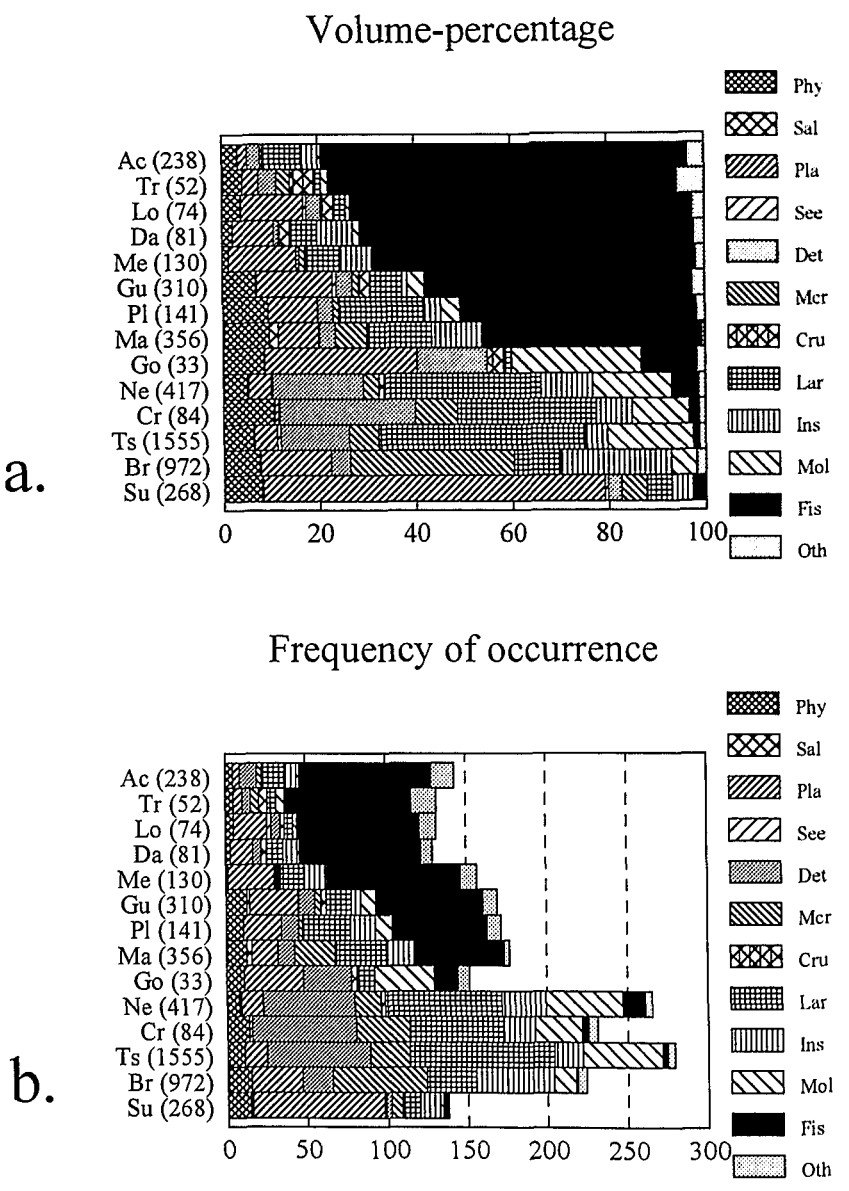


Fig. 7.2. Volume-percentages (**a**, cf. Table 7.3) and frequency of occurrence (**b**, cf. Table 7.2) of the food types in the gut contents of *Barbus* specimens larger than 15 cm fork length. The larger the sum of the frequency of occurrence percentages, the more generalist a species feeds. The number of specimens for which the gut contents was analysed is indicated behind the species name. Abbreviations: Ac = *B.acutirostris*, Cr = *B.crassibarbis*, Ma = *B.macrophtalmus*, Da = *B.dainellii*, Go = *B.gorgorensis*, Gu = *B.gorguari*, Ts = *B.tsanensis*, Ne = *B.nedgia*, Lo =*B.longissimus*, Me = *B.megastoma*, Br = *B.brevicephalus*, Tr = *B.truttiformis*, Pl = *B.platydorsus*, Su = *B.surkis*, Phy = phytoplankton, Sal = sessile algae, Pla = macrophytes, See = seeds, Det = detritus/ substratum, Mcr = micro-crustaceans, Cru = macro-crustaceans, Lar = larvae/worms, Ins = macro-insects, Mol = molluscs, Fis = fish, Oth = other food types.

in the context of the Lake Tana ecosystem, since food availability and other system parameters might influence the results

Method 2. Graphic (multivariate) comparison of predictions and gut data

To evaluate fits between predictions and gut data, we used an alternative approach, that was independent from the correlation calculations. If two independent methods for analysing the data give similar results this is a strong indication that our interpretation of the data is correct. This is especially important in cases in which large data-sets have to be summarized into few numbers (such as gap-codes or correlation coefficients), which inevitably results in the loss of some information and can lead to possible distortion. Similar results from independent methods indicate that such distortion was limited

The quantitative predictions and gut data were graphically compared in the two following ways:
1) Non-metric 1-dimensional scaling was performed. This is a method in which as much of the variation in which we are interested is represented in one dimension. The closer objects (species or food types in this case) are, the more overall similarity they have. 1-Dimensional scaling was performed separately on the prediction matrix (Table 7.1) and on the matrices with frequency of occurrence (Table 7.2) and gap-codes of volume-percentage data (Table 7.3). The graphical similarity between these 3 1-dimensional scalings was evaluated.

This method is a dimension-reduction method similar to principal components analysis (PCA), but subsequent dimensions need not be uncorrelated as in PCA. This results in the better preservation of small distances between points (Rohlf 1993; cf. Fig. 7.3: diet predictions v. actual diets, and Fig. 7.4: food partitioning predictions v. actual food partitioning).
2) Unweighted pair-group method clustering, using the arithmetic average (UPGMA-clustering; Rohlf 1993) was performed on the same data matrices that were used for the non-metric 1-dimensional scaling to compare predicted and actual food partitioning (Fig. 7.5). The presence and absence of clusters can be graphically compared between predictions and actual gut data. This method shows a hierarchy in relations.

Software

Unplanned pairwise comparisons of means and van der Waerden's transformations of ranks were performed with Statistical Analysis Software (SAS). All multivariate and clustering techniques were performed with NTSYS-pc, version 1.80 (Exeter Software, Setauket, New York).

RESULTS

Gut contents of the 14 Lake Tana *Barbus* species

Some food types are much less utilized by the barbs than others (Tables 7.2 and 7.3, Fig. 7.2). The average volume-percentage of seeds (0.3%), sessile algae (0.3%) and macro-crustaceans

Table 7.4. Predicted v. actual diet spectra. Values are correlations between hypothesized and actual (gap-codes of volume-percentages [top] and frequency of occurrence [bottom]) diet spectra within the *Barbus* species after standardisation of both data-sets. Italics indicate minimum and maximum values per row; minimum and maximum values per column are underlined. Note that only bold correlation coefficients (>0.532) are significant, however, we are mainly interested in the pattern of relative values (their ranks) of correlations, not in testing significances.

Gut data		Diet spectra Predictions													
		Ac	*Br*	*Cr*	*Da*	*Go*	*Gu*	*Lo*	*Ma*	*Me*	*Ne*	*Pl*	*Su*	*Tr*	*Ts*
Volume-percentages	*B.acutirostris*	0.524	***-0.623***	0.261	**0.765**	-0.456	***0.667***	0.342	-0.132	0.180	-0.280	0.486	***-0.782***	-0.031	-0.410
	B.brevicephalus	-0.094	***0.630***	-0.486	-0.530	-0.149	-0.307	-0.507	***0.554***	-0.015	0.316	0.081	0.092	0.085	0.448
	B.crassibarbis	**-0.563**	0.464	-0.062	-0.425	***0.628***	-0.525	***-0.756***	0.020	***-0.545***	***0.698***	***-0.543***	0.507	*-0.492*	***0.742***
	B.dainellii	0.360	**-0.609**	0.346	0.455	-0.352	0.488	**0.748**	-0.179	0.419	**-0.606**	0.017	-0.197	0.151	**-0.671**
	B.gorgorensis	-0.308	0.054	0.156	-0.278	0.333	-0.377	0.235	-0.422	-0.080	-0.067	-0.337	***0.615***	0.193	-0.095
	B.gorguari	0.376	-0.346	0.075	0.309	*-0.467*	0.337	**0.570**	-0.144	0.333	-0.397	0.243	-0.268	0.338	-0.452
	B.longissimus	***0.545***	-0.414	-0.070	0.434	-0.275	**0.568**	**0.574**	0.043	0.417	**-0.582**	0.370	-0.519	0.111	**-0.569**
	B.macrophtalmus	0.294	-0.226	-0.017	0.398	-0.175	0.313	0.056	0.000	0.013	-0.121	0.492	**-0.545**	0.035	-0.155
	B.megastoma	0.409	-0.474	0.086	0.265	-0.292	0.441	***0.772***	-0.123	*0.460*	***-0.681***	0.301	-0.255	*0.400*	***-0.722***
	B.nedgia	-0.439	-0.144	**0.587**	0.192	0.343	-0.232	-0.394	*-0.452*	**-0.532**	0.490	-0.387	0.260	-0.437	0.338
	B.platydorsus	0.447	**-0.583**	0.225	**0.649**	-0.329	0.527	**0.551**	-0.297	0.222	-0.466	***0.550***	**-0.600**	0.227	**-0.584**
	B.surkis	-0.135	**0.594**	*-0.508*	***-0.649***	-0.114	-0.384	-0.206	0.428	0.125	0.102	0.057	0.259	0.387	0.237
	B.truttiformis	0.398	-0.444	0.020	0.331	0.068	**0.608**	0.484	0.192	0.393	**-0.600**	-0.062	-0.281	-0.290	-0.525
	B.tsanensis	***-0.576***	**0.549**	-0.144	*-0.496*	**0.625**	***-0.587***	**-0.719**	0.081	-0.461	**0.605**	-0.466	0.520	-0.377	**0.681**
Frequency of occurrence	*B.acutirostris*	*0.446*	**-0.536**	0.171	**0.615**	-0.307	**0.534**	0.372	-0.226	0.146	-0.301	**0.567**	***-0.680***	0.131	-0.432
	B.brevicephalus	0.183	0.408	-0.472	-0.283	-0.290	0.067	-0.336	***0.725***	0.203	0.082	0.115	-0.187	-0.099	0.238
	B.crassibarbis	-0.165	0.439	-0.187	-0.207	0.059	-0.200	***-0.749***	0.359	-0.305	**0.638**	-0.306	0.078	***-0.535***	***0.708***
	B.dainellii	0.373	***-0.758***	0.468	***0.616***	-0.319	***0.535***	***0.766***	-0.384	0.307	***-0.613***	0.295	-0.368	0.256	***-0.759***
	B.gorgorensis	-0.312	0.178	0.068	-0.331	0.333	-0.364	0.051	-0.179	-0.058	0.042	***-0.533***	***0.629***	-0.061	0.077
	B.gorguari	0.046	0.016	-0.215	-0.163	0.093	-0.011	0.313	-0.028	0.182	-0.211	-0.110	0.146	0.205	-0.152
	B.longissimus	-0.030	-0.350	0.236	0.252	0.340	0.112	0.369	-0.301	0.033	-0.359	-0.060	0.037	-0.022	-0.374
	B.macrophtalmus	0.114	0.373	*-0.521*	-0.340	-0.191	-0.043	-0.230	0.391	0.042	0.199	0.150	-0.093	0.144	0.294
	B.megastoma	0.325	**-0.632**	0.390	**0.553**	*-0.339*	0.389	**0.662**	*-0.446*	0.221	**-0.554**	***0.641***	-0.457	*0.507*	***-0.731***
	B.nedgia	*-0.524*	-0.027	*0.477*	-0.045	*0.444*	-0.332	-0.390	-0.372	-0.477	0.470	-0.473	0.420	-0.357	0.350
	B.platydorsus	0.288	-0.172	-0.088	0.273	-0.333	0.247	0.155	-0.091	0.145	-0.082	**0.572**	**-0.555**	0.316	-0.182
	B.surkis	-0.289	***0.568***	-0.402	***-0.645***	0.132	***-0.567***	-0.092	0.138	0.024	0.038	0.011	0.456	0.476	0.155
	B.truttiformis	0.383	**-0.597**	0.301	0.485	-0.239	**0.534**	**0.655**	-0.154	*0.326*	**-0.548**	-0.016	-0.218	-0.023	**-0.589**
	B.tsanensis	-0.428	0.289	0.147	-0.115	0.340	-0.380	**-0.690**	-0.084	*-0.529*	***0.658***	-0.361	0.287	-0.481	**0.636**

Table 7.5. Correlations and fits of the predicted and actual diet spectra within the *Barbus* species. The calculation of the fit is explained in the text and based on ranks of the correlations and their significance. The average fit is the arithmetic mean of the fit based on gap-codes of the volume-percentages and the fit based on the frequency of occurrence. The minimum and maximum value per column are underlined. A qualitative interpretation is also listed.

	Volume-percentages		Frequency of occurrence		Average fit	Qualitative
	Correlation	Fit	Correlation	Fit		
B.acutirostris	0.524	0.685	0.446	0.685	0.685	fair
B.brevicephalus	0.630	1.000	0.408	0.685	0.843	good
B.crassibarbis	-0.062	0.463	-0.187	0.444	0.454	poor
B.dainellii	0.455	0.667	0.616	0.981	0.824	good
B.gorgorensis	0.333	0.667	0.333	0.667	0.667	fair
B.gorguari	0.337	0.574	-0.011	0.481	0.528	poor
B.longissimus	0.574	0.963	0.369	0.667	0.815	good
B.macrophtalmus	0.000	0.500	0.391	0.722	0.611	fair
B.megastoma	0.460	0.722	0.221	0.574	0.648	fair
B.nedgia	0.490	0.685	0.470	0.685	0.685	fair
B.platydorsus	0.550	0.963	0.572	0.981	0.972	good
B.surkis	0.259	0.611	0.456	0.685	0.648	fair
B.truttiformis	-0.290	0.370	-0.023	0.463	0.417	poor
B.tsanensis	0.681	0.981	0.635	0.963	0.972	good

(1.3%) is very low when compared with the average volume-percentage of larvae/worms (12.9%), macrophytes (14.4%) and fish (37.7%). This is also reflected in the f.o.o. of these food types (seeds, sessile algae and macro-crustaceans 0.4, 0.5, and 1.8% respectively, larvae/worms, macrophytes and fish 28.5, 23.1, and 44.1% respectively). The reason for this limited utilization can be the low abundance in the environment, but also some intrinsic characters of the food (difficult to process, low quality etc., see Discussion). Note that the number of samples and (pooled) specimens widely varies among species, from 33 specimens in 27 samples for *B. gorgorensis* to 1555 specimens in 195 samples for *B. tsanensis*. This more or less reflects the relative abundance of the species in the sampling area.

The gap-codes that were assigned to the volume-percentages of the food types after pairwise comparison often differ, depending on whether they were compared among (GC_p: food partitioning) or within species (GC_d: diet spectra)(Table 7.3). The less utilized food types show little differentiation in gap-codes among species, i.e. they do not differ significantly in volume-percentages among species. Sessile algae and macro-crustaceans do not show any significant differences among species at all. However, this can be an artefact, because the relative errors in the estimates of small volumes are larger.

The sum of all f.o.o. percentages gives an indication as to how generalized or specialized a species feeds. The theoretical minimum value is 100%. The lowest value we found was 129% for *B. dainellii* (including the 'other' food category), the highest was 279% for *B. tsanensis*, making the former a 'specialist' and the latter a 'generalist' (see also Discussion).

Several 'diet groups' can be distinguished from the gut contents data of Fig. 7.2 and Tables &.2 and 7.3, as visualised in the clustering of the *Barbus* species, using either the gap-codes of the volume-percentages (GC_p, Fig. 7.5*a*) or the f.o.o. (Fig. 7.5*c*).

1. Piscivores. This group (of rather specialized feeders) can be subdivided in:
   1a. almost exclusive piscivores that eat some other food types, but all in very small proportions: *B. acutirostris* and *B. truttiformis*.
   1b. almost exclusive piscivores that eat some other food types, of which macrophytes is the most important: *B. longissimus*, *B. dainellii*, *B. megastoma*, and *B. gorguari*.
   1c. predominant piscivores that eat some other food types in considerable quantities, especially plants and larvae/worm: *B. platydorsus* and *B. macrophtalmus*.
2. Benthivores. This group mainly feeds rather generalized on larvae/worms, detritus/substratum, and molluscs: *B. nedgia*, *B. tsanensis*, and *B. crassibarbis*.
3. Zooplanktivore/insectivore. This group only contains the rather generalized feeding *B. brevicephalus*.
4. Molluscivore/macrophytivore. This group only contains the rather specialized feeding *B. gorgorensis*.
5. Almost exclusive macrophytivore. This group only contains the rather specialized feeding *B. surkis*.

Correlations between hypotheses and gut contents data

The correlation between predicted and actual diets is very dependent on what is actually available in the ecosystem. We have no quantitative data on the relative abundances of the food types, but there is a consistent qualitative picture that can be drawn of the distribution of the different food types. Phytoplankton, microcrustaceans, detritus/substratum, larvae/worms, and small fish are omnipresent and relatively abundant. Macrophytes have a very patchy distribution, and therefore also the associated sessile algae, molluscs, and macro-insects (some other sessile algae and molluscs are more abundant, being associated with a rocky substratum). Macro-crustaceans and seeds appear to be rare in the until thusfar investigated ecosystem. These differences in distributions and abundances will affect the fit of predicted and actual diets.

Predicted v. actual species diet spectra

The correlations of predicted and actual diet spectra are usually positive (Tables 7.4 and 7.5) and never significantly negative. *B. crassibarbis* and *B. truttiformis* show (non-significant) negative correlations using both the volume-percentages and f.o.o. data. *B. gorguari* only shows a (non-significant) negative correlation when using f.o.o. data. All other correlations are positive, although not always significant ($r>0.532$). *B. brevicephalus* and *B. longissimus* show significant positive correlations between prediction and volume-percentage data; *B. dainellii* between its hypothesis and the f.o.o. data. *B. platydorsus* and *B.tsanensis* even show significant positive correlations between predicted and actual diet spectra for both the volume-percentage and f.o.o. data.

Table 7.6. Predicted v. actual food partitioning among species. Values are correlations between predicted and actual (gap-codes of volume-percentages [top] and frequency of occurrence [bottom]) gut distribution of food types among the 14 *Barbus* species. Italics indicate minimum and maximum values per row; minimum and maximum values per column are underlined. Note that only bold correlation coefficients (>0.576 for volume-percentages; >0.532 for frequency of occurrence data) are significant, however, we are mainly interested in the pattern of relative values of correlations (their ranks), not in testing significances.

		Food Partitioning Predictions													
Gut data		Phyto-plankton (townet)	Phyto-plankton (pump)	Sessile algae	Macro-phytes	Seeds	Detritus/ substratum	Micro-crustaceans (townet)	Micro-crustaceans (pump)	Macro-crustaceans	Larvae/ worms	Macro-insects	Molluscs	Fish (pursuit)	Fish (ambush)
Volume-percentages	Phytoplankton	-0.056	-0.282	-0.043	0.294	0.026	-0.357	0.026	-0.249	0.344	-0.274	0.128	0.069	0.164	0.269
	Sessile algae	0.034	**-0.551**	-0.124	*0.362*	0.015	-0.392	0.046	***-0.641***	***0.562***	-0.349	0.284	0.142	0.424	0.256
	Macrophytes	0.099	0.036	0.096	0.088	0.333	-0.404	0.132	0.037	0.111	-0.453	-0.045	0.325	-0.067	0.029
	Seeds	0.035	0.203	0.209	-0.231	0.442	0.116	-0.056	-0.030	0.165	-0.019	-0.274	0.419	-0.194	-0.350
	Detritus/substratum	***-0.541***	0.272	0.197	-0.319	0.275	***0.762***	-0.622	0.025	-0.230	***0.746***	-0.253	0.261	-0.410	-0.286
	Micro-crustaceans	0.040	***0.610***	0.311	0.093	-0.100	0.288	-0.017	***0.729***	-0.385	0.120	-0.346	-0.203	***-0.468***	*-0.467*
	Macro-crustaceans	*0.034*	***-0.551***	-0.124	*0.362*	*0.015*	-0.392	*0.046*	***-0.641***	***0.562***	-0.349	0.284	0.142	0.424	0.256
	Larvae/worms	-0.194	0.265	0.100	*-0.368*	-0.006	**0.665**	-0.263	0.212	-0.387	**0.681**	-0.301	-0.018	-0.297	-0.262
	Macro-insects	0.346	0.518	0.216	-0.167	-0.104	0.314	0.246	**0.702**	***-0.561***	0.167	*-0.493*	-0.154	-0.381	-0.459
	Molluscs	-0.491	0.121	*0.352*	-0.244	***0.687***	**0.641**	***-0.624***	-0.328	-0.058	**0.564**	-0.390	***0.697***	-0.386	-0.378
	Fish	*0.349*	***-0.708***	***-0.577***	0.281	***-0.597***	***-0.799***	*0.510*	-0.476	0.432	***-0.599***	***0.751***	***-0.544***	***0.834***	***0.746***
Frequency of occurrence	Phytoplankton	-0.134	-0.044	0.072	0.206	0.278	-0.308	-0.073	0.026	0.265	-0.309	0.005	0.284	-0.049	0.031
	Sessile algae	0.254	**-0.571**	-0.314	0.274	-0.275	**-0.549**	0.316	-0.507	**0.619**	-0.452	0.460	-0.197	**0.562**	0.386
	Macrophytes	0.018	0.147	0.354	0.136	0.525	-0.109	-0.049	0.031	0.103	-0.262	-0.340	**0.551**	-0.277	-0.296
	Seeds	0.125	**-0.632**	-0.270	*0.335*	-0.208	-0.467	0.176	**-0.662**	***0.632***	-0.355	0.435	-0.107	**0.557**	0.401
	Detritus/substratum	***-0.557***	0.255	0.227	*-0.358*	0.449	***0.785***	***-0.653***	-0.018	-0.212	***0.762***	-0.341	0.425	-0.439	-0.357
	Micro-crustaceans	0.099	0.468	0.259	0.097	-0.078	0.260	0.021	**0.567**	-0.253	0.104	-0.344	-0.127	-0.358	*-0.462*
	Macro-crustaceans	0.059	**-0.605**	-0.214	0.322	-0.085	-0.470	0.126	***-0.727***	**0.569**	-0.352	0.435	-0.028	0.490	0.437
	Larvae/worms	-0.200	*0.472*	0.170	-0.324	-0.070	**0.700**	-0.274	0.446	*-0.477*	**0.658**	-0.334	-0.117	-0.434	-0.347
	Macro-insects	0.222	0.399	0.199	0.130	-0.254	0.221	0.146	***0.578***	-0.374	0.088	-0.327	*-0.271*	-0.274	-0.361
	Molluscs	-0.465	0.315	*0.434*	-0.255	***0.624***	**0.653**	**-0.570**	-0.109	-0.369	**0.569**	*-0.471*	***0.583***	*-0.520*	-0.356
	Fish	*0.392*	***-0.647***	***-0.644***	0.136	***-0.578***	***-0.875***	***0.581***	-0.357	0.392	***-0.659***	***0.783***	***-0.546***	***0.824***	***0.793***

However, the absolute correlation value is not as interesting as the relative correlation value, since we are mainly interested in comparison within the Lake Tana *Barbus* group. For example, the absolute correlation between the predicted and actual diet of *B. surkis* (volume-percentages) is 0.259 (Table 7.4), the lowest positive correlation value between predicted and actual diets for any species, but there are only four actual diets that have higher correlations with the prediction for *B. surkis* (*B. crassibarbis*: 0.507, *B. gorgorensis*: 0.615, *B. nedgia*: 0.260, and *B. tsanensis*: 0.520; comparison within the table column). The rank value of this correlation is therefore 10 (maximum is 14). On the other hand there are correlation values that are higher than 0.259 (such as 0.337 for the predicted and actual diet spectrum of *B. gorguari*), that have a lower rank value (in this case 8).

In order to take both the relative correlation as well as the significance of the correlations into account, a fit value was calculated (see Material and methods). The values were calculated for the volume-percentage data and the f.o.o. data separately, and listed in Table 7.5, as well as an arbitrary, qualitative interpretation of these values. The fits, calculated with the volume-percentages and the f.o.o. were rather similar, except for *B. brevicephalus*, *B. longissimus*, and *B. megastoma*, which fit better with the volume-percentage data, and *B. dainellii* and *B. macrophtalmus*, which fit better with f.o.o. data.

In short, the diets of *B. brevicephalus*, *B. dainellii*, *B. longissimus*, *B. platydorsus*, and *B. tsanensis* can be predicted well (fit>0.8), the diets of *B. acutirostris*, *B. gorgorensis*, *B. macrophtalmus*, *B.megastoma nedgia*, and *B. surkis* can be predicted fairly (0.6<fit<0.8), and the diets of *B. crassibarbis*, *B. gorguari*, and *B. truttiformis* can be predicted poorly (fit<0.6).

Predicted v. actual food partitioning

The correlations of predicted and actual food partitioning among species are also usually positive (Tables 7.6 and 7.7), and never significantly negative (<-0.532). Detritus/substratum, micro-crustaceans (pump), macro-crustaceans, larvae/worms, molluscs, and fish (pursuit and ambush) all show significantly positive correlations for volume-percentage as well as for f.o.o. data. Phytoplankton (townet and pump feeding-modes), sessile algae, and macro-insects show (non-significant) negative correlations for both the volume-percentage and f.o.o. data. Micro-crustaceans (townet feeding-mode) only show a (minor) negative correlation for the volume-percentage data, seeds only for the f.o.o.

Fit values were calculated in the same way as in the diet comparisons. The values were calculated for the volume-percentage data and the f.o.o. data separately, and listed in Table 7.7, as well as the arbitrary, qualitative interpretation of these values. The fits, calculated from the volume-percentages and f.o.o. data were rather similar, except for seeds, which had a fair fit for the volume-percentage (0.716) data, and a poor fit for the f.o.o. data (0.425).

In short, the food partitioning of detritus/substratum, micro-crustaceans (pump), macro-crustaceans, larvae/worms, molluscs, and fish (pursuit and ambush) can be predicted well, and the food partitioning of phytoplankton (townet and pump), macrophytes, sessile algae, seeds, micro-crustaceans (townet), and macro-insects can be predicted poorly.

It is important to note that all food types that are relatively abundant, and easily distinguishable in the gut contents have (very) high predictabilities! Macrophytes (both abundant and well distinguishable, but patchily distributed) are the only exception. The poor predictability of townet feeding most likely means that this feeding mode is not used by the barbs to feed on phytoplankton and micro-crustaceans. It has never been reported as an observed strategy within the cyprinid family.

Table 7.7. Correlations and fits of the predicted and actual food partitioning among the 14 *Barbus* species. The calculation of the fit is explained in the text and based on ranks of the correlations and their significance. The average fit is the arithmetic mean of the fit based on gap-codes of the volume-percentages and the fit based on the frequency of occurrence. The minimum and maximum value per column are underlined. A qualitative interpretation is also listed.

	Volume-percentages		Frequency of occurrence		Average fit	Qualitative
	Correlation	Fit	Correlation	Fit		
Phytoplankton (townet)	-0.056	0.406	-0.134	0.369	0.387	poor
Phytoplankton (pump)	-0.282	0.350	-0.044	0.448	0.399	poor
Sessile algae	-0.124	0.382	-0.314	0.359	0.371	poor
Macrophytes	0.088	0.509	0.136	0.547	0.528	poor
Seeds	0.442	0.716	-0.208	0.425	0.570	poor
Detritus/substratum	0.762	1.000	0.785	1.000	1.000	good
Micro-crustaceans (townet)	-0.017	0.467	0.021	0.491	0.479	poor
Micro-crustaceans (pump)	0.729	1.000	0.567	0.976	0.988	good
Macro-crustaceans	0.562	0.976	0.559	0.953	0.964	good
Larvae/worms	0.651	0.976	0.658	0.958	0.967	good
Macro-insects	-0.493	0.279	-0.327	0.416	0.348	poor
Molluscs	0.697	1.000	0.583	0.963	0.981	good
Fish (pursuit)	0.834	1.000	0.824	1.000	1.000	good
Fish (ambush)	0.746	0.963	0.793	0.981	0.972	good

Graphic (multivariate) comparison of hypotheses and gut data

In order to visualize the comparison between the predictions of diet spectra and food partitioning, and the actual gut contents data, they have been separately visualized using predictions, f.o.o. and volume-percentage data (Gc_p) (Tables 7.1, 7.2 and 7.3) directly, without calculating correlations between them, as in the previous section. Two approaches have been taken: 1) 1-dimensional non-metric scaling of species (food partitioning) and food types (diet spectra),, and 2) UPGMA clustering of the species. The actual correlation values are decisive in evaluating the predictions, not the visualisations, since the latter only contain limited information.

Predicted v. actual diet spectra

The nonmetric 1-dimensional scaling (Fig. 7.3) shows a rather chaotic picture when all food types are taken into account. However, there are three consistent food type groups: 1) molluscs,

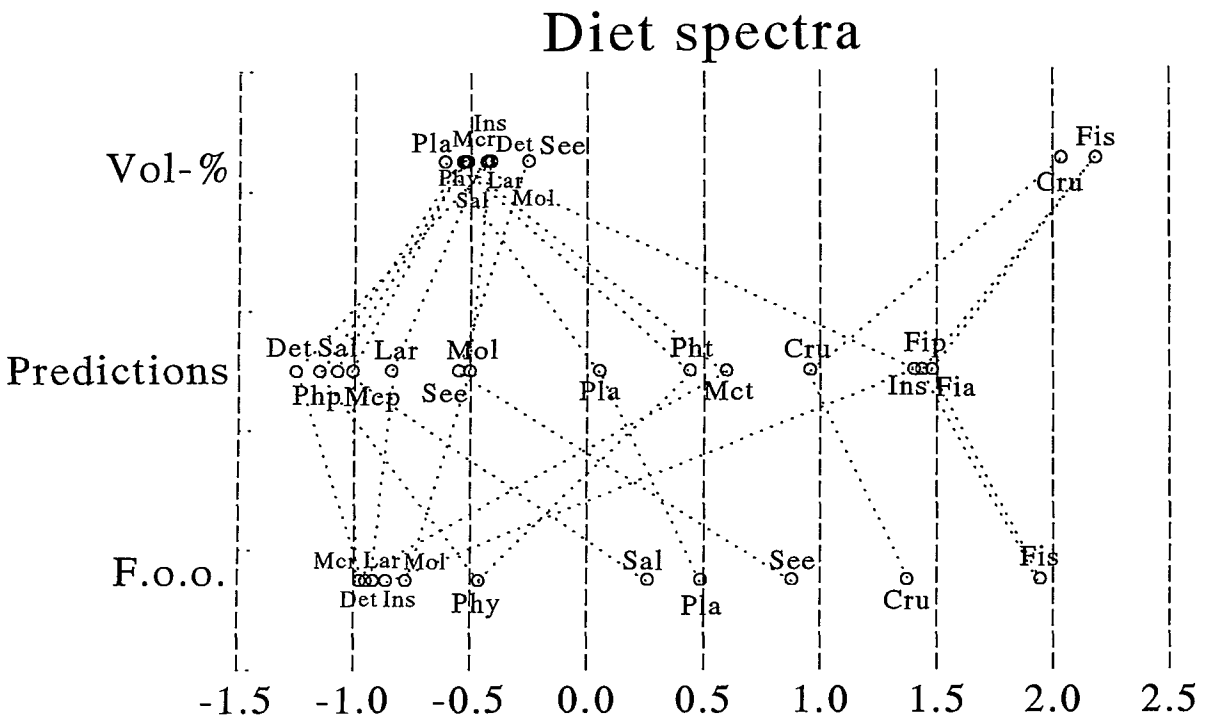


Fig. 7.3. Predicted v. actual diet spectra: nonmetric 1-dimensional scaling. The mutual distances on one line (1 dimension) represent the overall differences among food types in the diet spectra. The this overall difference as closely as possible. The lines of volume-percentage (top), predictions (middle), and frequency of occurrence (bottom) were calculated separately. They were based on 1) the gap-codes (GC_d) of the volume-percentages of the food types in the gut (top, stress value: 0.15, indicating a good representation of the original data), 2) the diet predictions (middle, stress: 0.25, indicating a fair representation of the original data), and 3) the frequency of occurrence of the food types in the gut (bottom, stress: 0.17, indicating a good representation of the original data). The same food types are connected by dotted lines. It is expected that lines should not cross between predictions and gut data, since we expect the mutual positioning of food types within each 1-dimensional scaling to be similar if predictions are accurate (e.g. the dotted lines connecting fish [Fis] with the predicted position [Fia and Fip] do not cross other dotted lines since the position of fish is consistently to the right of the group; the dotted lines connecting insects [Ins] to the predictions cross many other lines, and therefore it is concluded that the importance of insects in the diet spectra is poorly predicted). Abbreviations: Pht = phytoplankton (townet), Php = phytoplankton (pump), Phy = phytoplankton, Sal = sessile algae, Pla = macrophytes, See = seeds, Det = detritus/ substratum, Mct = micro-crustaceans (townet), Mcp = micro-crustaceans (pump), Mcr = micro-crustaceans, Cru = macro-crustaceans, Lar = larvae/worms, Ins = macro-insects, Mol = molluscs, Fip = fish (pursuit), Fia = fish (ambush), Fis = fish.

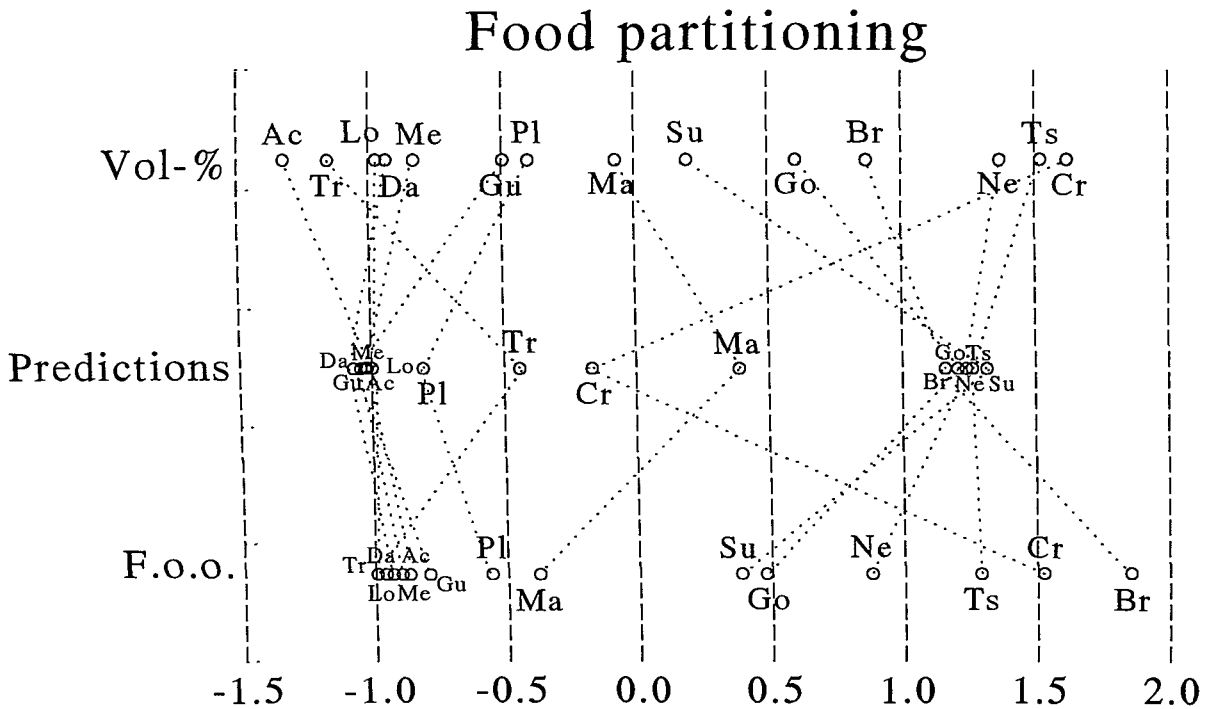


Fig. 7.4. Predicted v. actual food partitioning among the 14 Lake Tana *Barbus* species: nonmetric 1-dimensional scaling. The mutual distances on one line (1 dimension) represent the overall differences among species in food partitioning as closely as possible. The lines of volume-percentage (top), predictions (middle), and frequency of occurrence (bottom) were calculated separately. They were based on 1) the gap-codes (GC_p) of the volume-percentages of the food types (top, stress: 0.14, indicating a good representation of the original data), 2) the diet predictions (middle, stress: 0.19, indicating a good representation of the original data), and 3) the frequency of occurrence of the food types (bottom, stress: 0.16, indicating a good representation of the original data). The same species are connected by dotted lines. It is expected that lines should not cross between predictions and gut data, since we expect the mutual positioning of species within each 1-dimensional scaling to be similar if predictions are accurate (e.g. the dotted lines connecting *B. macrophtalmus* [Ma] with the predicted position do not cross other dotted lines (except for the ones of Cr) since the position of this species is consistently central in the group; the dotted lines connecting *B. crassibarbis* [Cr] to the predictions cross many other lines, and therefore it is concluded that the food partitioning of this species is poorly predicted). Abbreviations: Ac = *B.acutirostris*, Cr = *B.crassibarbis*, Ma = *B.macrophtalmus*, Da = *B.dainellii*, Go = *B.gorgorensis*, Gu = *B.gorguari*, Ts = *B.tsanensis*, Ne = *B.nedgia*, Lo =*B.longissimus*, Me = *B.megastoma*, Br = *B.brevicephalus*, Tr = *B.truttiformis*, Pl = *B.platydorsus*, Su = *B.surkis*.

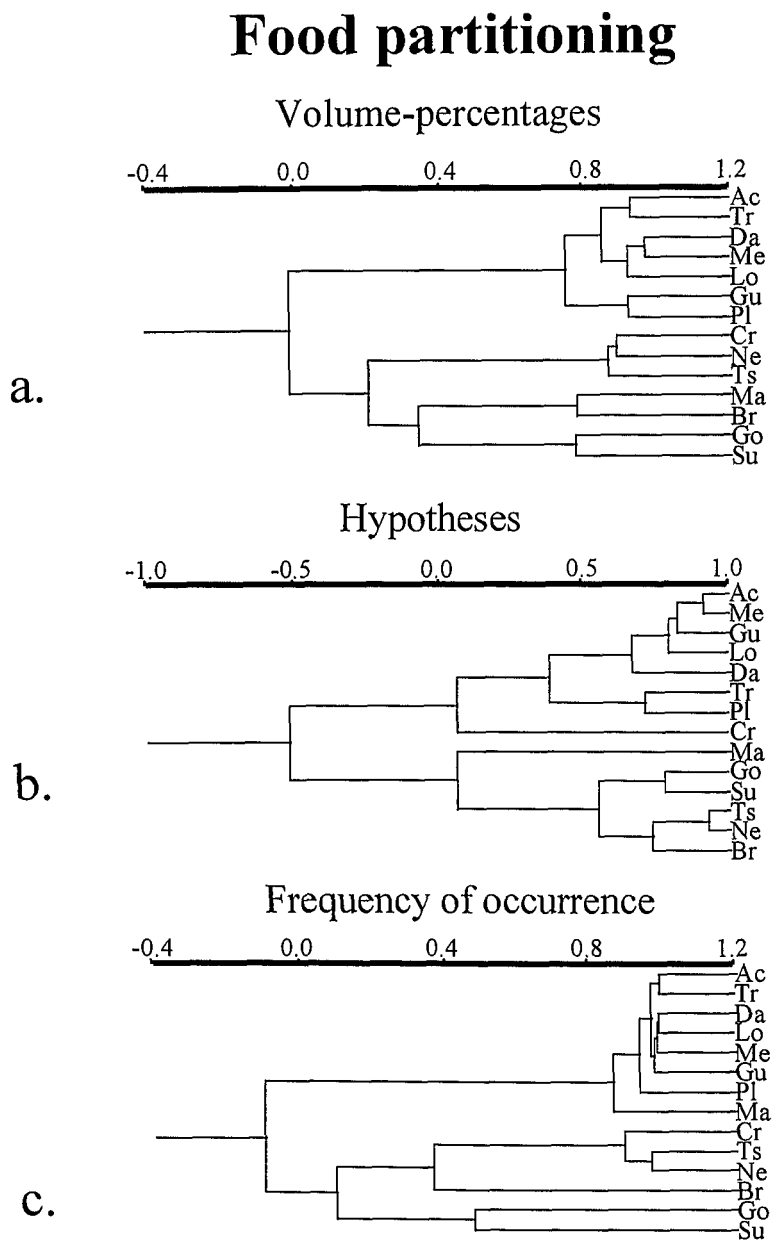


Fig. 7.5. Predicted v. actual food partitioning. UPGMA-clusterings of the 14 *Barbus* species are based on (a) the gap-codes of the volume-percentages of the food types (top, cophenetic value: 0.82, indicating a good representation of the original data), (b) the diet hypotheses (cf. Fig. 6.11) (middle, cophenetic value: 0.89, indicating a good representation of the original data), and (c) the frequency of occurrence of the food types (bottom, cophenetic value: 0.95, indicating a very good representation of the original data). This figure gives an impression of the predicted and actual trophic hierarchy in Lake Tana. Abbreviations: Ac = *B.acutirostris*, Cr = *B.crassibarbis*, Ma = *B.macrophtalmus*, Da = *B.dainellii*, Go = *B.gorgorensis*, Gu = *B.gorguari*, Ts = *B.tsanensis*, Ne = *B.nedgia*, Lo =*B.longissimus*, Me = *B.megastoma*, Br = *B.brevicephalus*, Tr = *B.truttiformis*, Pl = *B.platydorsus*, Su = *B.surkis*.

larvae/worms, detritus/substratum, and micro-crustaceans (pump), 2) macro-crustaceans, in between the former group and the next and 3) fish. These are exactly the food types of which the partitioning among species could also be well predicted.

Predicted v. actual food partitioning

The nonmetric 1-dimensional scaling (Fig. 7.4) and UPGMA-clustering of the species (Fig. 7.5), (based on predicted and actual food partitioning) show a similar and much more consistent picture than the grouping of predicted and actual diet spectra. There are three species groups that are consistent with the hypotheses in both the volume-percentage and f.o.o. data, and which are very similar to the 'diet groups' we described in the section on gut contents data: 1) the duo *B. tsanensis* and *B. nedgia*: benthivores 2) the duo *B. gorgorensis* and *B. surkis*: mollusci-macrophytivores, and 3) a group consisting of *B. acutirostris*, *B. dainellii*, *B. gorguari*, *B. longissimus*, *B. megastoma*, *B. platydorsus*, and *B. truttiformis*: the piscivores. The predicted peripheral position of *B. platydorsus* in the group of piscivores is consistently found in the gut contents data (both in 1-dimensional scaling and clustering). The predicted intermediate position of *B. macrophtalmus* between the piscivores and non-piscivorous groups in the clusterings is consistently found, which is especially visible in the 1-dimensional scaling plots (approximately central in the plot). The group of *B. surkis*, *B. gorgorensis*, *B. brevicephalus*, *B. nedgia*, and *B. tsanensis* is much more compact in the hypotheses, than it is in the gut data, but their relative positions are rather similar (except *B. brevicephalus*, as can be seen in the clusterings). The most marked differences between predictions and gut contents data are *B. truttiformis*, which was predicted to be at the periphery of the piscivorous group, while it is central in this group in the gut data, and *B. crassibarbis*, which is close to the piscivores in the predictions, and very close to *B. tsanensis* and *B. nedgia* in the gut data.

DISCUSSION

Predictability of diet spectra and food partitioning

Predictability of the diet spectra

The diet spectra of most species can be predicted well or fairly well (Table 7.5), especially those of *B. brevicephalus*, *B. dainellii*, *B. longissimus*, *B. platydorsus*, and *B. tsanensis*. The diets of *B. crassibarbis*, *B. gorguari*, and *B. truttiformis* are harder to predict. The predictability of the overall occurrence of different food types in the diet spectra differs (Fig. 7.3). Especially food types that are overall rare (see Chapter 1), such as sessile algae, seeds, and macro-insects were predicted poorly. More or less omnipresent, relatively abundant food types, such as larvae/worms, detritus, molluscs, fish and micro-crustaceans were predicted more accurately. The strong influence that the relative rarity of some food types has on the predictability of diet spectra is in concordance with what is expected, when the complications of the method are taken into account (as discussed later).

Some species are rare (e.g. *B. gorgorensis*), and only few samples could be collected from them. Therefore their average volume-percentages and f.o.o. of the food types were based on few specimens, which could lead to artefacts, especially when the samples were not collected evenly over the seasons.

Predictability of food partitioning among Lake Tana Barbus *species*

The predictability of food partitioning over the *Barbus* species is generally fairly good, especially for the most abundant food types. The partitioning of the rare food types is poorly predicted (sessile algae, seeds, macro-insects). This is not according to our expectations, since the partitioning among species should be independent of the absolute abundance of a food type. However, if the abundance drops below a certain point, the encounter rate of a fish with that food type will be mainly based on chance, in which case our predictions cannot hold. Moreover, low volume-percentages always produce a larger relative error that can influence the result. Macro-insects are often difficult to distinguish from insect larvae in samples, which further complicates the matter. The low predictability of eating micro-crustaceans and phytoplankton by means of townet filter-feeding can be explained by the fact that this feeding mode does not occur in cyprinids (Sibbing 1991*a*). The reason why the partitioning of macrophytes is rather poor is unresolved, but could be connected with the uneven and patchy distribution over the lake environment.

Our results (predictions and gut contents) suggest that the trophic hierarchy in Lake Tana is based on three large groups, with a total of 5 subgroups (Fig. 7.5): 1) a group of piscivores, of which 1a) *B. acutirostris*, *B. dainellii*, *B. gorguari*, *B. longissimus*, *B. megastoma* and *B. truttiformis*, are rather strict and 1b) *B. platydorsus* is a less specialized piscivore; 2) *B. macrophtalmus*, which is intermediate between piscivores and non-piscivores; 3) non-piscivores with 3a) the benthivores: *B. nedgia* and *B. tsanensis* and 3b) the macrophyti-/molluscivorous *B. gorgorensis* and *B. surkis*.

B. crassibarbis's position is less consistent, since it is predicted to be intermediate between piscivores and non-piscivores, and feeds most similarly to the benthivores (Fig. 7.2). The non-piscivore *B. brevicephalus*'s position is not completely consistent: it was predicted to be close to the benthivore group in food partitioning, but it feeds to a large extent on micro-crustaceans. It's individual prediction for feeding on micro-crustaceans by pump filter-feeding (0.446, Table 7.1) was high, which is in accordance with its gut contents data.

The relevance of the method is shown, since the distinction of the three large trophic groups and their subgroups proves that it can attain high resolving power combined with high accuracy. There is evidence that the method is even more powerful than this. The hypotheses predict e.g. that *B. acutirostris* is a good pursuit hunter of fish (Table 7.1), and not a good ambush hunter, while *B. platydorsus* is predicted to be the opposite. It is also predicted that micro-crustaceans are most likely taken by pump filter-feeding by most species and not by townet filter-feeding. These (rather detailed) predictions of feeding modes call for additional tests of performance and behaviour in which the feeding of these species is directly observed. The method could also be extended to

include the prediction of distribution patterns (spatial and temporal) of the large Lake Tana barbs, once the appropriate fish parameters can be defined.

Complications of effective predictions

In general, food partitioning is better to predict than diet spectra. This is to be expected, since this ecomorphological method is based on the comparison among species. Even if the abundance of different food resources is uneven, this holds for each of the species. However, uneven availability of different food sources will inevitably decrease the predictability of diet spectra within separate species, since the relative amounts of food types that are taken by individual fish will, to a large extent (sometimes even exclusively) reflect the relative availability of the food types, and not so much its (in)abilities to utilize particular food types.

In testing our predictions, we assumed that all food types and species are homogeneously distributed so that all food types are equally available to all species. This is a reasonable assumption in most cases, but there are e.g. species that preferably live in open water, over muddy substrate without vegetation, that do hardly encounter sessile algae, snails and macrophytes. For more thorough tests, it is therefore necessary to have some data on the quantitative distribution of food types. Habitat use might also be predictable from morphology (Webb 1984) and could be included in a further analysis.

There are several factors complicating the effective prediction of diet spectra and food partitioning:

1) Methodological factors

a) Complexity of the method

There are many steps involved before the predictions of diet spectra and food partitioning are constructed, and even more before they are tested. This is difficult to avoid when many parameters are analysed simultaneously. In every step information may get lost or distorted. It is very important to have continuous feed-back with the original data throughout the process. On the other hand, using a cumulative set of many parameters, accounting for many different aspects of feeding is also the strength of the approach, as will be discussed in the section on which characters should be measured.

Throughout the whole analysis we have tried not to overestimate differences. This is one of the reasons to use gap-codes which only differ when statistically significant differences occur in the original data. This results in a conservative estimate of the differences between species and food types. However, our study shows that despite these complications the multivariate approach is more powerful than univariate approaches in predicting diet spectra and food partitioning.

b) The food-fish model (FFM)

It is essential for effective diet predictions that the mechanistic - not just the correlative - relationship between a structure and the performance of an organism is known (Chapter 6, Barel et al. 1989, Sibbing et al. 1994, Wainwright & Richard 1995). We have tried only to use parameters that have such an unambiguous relationship with performance, but we largely depended on the extrapolation of results from earlier studies. If some of these results are in fact not as universal as

we took them to be (e.g. due to phylogenetic constraints), inaccuracies might have affected the FFM.

The better we understand the whole process of foraging and processing of food, the more detailed our hypotheses will be, and the better our predictions. The mechanisms to deal with food types that pose high demands on predators (e.g. fine mesh-size of the branchial sieve, high pursuit speeds, strong pharyngeal crushing capacity) are often better understood than more subtle mechanisms, such as prey detection systems. Therefore the (in)ability to utilize these highly demanding types of food are easier to predict. Also, in a situation that there is competition for resources, especially these high-demand food types will initiate food partitioning among species. Therefore the high predictability of high-demand food types as compared to others might be intrinsic.

Moreover, the FFM is based on (mechanical) properties of the food, which are not always congruent with the taxonomic group of the food types (cf. Chapter 6, Barel et al. 1989). For example, beetles and seeds are both strong, stiff, encapsulated, and protein-rich foods, but taxonomically they are far apart. There is therefore a need to quantify food properties. The FFM will predict mechanical food types and modes of feeding (such as filtering or pursuit) better than taxonomic food type groups (Motta 1988).

2) Biological factors:

a) The uneven distribution of food types, as discussed above, which mainly affected the predictions of diet spectra, and not so much of food partitioning.

b) Food quality differences and competition for food resources

A situation of competition is necessary for the successful prediction of diet spectra and food partitioning. It is e.g. possible that a species is better equipped for the utilization of detritus than for zooplankton. However, it is possible that zooplankton (which is of much higher nutritional quality), gets so abundant, that it is more profitable for the species to use this food source, instead of detritus, for which it is specialized. This will decrease the predictability of both diet spectra and food partitioning. Behavioural adaptability allows for wider resource use than only the optimal as suggested by morphology. For example many species, including the herbivorous *B. surkis*, were found to feed on fish offal where it was abundant, i.e. where it was discarded into Lake Tana by fishermen.

3) Technical factors:Gut contents

It can be a problem to determine what the actual diets in the field are. Some food types are difficult to distinguish (e.g. insect larvae and macro-insects) and some are more easily digestible than others, causing them to be underestimated in presence. Ideally, only freshly ingested food in the stomach should be considered. However, cyprinids do not have a separate stomach, in which the most recently ingested food is present, so we somewhat arbitrarily had to collect the anterior part of the intestine. Certain food types are almost always only present as a minor volume-fraction (e.g. sessile algae, seeds), thereby making the relative errors of the volume-estimates consistently larger.

Moreover, it was necessary to include intestine samples from fish that were caught by gill-netting, and were therefore not completely fresh, to get a sufficient number of samples. Therefore, the representation of the diets will inevitably show some bias, for which we tried to compensate (within the given possibilities) by including both average volume-percentages and frequency of occurrence (f.o.o.) data in the analysis.

In conclusion, the predictability of food types in the diet works best when there is (1) a competitive situation, in which (2) food is overall scarce, and for (3) food types that are equally available to all species in the comparison, that are of (4) relatively high quality, and of which (5) the feeding mechanism is well understood (usually food types that pose high demands on the predators).

Lake Tana has low productivity, and food is relatively scarce (Admasu 1986, Rzóska 1976). The lake is also well mixed, and most of its area outside the littoral zone is rather homogeneous. Detritus/substratum, micro-crustaceans (pump), larvae/worms, molluscs, and fish can be found in most localities of the lake (although some food types may be patchy distributed), the mechanisms for their processing are fairly well understood, and the food is of high quality (except for detritus/substratum). Phytoplankton is also readily available, but this food type is of very low quality and demands rather extreme specializations to be utilized.

Which characters should be measured?

In our previous paper on this subject (Chapter 6), we showed that some of the measured fish parameters were intercorrelated, and also that not all measuring parameters contribute to the total variation in morphology of our species to the same extent. Therefore we performed a principal components analysis (PCA), resulting in (by definition) uncorrelated new parameters (the PCs). The result of the method, whether it was performed with the original parameters or with the PCs, was very similar. We also noticed that the method is rather robust, i.e. when we repeated the analysis after addition or deletion of some measuring parameters, the overall picture of the hypotheses remained almost identical.

Because of the intercorrelation of measuring parameters and the insensitivity of the method to the deletion of one or several measuring parameters, we concluded that in the particular case of the Lake Tana barbs there is a redundancy of measurements. This is of more than theoretical importance, as taking measurements is a time-consuming activity. Moreover, if the more difficult (or more inaccurate) measurements could be replaced with easier or more precise measurements, the method could gain power. The refinement of the method is currently investigated by our research group, and there are two approaches we would like to mention.

A first way to approach the, possible, redundancy problem is by regarding the fish as a complex of functional units for different tasks, such as detection, pursuit, or chewing. We are currently investigating whether it is possible to find one, or a few key characters for each of these functional

units to define its (in)ability to deal with a range of food types. The result could be a compact group of key characters which sufficiently predicts diet in natural circumstances.

An additional approach is that of the 'overruling characters', which does not consider all characters to be equally important for food utilization, but takes into account that there is a hierarchy in importance, with some characters 'overruling' others. If e.g. a fish has heavy pharyngeals with long symphyses, excellently suited for stabilising the large forces that are needed to crush large molluscs, but it has a narrow oral gape, the fish will never be able to eat these large molluscs. Mouth size has priority over pharyngeal parameters in this case (and even excludes the use of large molluscs). In the analysis relative importance could be included by weighting of characters.

The idea that measuring many, often intercorrelated, characters leads to redundancy in the data set, might be misleading. All structures in an organism are influenced by the presence of other structures (constructional constraints: Barel 1983, 1993). Therefore, all characters carry an amount of 'noise' which cannot be directly interpreted functionally. When only a single or a few characters are taken into account, this noise may obscure the (functional) differences we are interested in. When we consider many parameters (such as in this study), individual characters will still carry noise, but the cumulative set of characters will still allow for a functional interpretation, since the noise is expected to be random. Only in the highly unlikely case that all noise will be directed in the same direction functional differences might still be obscured completely. Therefore, the fact that many characters are taken into account (even if they are correlated) is itself a prerequisite for the success of the method.

Moreover, a character may only account for little of the total variation, and be almost completely correlated with another character, but it is still possible that this character holds the key to the trophic distinction of two rather similar species. For example, eye size might account for only a small fraction of morphological differentiation among species, but it could give an indication of day/night activity patterns. Such different activity patterns can effectively create niche differences between species that are otherwise feeding on the same food type (such as zooplankton). We believe that even more characters are needed if one wishes to increase the resolving power of the method for detailed predictions over the whole range of trophic groups. If the goal is to make approximate trophic groups (piscivores, non-piscivores, e.g. for fisheries purposes), it will suffice to measure less characters than when a more intricate question is asked.

Specialists versus generalists

Initially, we have characterized food specialists and generalists on the basis of the summed f.o.o. percentages. We found that most specialists (summed f.o.o. percentages < 150) are piscivores (*B. dainellii*, *B. longissimus*, *B. truttiformis*, and *B. acutirostris*), except for *B. surkis*, which is predominantly herbivorous. *B. brevicephalus*, *B. crassibarbis*, *B. nedgia*, and *B. tsanensis* are generalists (summed f.o.o. percentages > 200). The former feeds mostly on macro-insects and micro-crustaceans, the other three are typical benthivores, mainly feeding on larvae/worms and

detritus/substratum, sometimes with large proportions of molluscs. However, when looking at the food partitioning predictions (Table 7.1, Figs 7.4 and 7.5, cf. Chapter 6), *B. nedgia* and *B. tsanensis* appear to be rather specialized with marked abilities for detritus/substratum and larvae/worm combined with inabilities for piscivory. The reason for this is that larvae/worms and detritus/substratum are food types that have relatively similar properties, which require similar feeding modes (Table 7.1: predictions are 0.467 and 0.618 respectively for *B. nedgia*, and 0.393 and 0.527 for *B. tsanensis*, all values significant; see also Fig. 6.11*a*).

This brings us to the definition of specialism and generalism. In the context of this study, the terms food specialist and food generalist should not be defined on the basis of the number of taxonomic groups that are found in the diets of the species, but on the number of feeding modes (Barel et al. 1989, Motta 1988). The groups of the piscivores and benthivores are in fact both rather specialized in their specific feeding modes. The real generalists among the Lake Tana barbs are the ones that combine conflicting feeding modes, such as piscivory and zooplanktivory (*B. macrophtalmus*), piscivory and herbivory (*B. gorguari*), or piscivory, herbivory and the eating of insect larvae (*B. platydorsus*). Generally, feeding mode specialism and generalism is well predicted by morphology, as is apparent from the intermediate positions of *B. macrophtalmus* and *B. platydorsus* in the food partitioning predictions (Figs 7.4 and 7.5).

It is remarkable that the differentiation of different parts of the feeding constructions in the Lake Tana barbs does not seem to have developed at the same evolutionary speed. In short, the foraging characters are much more differentiated than the food processing characters. Spatially this means that most extreme specializations are found anteriorly in the head, while the posterior part, e.g. the pharyngeal jaws, are much less differentiated. An indication for this are the gap-codes that were assigned to the measured parameters, after their differences were tested for significance (Table 7.5 in Chapter 6): the more gap-code levels, the more the parameters are differentiated. Foraging parameters have maximum gap-codes of 6,7 or 8 (e.g. Gape area/Body area, anterior barbel length/fork length, eye diameter/fork length), while pharyngeal jaw parameters usually have maximum values of 3 or 4 (robustness: pharyngeal mass/pharyngeal length^3, pharyngeal symphysis length).

If adaptive differentiation is initiated by preferential behaviour for particular food types, we would expect that structures that form the first interface with the prey (such as detection or capture structures) are initially under stronger selective forces than the structures that are only of importance later in the process of feeding (such as mastication structures). It can also be expected that in the cause of evolutionary time, the differentiation in the latter structures would 'catch up'. The fact that this did not happen (yet) in the Lake Tana barbs, suggests the recent origin of the species flock.

Extrapolation of the method and the predictability of ecology from morphology

Studies on the relationship between morphology and (especially) gut data have, until recently, mainly been correlative (Gatz 1979, Findley & Black 1983, Felley 1984, Winnemiller 1991), with

varying results. In this study we predicted diet spectra and food partitioning, explicitly based on the results of previous studies on the functional morphology and biomechanics of fish feeding. Subsequently we tested these predictions. We have tried to provide a sound methodology for constructing diet predictions as well as for the test of these predictions. The results from this study are encouraging for a more general applicability of the method.

Initially we focussed on predictions in a comparative way among the 14 Lake Tana *Barbus* species, and did not extrapolate our findings to other fish groups, bearing in mind that phylogenetic history of a group can obscure trophic adaptations (Westneat 1995). However, we are now convinced that the demands that some food types pose on the structures of fish are so strong, that similar (convergent) solutions must be found in different phylogenetic groups (Wainwright & Richard 1995). Jaw mechanics for optimal suction (Muller 1987) is such a biomechanical optimization found in various, diverse fish groups.

Importance of the ecomorphological method for the understanding of the ecosystem

The relationships among different fish species in an aquatic ecosystem can be deduced from an extensive sampling program over several years, accounting for diurnal, seasonal and spatial variation. Such a study will analyse the situation as it is, but has no predictive value, once environmental circumstances change (Sibbing et al. 1994). The ecomorphological method considers structural solutions organisms have, to deal with various features of food. It provides a tool not only to reconstruct trophic interactions, from the present situation, but can, ideally, also predict the changes in these interactions due to changes in the environment (either naturally or human-induced). It would e.g. be useful to predict the impact of selective fishing on certain fish stocks. It is imaginable that trophic shifts can result from the strong numeric reduction of certain species due to selective (over)fishing of the stock. Other species may fill the gap and start using the resource which was previously used by the species that is overfished. A realistic example is the overfishing of the large piscivores. Of all Lake Tana barbs they become largest and are preferred by the fishermen. If *B. dainellii*, *B. gorguari*, *B. megastoma*, *B. acutirostris*, and *B. longissimus* were strongly overfished, we would predict that *B. platydorsus* and *B. macrophtalmus* would start to eat more small fish, as they would now be the lake's best piscivores. This would also create space for other species to feed on the food which *B. platydorsus* and *B. macrophtalmus* used more commonly before the overfishing, resulting in cascading effects through the trophic community structure. Experiments in ponds or enclosures are needed to further test this idea.

Food web reconstruction

The trophic interactions that were studied in this paper enabled us to reconstruct a food web of Lake Tana (Fig. 7.7). Note that different *Barbus* species play different ecological roles, from primary consumers (such as the herbivorous *B. surkis*) to tertiary consumers (such as the mainly piscivorous *B. megastoma*). One of the surprising phenomena in Lake Tana is the large number of piscivorous species (8). Cyprinids are not well equipped for piscivory, because they lack oral teeth

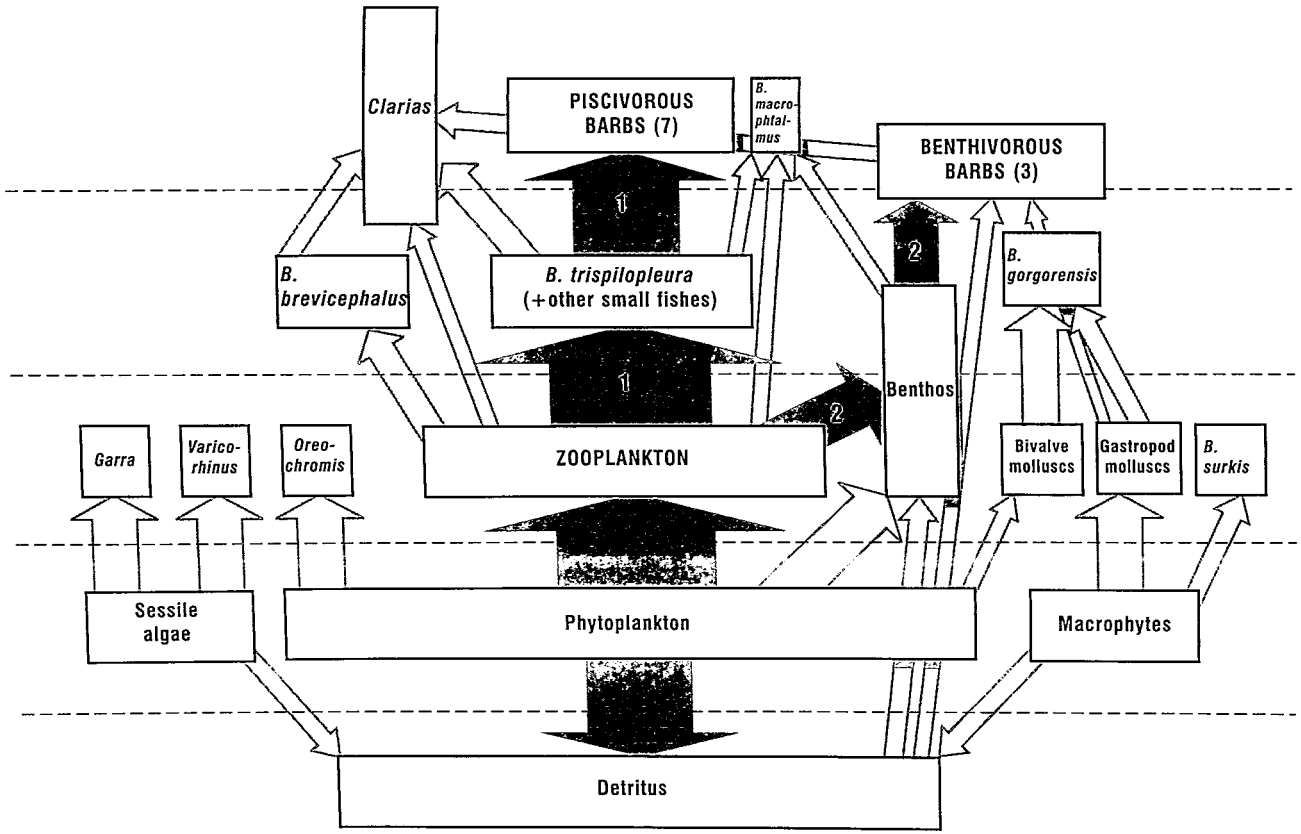


Fig. 7.6. Food web reconstruction of Lake Tana showing the 'zooplankton bottleneck'. The arrows indicating energy flow are not to scale between levels, although they are qualitatively scaled within levels. Note that the most important energy flow towards *Barbus* biomass production is directed from phytoplankton, via zooplankton, and then especially via *B. trispilopleura* (1), and to a lesser extent via benthos (2) (see text).

and a distinct stomach. We believe that one of the reasons for this multitude of piscivores lies in what we will call the 'zooplankton bottleneck'.

Lake Tana has a very low productivity (Wudneh 1997), and most of its primary production is phytoplankton. If a fish is to eat phytoplankton successfully, it will have to have an elaborate branchial sieve and a long intestine. *Oreochromis niloticus* is a specialized phytoplankton eater (Getachew & Fernando 1989), and fills this niche in the Lake Tana ecosystem. It is reasonable to assume that the ancestral barbs of Lake Tana were benthivorous like the present day, riverine barbs of Ethiopia, without the rather extreme specializations for eating minute particles. It was therefore not only difficult to utilize this food resource, but since it is also of low quality there will not have been a strong evolutionary drive to start using it, if alternatives were available (especially because there was already a specialist for this food type present).

The difficulty of eating small particles holds to a lesser extent for zooplankton, the main consumers of the phytoplankton. However, the quality of zooplankters is high, and all barbs eat zooplankton when they are small. When they become larger than 15 cm fork length it becomes increasingly difficult for them to retain zooplankters. The impossibility for cyprinids to retain enough energy from zooplankton when they grow larger has been described for Dutch cyprinids (Van den Berg et al. 1994), and will be even stronger in a tropical system as Lake Tana, where average zooplankton sizes are smaller than in temperate regions. The only barb species eating considerable amounts of zooplankton when adult are *B. brevicephalus* and *B. macrophtalmus*, of which especially the former stays small (maximum of 25 cm FL). In short, zooplankton is only an interesting food source for the 'large' Lake Tana barbs when the barbs are relatively small.

Probably the most effective zooplanktivorous fish in Lake Tana is the small *Barbus (Enteromius) trispilopleura*. This abundant fish reaches a maximum size of c. 8 cm FL and feeds almost exclusively on zooplankton. *B. trispilopleura* is itself almost the sole food source of the piscivorous 'large' barbs. As this species is more or less omnipresent in the lake, in all habitats, it can be imagined that the ancestral Lake Tana barbs switched to this prey item in a lake where utilizable food is scarce. They may not have been optimally equipped for catching fish, but the high profitability of eating it compensated for this, especially since there probably was no competition from specialized piscivores. Other effective zooplanktivores are certain benthic invertebrates (such as chaoborids). These organisms are an important food source for most of the non-piscivorous *Barbus* species.

The above considerations produce a picture of the Lake Tana ecosystem in which the zooplankton is the main gateway for energy to be transported from the primary producers to large barbs (Fig. 7.6), especially via *Barbus trispilopleura*, and to a somewhat lesser extent via benthic organisms: the 'zooplankton bottleneck'. *Barbus* species that feed largely independent of the zooplankton are *B. surkis* (primarily herbivorous), and *B. gorgorensis* (mainly feeding on molluscs, that in their turn eat primary producers, such as macrophytes and phytoplankton). Epilithic grazers of diatoms (*Varicorhinus beso* and *Garra* spp.) fill up a very specific niche in Lake Tana, as does the tilapia *Oreochromis niloticus* (phytoplankton). Finally, *Clarias gariepinus* is an opportunistic

eater of pelagic zooplankton and insect-larvae like *Chaoborus* (Wudneh 1997). It is also the only species that can eat larger fish (> 20 cm FL) than any of the piscivorous *Barbus* species.

An evolutionary scenario

In previous papers we have hypothesized that the ancestral Lake Tana barb species probably was very similar to the contemporary variable riverine *B. intermedius*, and that it radiated into the new niches of the newly-formed Lake Tana (Nagelkerke et al. 1994, 1995*a*, Nagelkerke & Sibbing 1996). We believe that the main driving force of the speciation has been trophic specialization and disruptive selection on feeding related characters. Especially in the open water, the major high quality food types that could be utilized were benthos and small fish ('the zooplankton bottleneck', see above). Since most barbs (and therefore probably also the ancestral barb species) are benthivores, no special adaptations were necessary for utilizing benthos as food source. Piscivory however, puts high demands on the capture and intake functions. Some individuals of the variable barb stock probably were better equipped for eating fish than others, which could lead to preferential feeding on fish (remember that probably no specialized piscivore was present in the lake) and gradually to structural adaptations for piscivory. Since the capture and intake structures of a predator form the first interface with the prey it can be expected that they initially were under stronger selective forces than other structures. The fact that we find the most extreme differentiation among the Lake Tana barbs in the capture and intake structures points in that direction, and also indicates that the Lake Tana barbs evolved relatively recently, since the differentiation of other structures did not 'catch up'. The evolutionary division between piscivores and non-piscivores seems to be basic to the Lake Tana *Barbus* flock and we expect it to be reflected in their phylogenetic relations.

Biodiversity, stability and production of the ecosystem

By using ecomorphological methods to predict the trophic interactions of different species (and the shifts in these interactions resulting from environmental changes), insights into the mechanisms and efficiency with which energy is transferred through the ecosystem along the trophic interactions will be gained. The stability, resilience, and productivity of these interactions will also be better understood. This is especially interesting in relation to the biodiversity of the system: what happens to the system when some species become extremely rare, or even become extinct?

Work on terrestrial ecosystems has shown that productivity and stability are greater when biodiversity is high (Naeem et al. 1994, Tilman & Downing 1994, Tilman et al. 1996), although for aquatic ecosystems such correlations have not been found unambiguously (Lévêque 1995). We have argued that when a species disappears from the ecosystem another species will probably, within its possibilities, take its ecological place. However, this still means that there is a difference with the ecological situation before the disappearance: total production and/or the quality of the production can be (strongly) affected. Notwithstanding the controversies over the role of biodiversity in the production of ecosystems, it seems safest to assume that productivity and

stability (and therefore sustainability) of fish production in Lake Tana will profit from a balanced exploitation of the fish species, keeping its biodiversity as intact as possible.

ACKNOWLEDGEMENTS

We thank the Ministry of Agriculture in Addis Ababa for its cooperation, as well as the Amhara National Regional State Bureau of Agriculture in Bahar Dar for cooperation in the local implementation of our work. We also acknowledge all the people that helped collecting in the field, Geert van Snik, Michiel Helmes, Hans van Oostenbrugge, Sander Kranenbarg, Arnold van den Burg, and Suzanne van Gaans. Furthermore, we thank Albert Otten for his help with the statistics. Jan Osse is acknowledged for valuable remarks, substantially improving this manuscript. This study was financed by the Netherlands Organization for the Advancement of Tropical Research (NWO/WOTRO), project W88-176, the Interchurch Foundation Ethiopia/Eritrea (ISE, Urk, The Netherlands), and the Interchurch Coordination Commission for Development Projects (ICCO, Zeist, The Netherlands).

Chapter 8

In Lake Tana, a unique fish fauna needs protection.

Leo A.J. Nagelkerke[1], Mikhail V. Mina[2], Tesfaye Wudneh[3],
Ferdinand A. Sibbing[1] & Jan W.M. Osse[1]

[1]*Department of Experimental Animal Morphology and Cell Biology, Agricultural University, Marijkeweg 40, 6709 PG Wageningen, The Netherlands*
[2]*Koltzov Institute of Developmental Biology, Russian Academy of Sciences, Vavilov Street 26, 117334 Moscow, Russia.*
[3] *Department of Fish Culture and Fisheries, Agricultural University,, Marijkeweg 40, 6709 PG, Wageningen, The Netherlands.*

Published in: *BioScience 45* (1995) **45**: 772-775.

ABSTRACT

In Lake Tana, Ethiopia, a unique group of large *Barbus* spp. (Cyprinidae, Teleostei) possibly constitutes the only known, intact, cyprinid species flock in the world. These fishes show a large morphological and ecological diversity. Fishing pressure is increasing, especially near the spawning grounds, where the largest catches are made during the reproductive season. This might pose a serious threat to the survival of the fish fauna.

INTRODUCTION

Discussions on the conservation of biodiversity usually focus on terrestrial habitats, especially on rain forest ecosystems (Myers 1979, Simberloff 1984, Wilson 1989). Because of this bias, the value of aquatic communities, less accessible for direct observations, is often not fully appreciated. The purpose of this article is to draw attention to a unique freshwater system - Lake Tana - and especially to its fishes. Thus we want to urge the international scientific community to increase knowledge on the origin and state of the current biodiversity, mobilize people in advocating the high value of such freshwater ecosystems, and promote sustainable fisheries with protection of the diverse natural resources.

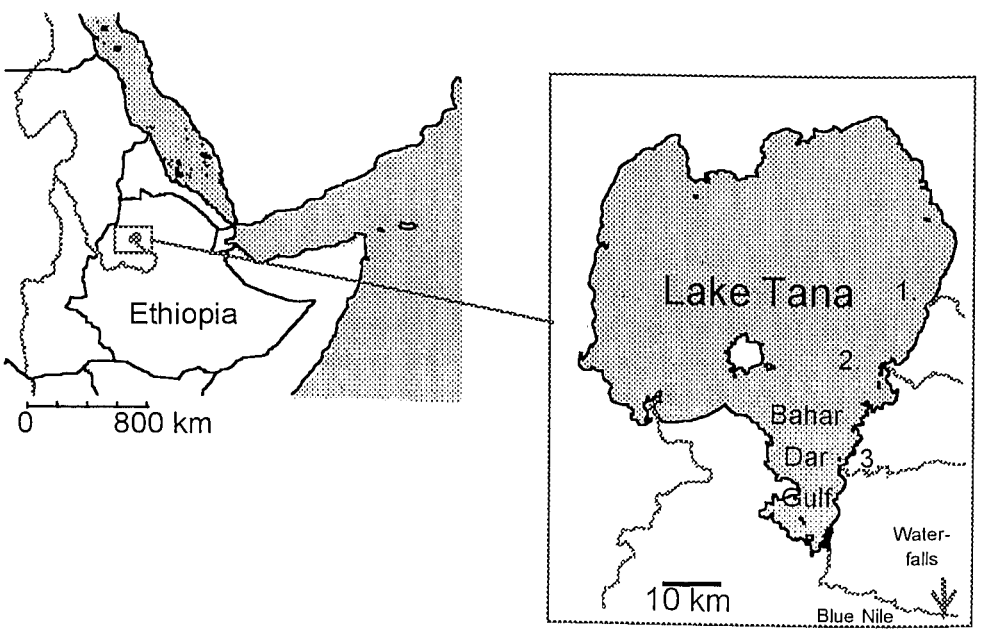


Fig. 8.1. Map of the Horn of Africa, indicating Lake Tana. The large river mouths along the east coast are: (1) Rib River, (2) Gumara River and (3) Gelda River. The southern Bahar Gulf is the research area, although fishermen range further north and west.

LACUSTRINE FISH COMMUNITIES

Lacustrine fish communities, exemplified by the cichlids in the African Lakes Victoria, Tanganyika and Malawi and by cyprinids in the Philippines Lake Lanao, are known to be exceptionally vulnerable to the deleterious influences of human activities (Bruton 1990, Kornfield & Echelle 1984). There are many examples of destruction of such communities through overfishing (Coulter et al. 1986), pollution (Coulter et al. 1986, Kornfield & Echelle 1984) and introduction of non-native species (Craig 1992, Witte et al. 1992) of which the Lake Victoria disaster is the most infamous. Introduction of the Nile perch in Lake Victoria dramatically changed the ecosystem at the cost of many haplochromine species (Barel et al. 1985, Bruton 1990, Witte et al. 1992). Some of these lakes contain or contained species flocks - monophyletic groups of species endemic to a geographically circumscribed area (Greenwood 1984). Such lakes are interesting because they form natural laboratories for studying evolutionary processes (Coulter et al. 1986).

Some lacustrine species flocks, such as the one in Lake Lanao in the Philippines (Kornfield & Carpenter 1984), were exterminated even before their evolution was studied. A potential species flock of barbs (*Barbus* spp., Cyprinidae) has been rediscovered in Lake Tana. Early records (Bini 1940, Boulenger 1902, 1907, 1911, Brunelli 1940, Rüppel, 1836) had pointed to the existence of this complex of species.

Lake Tana is Ethiopia's largest lake (3150 - 3500 km^2) and is situated in the northwestern highlands at an altitude of ca. 1800 m (Fig. 8.1; Nagelkerke et al. 1994). The lake was formed by volcanic blocking of the Blue Nile, probably in early Pleistocene times (Mohr 1962). It is shallow (maximal depth 14 m, mean 8 m) and oligo-mesotrophic (Rzóska 1976). Several small rivers (maximal length of 60 km) enter the lake, the Blue Nile being its only outflow. After 30 km this river plunges down 40-meter-high waterfalls, isolating Lake Tana and its tributaries from other parts of the Nile basin.

The large barbs of Lake Tana are noteworthy because of the variety of morphologically distinct forms (morphotypes) they exhibit. The other fish species found in Lake Tana are widespread in the lakes and rivers of the Ethiopian highlands: representatives of the genera *Oreochromis* (Cichlidae), *Clarias* (Clariidae) and *Nemacheilus* (Balitoridae) and of the cyprinid genera *Garra* and *Varicorhinus*, as well as at least two species of small barbs.

Some of the Lake Tana large *Barbus*, which are hexaploids in contrast to the small, diploid African *Barbus*, reach a body length of 85 cm and a weight of 12 kg. Six species of this group were described from the lake by Rüppell (1836). Boulenger (1907, 1911) added five new species, and Bini (1940) distinguished a total of 10 species and 23 subspecies. Brunelli (1940) suggested that some of the species might be morphs of one polymorphic species. Banister (1973) revised the East African large *Barbus* classification and lumped 50 nominal species and subspecies into one species: *B. intermedius* Rüppell, 1836, including all large *Barbus* from Lake Tana.

Recently Mina et al. (1993) suggested that morphological diversification in the Lake Tana barbs continues after the fishes attain sexual maturity. Old individuals identified as belonging to different morphotypes might be morphologically similar during early years of their life.

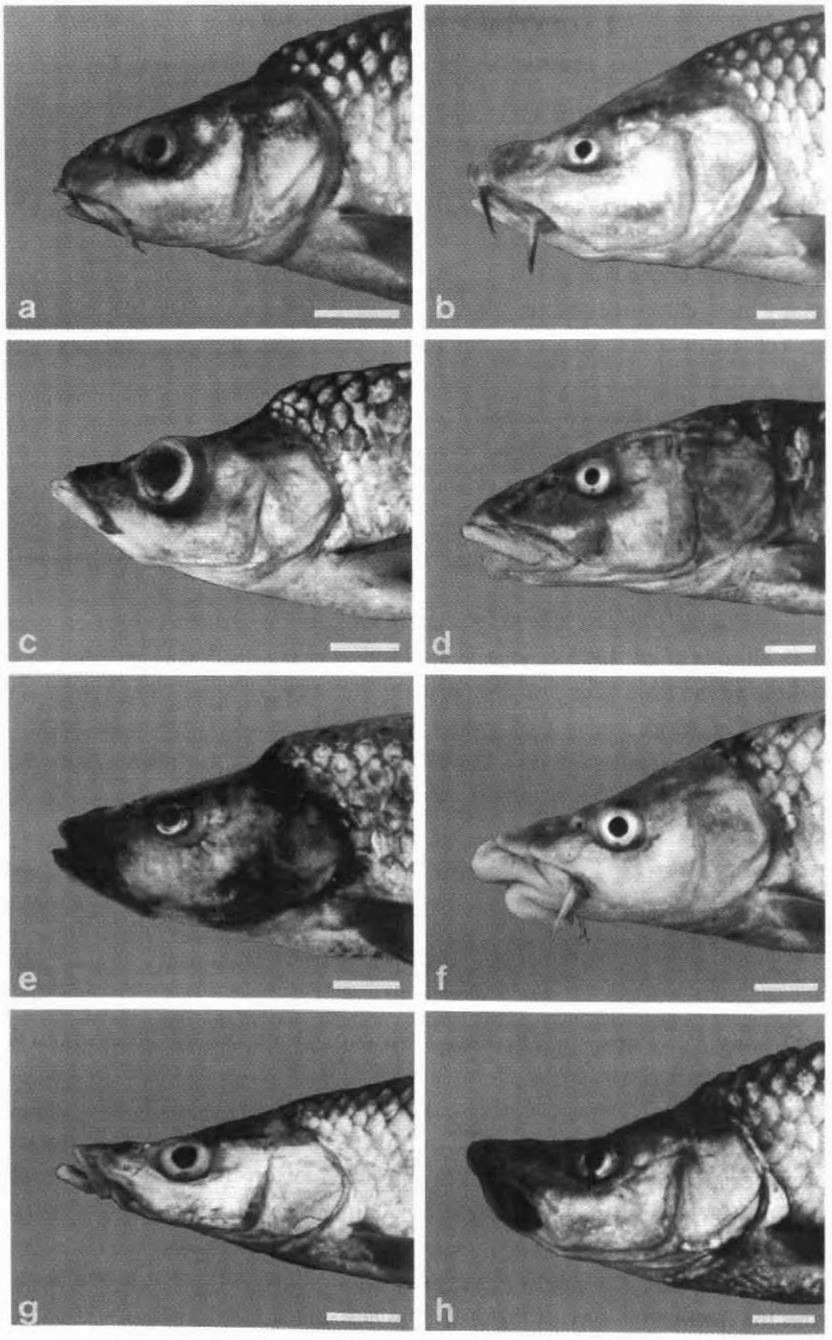


Fig. 8.2. Heads of 8 of the 13 *Barbus* morphotypes from Lake Tana. No scientific names have been yet given to the morphotypes (Nagelkerke et al. 1994). Their common names are **(a)** intermedius, **(b)** barbel, **(c)** bigmouth big-eye, **(d)** bighead, **(e)** dark, **(f)** lip, **(g)** acute, **(h)** bigmouth small-eye. Bars are 2 cm.

Whatever the exact taxonomic status of the Lake Tana barbs, recent morphometric results from a team of the Agricultural University of Wageningen in the Netherlands showed that 13 distinct morphotypes are present (Nagelkerke et al. 1994), some of them differing in appearance no less than do different species or even genera of, for example, European cyprinids (Fig. 8.2). Ecological differences (food types and distribution patterns) between the morphotypes are also substantial. Moreover, in September 1994, Nagelkerke and his colleagues observed that different morphotypes are spatially and/or temporally segregated during spawning.

This evidence supports the hypothesis that the Lake Tana barbs constitute an endemic species flock, making it the only cyprinid species flock known that has not been irreversibly damaged by human influences. The phylogenetic relations between the species are still unclear. The first step to determining their taxonomic status is to assess whether they are in fact reproductively isolated and to document their genetic differences. We initiated analyses of allozymes and the major histocompatibility complex (MHC) loci of the nuclear genome in cooperation with other research groups. An investigation of mitochondrial DNA is planned.

Studies of the large barbs in Lake Tana may contribute considerably to our understanding of evolutionary mechanisms. The fact that the barb species are endemic to the lake strongly suggests that intralacustrine speciation is occurring (Coulter et al. 1986).

HUMAN INFLUENCES

Lake Tana is one of the few African lakes which have not yet been damaged by human activities. There are no introduced fish species or major sources of pollution. Since 1986, commercial fisheries are developing in the southern part of the lake, where the large barbs constitute approximately 35% of the total commercial catch. The demand for *Barbus* and *Oreochromis* is higher than for the catfish *Clarias*, especially during the many fasting days of the Ethiopian Orthodox Church.

The central and regional Ethiopian administration seeks to develop fisheries for sustainable production. The Ministry of Agriculture has initiated fishery management studies on Lake Tana. It is important to know which fish stocks are present and to characterize the fishery pressure on these separate stocks before management programs can be designed.

In the past three years, the fishing grounds in the southern part of the lake have extended from an area close to the main landing site near Bahar Dar town to the mouths of the rivers 35-50 km to the north along the east coast. There are no signs of overfishing yet, but fishermen take their largest catches at or near the spawning grounds at the mouths of the large rivers (Fig. 8.3). Here most ripe barbs (i.e., sexually mature fish with highly developed gonads) from the lake aggregate during the spawning season. During September 1994, at two of the river mouths (Gumara and Rib Rivers) more than 90% of all the barbs collected were ripe and about to spawn, and more than 60% were ripe at a third river mouth (Gelda River; Fig. 8.4).

Fishes on spawning migrations are especially vulnerable to overfishing (Craig 1992), because their exploitation can, in extreme cases, lead to a dramatic decrease in the number of recruits

(Gabriel et al. 1989). Moreover, at present there is no limitation on the number of gill nets used, although the most commonly used mesh size (100 mm) ensures that the smallest fishes caught are sexually mature.

In view of the importance of the Lake Tana fishery for the local population, the tendency to raise fishing pressure is understandable. Yet, this increase might, after a temporary rise in the yield, result in a decreasing production. Furthermore, if fishing continues to be intense at the time of spawning, the barb populations are expected to decrease rapidly.

NEED FOR A STRATEGY

A fishery strategy providing both optimal sustainable yield and preservation of the unique natural diversity of the Lake Tana barbs is urgently needed. Such a strategy can be elaborated only after the necessary data on fish and fishery biology are obtained. The collection of such a dataset has been started by the Ethiopian Ministry of Agriculture, by the Agricultural University of Wageningen and by the Freshwater Biology group of the Joint Ethio-Russian Biological Expedition. Data on the reproductive and genetic status and distribution dynamics of the different *Barbus* stocks are incomplete and limited to the southern Bahar Dar Gulf.

Joint efforts of Ethiopian administrative and scientific institutions and specialists from different

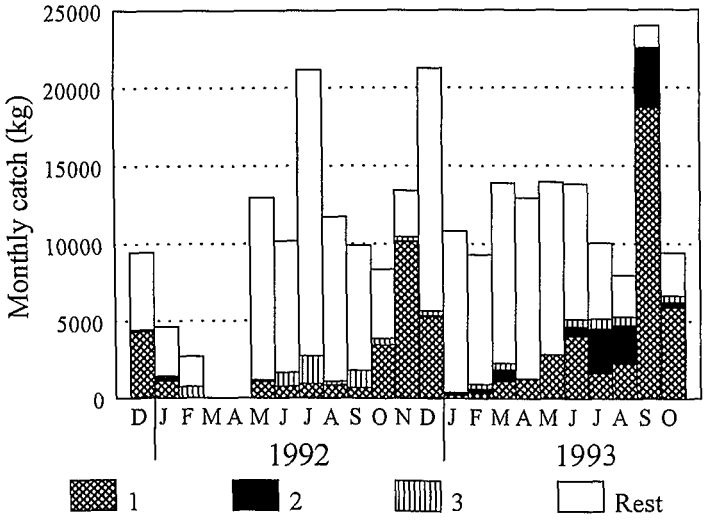


Fig. 8.3. Total monthly catches from the motorized fishing boats during the period December 1991 until October 1993 (because of the civil war there was no catch recorded in March and April of 1992). The areas 1, 2 and 3 are large river mouths (shown on Fig. 8.1) and presumed spawning areas of *Barbus* along the east-coast of the lake. At the end of the rainy season (September-November) fishes aggregate at the mouths for the spawning period. Especially in September 1993, a larger catch of *Barbus* was taken from the river mouths.

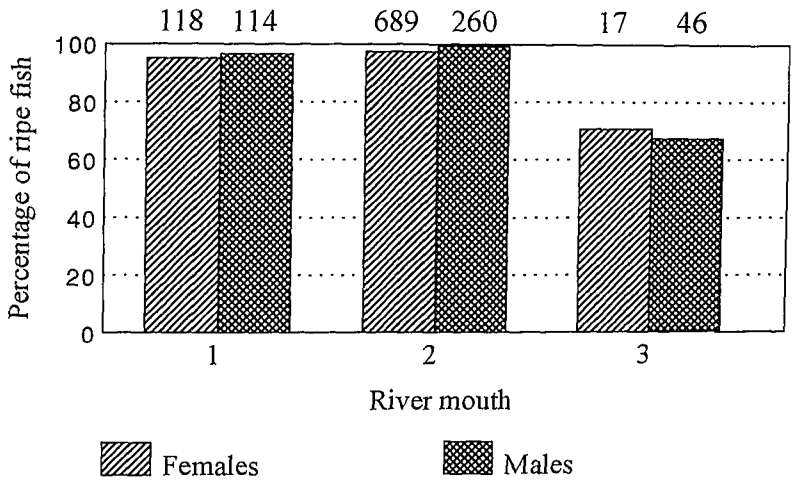


Fig. 8.4. Percentage of ripe female and male barbs in the catch of three river mouths (see Fig. 8.1) during September 1994. The total numbers of examined barbs is indicated at the base of the bars.

countries would greatly enhance our knowledge and consequently the possibilities of developing a strategy balancing sustainable fish production and conservation of biodiversity. Such a strategy might include a law limiting the mesh sizes and the number of fishing boats or nets, or closing specific areas or seasons (Coulter et al. 1986, Craig 1992, Ribbink 1987).

Permanent monitoring of size and species-composition of the catch is important to signal overfishing. This work should be performed by trained local people (some already present), preferably in cooperation with national and international conservation and fishery institutions. The establishment of a permanent hydrobiological station would be desirable for monitoring water quality, in view of the rapidly increasing human population around the lake. Even more important, however, is that local fishermen and fishery experts realize their responsibility, because they are the only persons who can make management of sustainable fisheries work (Craig 1992).

CONCLUSIONS

The international scientific community urgently needs to be informed about the unique ecosystem of Lake Tana. Preventive measures must be initiated now, before an ecological crash occurs and we are left only to rescue the survivors. We should learn from the experience elsewhere, such as Lake Victoria.

ACKNOWLEDGEMENTS

We thank M. Machielse, F. Witte, C.D.N. Barel and W.L.T. van Densen for their stimulating discussions and valuable remarks on the manuscript. This study was financially supported by the Netherlands Organization for the Advancement of Tropical Research (NWO-WOTRO project W88-176, L.A.J. Nagelkerke) and by the Interchurch Foundation Ethiopia (ISE, Urk) and the Interchurch Coordination Commission of Developmental Projects (ICCO, Zeist: L.A.J. Nagelkerke and T. Wudneh), both from the Netherlands. The Ethiopian Ministry of Agriculture (Addis Ababa and Bahar Dar) supported the local field and laboratory work.

REFERENCES

Admasu, D. (1986). *Report on limnological studies on Lake Tana*, pp. 1-44. Addis Ababa, Ethiopia: Addis Ababa University, Department of Biology, internal report.

Albrecht, G.H. (1978). Some comments on the use of ratios. *Systematic Zoology* **27**: 67-71.

Archie, J.W. (1985). Methods for coding variable morphological features for numerical taxonomic analysis. *Systematic Zoology* **34**: 326-345.

Atema, J. (1971). Structures and functions of the sense of taste in catfish (*Ictalurus natalis*). *Brain, Behaviour and Evolution* **4**: 273-294.

Baker, B.H., P.A. Mohr & L.A.J. Williams (1972). Geology of the eastern riftsystem of Africa. *The Geological Society of America, special paper* **136**: 1-67.

Balon, E.K. (1988). Tao of life: universality of dichotomy in biology. 2. The epigenetic mechanisms. *Rivista di Biologia/ Biology Forum* **81**: 339-380.

Balon, E.K. (1992). How dams on the River Danube might have caused hybridization and influenced the appearance of a new cyprinid taxon. *Environmental Biology of Fishes* **33**: 167-180.

Banister, K.E. (1973). A revision of the large *Barbus* (Pisces, Cyprinidae) of East and Central Africa. Studies on African Cyprinidae, part 2. *Bulletin of the British Museum of natural History (Zoology)* **26**: 1-148.

Baras, E. & Cherry, B. (1990). Seasonal activities of female barbel *Barbus barbus* (L.) in the River Ourthe (Southern Belgium), as revealed by radio tracking. *Aquatic Living Resources* **3**: 283-294.

Barel, C.D.N. (1983). Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Netherlands Journal of Zoology* **33**: 357-424.

Barel, C.D.N. (1993). Concepts of an architectonic approach to transformation morphology. *Acta Biotheoretica* **41**: 345-381.

Barel, C.D.N., G.Ch. Anker, F. Witte, R.J.C. Hoogerhoud & T. Goldschmidt (1989). Constructional constraints and its ecomorphological implications. *Acta Morphologica Neerlando-Scandinavica* **27**: 83-109.

Barel, C.D.N., P. Dorit, P.H. Greenwood, G. Fryer, N. Hughes, P.B.N. Jackson, H. Kawanabe, R.H. Lowe-McConnell, M. Nagoshi, A.J.R. Ribbink, E. Trewavas, F. Witte, and K. Yamoaka (1985). Destruction of fisheries in Africa's lakes. *Nature* **315**: 19-20.

Barel, C.D.N., M.J.P. van Oijen, F. Witte & E.L.M. Witte-Maas (1977). An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. *Netherlands Journal of Zoology* **27**: 333-389.

Beadle, L.C. (1981) Lake Tsana. In: *The inland waters of tropical Africa: an introduction to tropical limnology* (L.C. Beadle), pp. 191-193. London: Longman.

Berg, C. van den, J.G.M. van den Boogaart, F.A. Sibbing & J.W.M. Osse (1994). Zooplankton feeding in common bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*): experiments, models and energy intake. *Netherlands Journal of Zoology* **44**: 15-42.

Berg, C. van den, F.A. Sibbing, J.W.M. Osse & W. Hoogenboezem (1992). Structure, development and function of the branchial sieve of bream (*Abramis brama*), white bream (*Blicca björkna*) and roach (*Rutilus rutilus*). *Environmental Biology of Fishes* **33**: 105-124.

Berrebi, P. (1995). Speciation of the genus *Barbus* in the north Mediterranean basin: recent advances from biochemical genetics. *Biological Conservation* **72**: 237-249.

Berrebi, P. & D.S. Valiushok. (Submitted) Genetic divergence among Lake Tana (Ethiopia) barb morphotypes. An allozymic study. *Biological journal of the Linnean Society.*

Bini, G. 1940. I pesci del Lago Tana (The fishes of Lake Tana). *Missione di Studio al Lago Tana richerge limnologiche. B. Chimica e Biologia, Reale Accademia d'Italia* **3**: 137-179.

Boulenger, G.A. (1902). Descriptions of new fishes from the collection made by Mr. E. Degen in Abyssinia. *The Annals and Magazine of Natural History, 7th Series* **10**: 421-437.

Boulenger, G.A. (1907). *Zoology of Egypt: the fishes of the Nile*, pp. 1-578. London: H.Rees.

Boulenger, G.A. (1911). *Freshwater fishes of Africa. Vol II*, pp. 1-512. London: British Museum (Natural History).

Brunelli, G. (1940). Le mutazioni del genere *Barbus* del Lago Tana. *Missione di Studio al Lago Tana richerge limnologiche. B. Chimica e Biologia, Reale Accademia d'Italia* **3**: 207-213.

Bruton, M.N. (1990). The conservation of the fishes of Lake Victoria, Africa: an ecological perspective. *Environmental Biology of Fishes* **27**: 161-175.

Buth, D.G., Dowling, T.E. & Gold, J.R. (1991). Molecular and cytological investigations. In *Cyprinid fishes: systematics, biology and exploitation* (Winfield, I.J. & Nelson, J.S. eds.) pp. 83-126. London: Chapman & Hall.

Cheesman, R.E. (1936) *Lake Tana and the Blue Nile*, pp. 1-400. London: Macmillan and Co.

Christensen, B. (1996). Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size-dependent predator-prey interactions. *Oikos* **76**: 368-380.

Chu, Y.T. (1935). Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. *Biological Bulletin of St. John's University Shanghai* **2**: 1-225.

Cooper, D.W. (1968). The significance level in multiple tests made simultaneously. *Heredity* **23**: 614-617.

Coulter, G.W., B.R. Allanson, M.N. Bruton, P.H. Greenwood, R.C. Hart, P.B.N. Jackson & A.J. Ribbink (1986). Unique qualities and special problems of the African Great Lakes. *Environmental Biology of Fishes* **17**: 161-183.

Craig, J.F. (1992). Human-induced changes in the composition of fish communities in the African Great Lakes. *Reviews in Fish Biology and Fisheries* **2**: 93-124.

Crawford, S.S. & E.K. Balon (1994). Alternative life histories of the genus *Lucania*: 3. An ecomorphological explanation of altricial (*L.parva*) and precocial (*L.goodei*) species. *Environmental Biology of Fishes* **41**: 369-402.

Cresko, W.A. & J.A. Baker (1996). Two morphotypes of lacustrine threespine stickleback, *Gasterosteus aculeatus*, in Benka Lake, Alaska. *Environmental Biology of Fishes* **45**: 343-350.

Crowder, L.W., J.A. Rice, T.J. Miller & E.A. Marchall (1992). Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. In: *Individual-based models and approaches in ecology: populations, communities and ecosystems* (D.L. DeAngelis & L.J. Gross, eds), pp. 237-255. London: Chapman & Hall.

DeAngelis, D.L. & L.J. Gross (1992). *Individual-based models and approaches in ecology: populations, communities and ecosystems* (D.L. De Angelis & L.J. Gross eds), pp. 1-525. London: Chapman & Hall.

Densen, W.L.T. van (1994). Predator enhancement in freshwater fish communities. In: *Rehabilitation of freshwater fisheries* (I.G. Cowx), pp. 102-119. Fishing News Books, Blackwell, Oxford.

De Silva, S.S., Schut, J. & Kortmulder, K. (1985). Reproductive biology of six *Barbus* species indigenous to Sri Lanka. *Environmental Biology of Fishes* **12**: 201-218.

Dgebuadze, Yu.Yu. (1995). The land/inland-water ecotones and fish population of Lake Valley (West Mongolia). *Hydrobiologia* **303**: 235-245.

Dgebuadze, Yu.Yu., A.S. Golubtsov, V.N. Mikheev & M.V. Mina (1994). Four fish species new to the Omo-Turkana basin, with comments on the distribution of *Nemacheilus abyssinicus* (Cypriniformes: Balitoridae) in Ethiopia. *Hydrobiologia* **286**: 125-128.

Dixon, B., Nagelkerke, L.A.J., Sibbing, F.A., Egberts, E. & Stet, R.J.M. (1994). Evolution of MHC class II beta chain polymorphism in the Barbus species flock of Lake Tana. *Developmental and Comparative Immunology* **18** (Sup.1): 49.

Dixon, B., L.A.J. Nagelkerke, F.A. Sibbing, E. Egberts & R.J.M. Stet (1996). Evolution of MHC class II β chain-encoding genes in the Lake Tana barbel species flock (*Barbus intermedius* complex). *Immunogenetics* **44**: 419-431.

Douglas, M.E. & W.J. Matthews (1992). Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* **65**: 231-244.

Douglas, M.E., W.L. Minckley & H.M. Tyus (1989). Qualitative characters, identification of Colorado River chubs (Cyprinidae: genus *Gila*) and the "Art of seeing well". *Copeia* **1989**: 653-662.

Dowling, T.E. & Moore, W.S. (1984). Level of reproductive isolation between two cyprinid fishes, *Notropis cornutus* and *N. chrysocephalus*. *Copeia* **1984**: 617-628.

Dumont, H.J. (1983). On the dragonflies of the Ethiopian plateau and Lake Tana. *Notulae odonatologiae* **2**: 10-11.

Dumont, H.J. (1986). The Nile River system. In: *The ecology of river systems* (B.R. Davies & K.F. Walker, eds), pp. 61-88. Dordrecht, The Netherlands: Dr. W. Junk publishers.

Ebenman, B. & L. Persson (1988). *Size-structures populations: ecology and evolution*, pp. 1-284. Heidelberg: Springer.

Elshoud, G.C.A. (1986). The opercular four-bar system in fishes. In: *Fish and Chips, computer models and functional morphology of fishes* (G.C.A. Elshoud), pp. 28-64. Leiden, The Netherlands: University of Leiden, Ph.D. thesis.

Evans, H.E. (1952). The correlation of brain pattern and feeding habits in four species of cyprinid fishes. *Journal of comparative Neurology* **97**: 133-142.

Felley, J.D. (1984). Multivariate identification of morphological-environmental relationships within the Cyprinidae (Pisces). *Copeia* **1984**: 442-455.

Fernald, R.D. (1988). Aquatic adaptations in fish eyes. In: *Sensory Biology of Aquatic Animals* (J. Atema, R.R. Fay, N.N. Popper & W.N. Tavolga eds), pp. 435-66. New York: Springer Verlag.

Findley, J.S. & H. Black (1983). Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* **64**: 625-630.

Finger, T.E. (1988). Sensorimotor mapping in oropharyngeal reflexes in goldfish, *Carassius auratus*. *Brain, Behaviour and Evolution* **31**: 17-24.

Fowler, H.W. (1976). A catalog of world fishes (25). *Quarterly Journal of the Taiwan Museum* **29**: 277-396.

Fryer, G. (1996). Endemism, speciation and adaptive radiation in great lakes. *Environmental Biology of Fishes* **45**: 109-131.

Gabriel, W.L., M.P. Sissenwine & W.J. Overholtz (1989). Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *North American Journal of Fisheries Management* **9**: 383-391.

Gasse, F. (1987). Éthiopie et Republique de Djibouti. In: *Zones humides et lacs peu profonds d'Afrique* (M.J. Burgis & J.J. Symoens, eds), pp. 248-261. Paris: Éditions l'ORSTOM 211.

Gatz, A.J, Jr. (1979*a*). Community organization in fishes as indicated by morphological features. *Ecology* **60**: 711-718.

Gatz, A.J. Jr. (1979*b*). Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* **21**: 91-124.

Getachew, T.& C.H. Fernando (1989). The food habits of an herbivorous fish (*Oreochromis niloticus* Linn.) in Lake Awasa, Ethiopia. *Hydrobiologia* **174**: 195-200.

Goldschmidt, T. & F. Witte (1990). Reproductive strategies of zooplanktivorous haplochromine cichlids (Pisces) from Lake Victoria before the Nile perch boom. *Oikos* **58**: 356-368.

Golubtsov, A.S.& Krysanov, E. Y. (1993). Karyological study of some cyprinid species from Ethiopia. The ploidy differences between large and small *Barbus* of Africa. *Journal of Fish Biology* **42**: 445-455.

GOPA-consultants (1996). Lake Tana. In: *Lake Fisheries Development project, phase II, working paper number twenty three, Lake management plans*, pp. 3-10. Addis Ababa, Ethiopia: Fisheries Resources Development Division (Ministry of Agriculture) & Commission of the European Communities (EDF VI).

Gordon, J.E. (1976). *The New Science of Strong Materials: or why you don't fall through the floor*, pp. 1-287. Harmondsworth, Middlesex, England: Pelican books.

Gosline, W.A. (1973). Considerations regarding the phylogeny of cypriniform fishes, with special reference to structures associated with feeding. *Copeia* **1973**: 761-776.

Goulding, M. (1985). Forest fishes of the Amazon. In: *Key Environments of Amazonia* (G.T. Prance & T.E. Lovejoy eds.), pp. 267-76. New York: Pergamon Press.

Greenwood, P.H. (1974). The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bulletin of the British Museum of natural History (Zoology)*, Suppl. 6: 1-134.

Greenwood, P.H. (1976). Fish fauna of the Nile. In: *The Nile, biology of an ancient river* (J. Rzóska, ed.), pp. 127-141. The Hague, The Netherlands: Dr. W. Junk Publishers.

Greenwood, P.H. (1984). What *is* a species flock?. In: *Evolution of Fish Species Flocks* (A.A. Echelle & I. Kornfield, eds), pp. 13-19. Orono: University of Maine at Orono Press.

Gromov, I.A. (1973). Morphological characteristics and local populations of the eastern carp (*Cyprinus carpio haematopterus* (Temm. et Schlegel). *Journal of Ichthyology* **13**: 335-347.

Grossman, G.D. (1986). Food resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology London* **1**: 317-355.

Guégan, J.-F., Rab, P., Machordom, A. & Doadrio, I. (1995). New evidence of hexaploidy in 'large' African *Barbus*, with some considerations on the origin of hexaploidy. *Journal of Fish Biology* **47**: 192-198.

Günther, A. (1868). *Catalogue of the fishes of the British Museum, vol. VII:* Physostomi, pp. 1-512. London: British Museum (Natural History).

Hambright, K.D. (1994). Morphological constraints in the piscivore-planktivore interaction: Implications for the trophic cascade hypothesis. *Limnology and Oceanography* **39**: 897-912.

Hambright, K.D., R.W. Drenner, S.R. McComas & N.G. Hairston Jr. (1992). Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. *Archives of Hydrobiology* **121**: 389-404.

Heckel, J.J. (1846). Die Fische Aegyptens. In: *Reisen in Europa, Asien und Africa, mit besonderer Rücksicht auf die naturwissenschaftliche Verhältnisse der betreffenden Länder unternommen in den Jahren 1835 bis 1841. Band 2: Reisen in Aegypten, Nubien und Ost-Sudan* (J. von Russegger, ed.), pp. 315-345. Stuttgart, Germany.

Herre, A.W.C.T. (1924). Distribution of the true fresh-water fishes in the Philippines. *Philippine Journal of Science* **24**: 249-306.

Hofer, R. (1988). Morphological adaptations of the digestive tract of tropical cyprinids and cichlids to diet. *Journal of Fish Biology* **33**: 399-408.

Hofer, R. (1991). Digestion. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 413-425. London: Chapman & Hall.

Holčik, J., P. Bănărescu & D. Evans (1989) .A general introduction to fishes. In: *The fresh water fishes of Europe. Vol.1, part 2: General introduction to fishes. Acipenseriformes* (J. Holčik, ed.), pp. 18-147. Wiesbaden, Germany: Aula Verlag.

Holling, C.S. (1966). The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**: 1-86.

Hoogenboezem, W., J.G.M. van den Boogaart, F.A. Sibbing, E.H.R.R. Lammens, A. Terlouw & J.W.M. Osse (1991). A new model of particle retention and branchial sieve adjustment in filter-feeding bream (*Abramis brama*, Cyprinidae). *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 7-18.

Howes, G.J. (1987). The phylogenetic position of the Yugoslavian cyprinid fish genus *Aulopyge* Heckel, 1841, with an appraisal of the genus *Barbus*, Cuvier & Cloquet, 1816 and the subfamily Cyprininae. *Bulletin of the British Museum of natural History (Zoology)* **52**: 165-196.

Howes, G.J. (1991). Systematics and biogeography: an overview. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 1-33. London: Chapman & Hall.

Hubbs, C.L. & K.F. Lagler (1947). *Fishes of the Great Lakes region*, pp. 1-213. Ann Arbor, Michigan: University of Michigan Press.

James, M. (1985). *Classification algorithms*, pp. 1-211. London: Collins professional and technical books.

James, F.C. & C.E. McCulloch (1990). Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics* **21**: 129-166.

Janssen, J. (1976). Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *Journal of the Fisheries Research Board of Canada* **33**: 1972-5.

Jeronomidis, G. (1991). Mechanical and fracture properties of cellular and fibrous material. In: *Feeding and the Texture of Food* (J.F.V. Vincent & P.J. Lillford, eds), SEB Seminar Series 44, pp. 1-17. Cambridge: Cambridge University Press.

Keast, A. & D. Webb (1966). Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Board of Canada* **23**: 1845-1874.

Kornfield, I. & K.E. Carpenter (1984). Cyprinids of Lake Lanao, Philippines: taxonomic validity, evolutionary rates and speciation scenarios. In: *Evolution of fish species flocks* (A.A. Echelle & I. Kornfield, eds), pp. 69-83. Orono, Maine: University of Maine at Orono Press.

Kornfield, I. and A.A. Echelle. (1984). Who's tending the flock? In: *Evolution of fish species flocks* (A.A. Echelle & I. Kornfield, eds), pp. 251-254. Orono, Maine: University of Maine at Orono Press.

Kotrschal, K. (1989). Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological role. *Environmental Biology of Fishes* **24**: 199-218.

Kotrschal, K., R. Brandstätter, A. Gomahr, H. Junger, M. Palzenberger & M. Zaunreiter (1991). Brain and sensory systems. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 284-331. London: Chapman & Hall.

Kramer, D.L. & M.J. Bryant (1995). Intestine length in the fishes of a tropical stream: 2. Relationships to diet - the long and short of a convoluted issue. *Environmental Biology of Fishes* **42**: 129-141.

Lammens, E.H.R.R., W.L.T. van Densen & R. Knijn (1990). The fish community structure in Tjeukemeer in relation to fishery and habitat utilization. *Journal of Fish Biology* **36**: 933-945.

Lammens, E.H.R.R. & W. Hoogenboezem (1991). Diets and feeding behaviour. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 353-376. London: Chapman & Hall.

Lammens, E.H.R.R., J. Geursen & P.J. McGillavry (1987). Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in eutrophicated lakes. In: *Proceedings of the 5th Congress of European Ichthyologists, Stockholm, 1985*, pp. 153-162.

Lauder, G.V. (1980). Hydrodynamics of prey capture by teleost fishes. In: *Biofluid Mechanics*, volume 2 (D. Schneck, ed.), pp. 161-81. New York: Plenum Press.

Law, R. & D.R. Grey (1988). Maximum sustainable yields and the self-renewal of exploited populations with age dependent vital rates. In: *Size-structured populations: ecology and evolution* (B. Ebenman & L. Persson, eds), pp. 140-156. Berlin: Springer-Verlag.

Lazzaro, X. (1987). A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* **146**: 97-167.

Leeuwen, J.L. van (1984). A quantitative study of flow in prey capture by rainbow trout, *Salmo gairdneri* with general consideration of the actinopterygian feeding mechanism. *Transactions of the Zoological Society of London* **37**: 171-227.

Leeuwen, J.L. van & M. Muller (1984). Optimum sucking techniques for predatory fish. *Transactions of the Zoological Society of London* **37**: 137-69.

Lévêque, C. (1995). Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquatic Living Resources* **8**: 59-78.

Lévêque, C. & J. Daget (1984). Cyprinidae. In: *Check-list of the freshwater fishes of Africa, volume I (CLOFFA 1)* (J. Daget, J.P. Gosse & D.F.E. Thys van den Audenaerde, eds), pp. 217-343. Paris: Éditions d' Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM) & Tervuren, Belgium: Musée Royal de l'Afrique Central.

Liem, K.F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *American Zoologist* **20**: 295-314.

Liem, K.F. (1980b). Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns. In: *Environmental Physiology of Fishes* (M.A. Ali, ed.), pp. 299-334. New York: Plenum Publishing Corporation.

Løvtrup, S. (1987). On the species problem and some other taxonomic issues. *Environmental Biology of Fishes* **20**: 3-9.

Machordom, A., P. Berrebi & I. Doadrio (1990). Spanish barbel hybridization detected using enzymatic markers: *Barbus meridionalis* Risso x *Barbus haasi* Mertens (Osteichthyes, Cyprinidae). *Aquatic Living Resources* **3**: 295-303.

Marsman, H. *Verzamelde Gedichten* (1938), pp. 1-195. Amsterdam: Querido.

Martin, W.R. (1949). The mechanics of environmental control of body form in fishes. *Publication of the Ontario Fishery Research Laboratory* **70**.

Matthes, H. (1963). A comparative study of the feeding mechanisms of some African Cyprinidae (Pisces, Cypriniformes). *Bijdragen tot de Dierkunde, Amsterdam* **33**: 1-35.

Mayr, E. (1942). *Systematics and the origin of species*, pp. 1-334. New York: Columbia University Press, New York.

Mayr, E. (1984). Evolution of fish species flocks: a commentary. In: *Evolution of fish species flocks* (A.A. Echelle & I. Kornfield, eds), pp. 3-11. Orono, Maine: University of Maine at Orono Press, pp. 3-11.

McPhail, J.D. (1993). Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. *Canadian Journal of Zoology* **71**: 515-523.

Meagher, S. & T.E. Dowling (1991). Hybridization between the cyprinid fishes *Luxilus albeolus*, *L. cornutus*, and *L. cerasinus* with comments on the proposed hybrid origin of *L. albeolus*. *Copeia* **1991**: 979-991.

Meer, H.J. van der & G.Ch. Anker (1984). Retinal resolving power and sensitivity of the photopic system in seven haplochromine species (Teleostei, Cichlidae). *Netherlands Journal of Zoology* **34**: 197-209.

Meyer, A. (1987). Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* **4**: 1357-1369.

Meyer, A. (1989). Cost of morphological specialization: feeding performance of the two morphs in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*. *Oecologia* **80**: 431-436.

Meyer, A., T.D. Kocher, P. Basasibwaki & A.C. Wilson (1990). Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* **347**: 550-553.

Mills, E.L., J.L. Forney & K.J. Wagner (1987). Fish predation and its cascading effects on the Oneida Lake food chain. In: *Predation: direct and indirect impacts on aquatic communities* (W.C. Kerfoot & A. Sih eds.), pp. 118-131. Hanover: University Press of New England.

Mina, M.V. (1992). *Microevolution of fishes. Evolutionary aspects of phenetic diversity* (Translation from Russian of: *Mikroe 'volyutsia Ryb. E 'volyutsionnye Aspekty Feneticheskogo Raznoobraziya*), pp. 1-215. Rotterdam, The Netherlands: A.A. Balkema.

Mina, M., A. Mironovsky & Y. Dgebuadze (1993). Allométrie et divergence entre les barbeaux du lac Tana (Éthiopie). *Cahiers d'Éthologie* **13**: 219-222.

Mina, M.V., A.N. Mironovsky & Y.Y. Dgebuadze (1996). Lake Tana large barbs: phenetics, growth and diversification. *Journal of Fish Biology* **48**: 383-404.

Mohr, P.A. (1962). *The geology of Ethiopia*, pp. 1- 268. Addis Ababa, Ethiopia: University College of Addis Ababa Press.

Moriarty, D.J.W. (1973). The physiology of digestion of blue green algae in the cichlid fish, *Tilapia nilotica*. *Journal of Zoology, London* **171**: 25-39.

Motta, P.J. (1984). Mechanics and functions of jaw protrusion in teleost fishes: a review. *Copeia* **1984**: 1-18.

Motta, P.J.. 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Enironmental Biology of Fishes* **22**: 39-67.

Motta, P.J., K.B. Clifton, P. Hernandez & B.T. Eggold (1995). Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. *Environmental Biology of Fishes* **44**: 37-60.

Motta, P.J. & K.M. Kotrschal (1992). Correlative, experimental and comparative evolutionary approaches in ecomorphology. *Netherlands Journal of Zoology* **42**: 400-415.

Motta, P.J., S.F. Norton & J.J. Luczkovich (1995). Perspectives on the ecomorphology of bony fishes. *Environmental Biology of Fishes* **44**: 11-20.

Muller, M. (1987). Optimization principles applied to the mechanisms of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *Journal of Theoretical Biology* **126**: 343-368.

Muller, M. & J.W.M. Osse (1984). Hydrodynamics of suction feeding in fish. *Transactions of the Zoological Society of London* **37**: 51-135.

Myers, N. (1988). Tropical-forest species: going, going, going... *Scientific American* **259**: 132.

Nagelkerke, L.A.J., M.V. Mina, T. Wudneh, F.A. Sibbing, & J.W.M. Osse (1995*a*). In Lake Tana, a unique fish fauna needs protection *Bioscience* **45**: 772-775.

Nagelkerke, L.A.J. & F.A. Sibbing (1996*a*). Reproductive segregation among the *Barbus intermedius* complex of Lake Tana, Ethiopia. An example of intralacustrine speciation? *Journal of Fish Biology* **49**: 1244-1266.

Nagelkerke, L.A.J. & F.A. Sibbing (1996*b*). Efficiency of feeding on zebra mussel (*Dreissena polymorpha*) by common bream (*Abramis brama*), white bream (*Blicca bjoerkna*), and roach (*Rutilus rutilus*): the effects of morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 2847-2861.

Nagelkerke, L.A.J. & F.A. Sibbing (accepted). A revision of the large barbs (*Barbus* spp., Cyprinidae, Teleostei) of Lake Tana, Ethiopia, with a description of seven new species. *Zoölogische Verhandelingen,Nationaal Natuurhistorisch Museum, Leiden*

Nagelkerke, L.A.J., F.A. Sibbing, J.G.M. van den Boogaart, E.H.R.R. Lammens, & J.W.M. Osse (1994). The barbs (*Barbus* spp.) of Lake Tana: a forgotten species flock? *Environmental Biology of Fishes* **35**: 1-22.

Nagelkerke, L.A.J., Sibbing, F.A. & Osse, J.W.M. (1995*b*). Morphological divergence during growth in the large barbs (*Barbus* spp.) of Lake Tana, Ethiopia. *Netherlands Journal of Zoology* **45**, 431-454.

Nelson, J.S. (1994). *Fishes of the World*, pp. 1-600. New York: John Wiley.

Nikolsky, G.V. (1963). *The Ecology of Fishes*, pp. 1-352. London: Academic Press.

Norton, S.F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environmental Biology of Fishes* **44**: 61-78.

Oellerman, L.K. & P.H. Skelton (1990). Hexaploidy in yellowfish species (*Barbus*, Pisces, Cyprinidae) from southern Africa. *Journal of Fish Biology* **37**: 105-115.

Oijen, M.J.P. van, F. Witte & E.L.M. Witte-Maas (1981). An introduction to ecological and taxonomic investigations on the haplochromine cichlids from the Mwanza Gulf of Lake Victoria. *Netherlands Journal of Zoology* **31**: 149-174.

Osse, J.W.M. (1985). Jaw protrusion, an optimization of the feeding apparatus of teleosts? *Acta Biotheoretica* **34**: 219-32.

Osse, J.W.M. (1990). Form changes in fish larvae in relation to changing demands of function. *Netherlands Journal of Zoology* **40**: 362-385.

Osse, J.W.M., F.A. Sibbing & L.A.J. Nagelkerke (1993). Diversité morphologique et écologique au sein des *Barbus intermedius* du Lac Tana. *Cahiers d'Éthologie* **13**: 217.

Pellegrin, J., 1905. Poissons d'Abyssinie et du Lac Rodolphe (collection Maurice de Rothschild). *Bulletin du Musée d'Histoire Naturelle, Paris* **11**: 290-294.

Pet, J.S., G.J.M. Gevers, W.L.T. van Densen, & J. Vijverberg (1996). Management options for a more complete utilization of the biological fish production in Sri Lankan reservoirs. *Ecology of Freshwater Fish* **5**: 1-14.

Poncin, P., J. Jeandarme, & P. Berrebi (1994). A behavioural study of hybridization between *Barbus barbus* and *Barbus meridionalis*. *Journal of Fish Biology* **45**: 447-451.

Povel, G.D.E. (1986). Pattern detection within the *Yponomeuta padellus*-complex of the European small ermine moths (Lepidoptera, Yponomeutidae). I. Biometric description and recognition of groups by numerical taxonomy. *Proceedings of the Royal Netherlands Academy of Sciences C* **89**: 425-441.

Protasov, V.R. (1970). *Vision and near orientation of fish* (Translation from Russian of: *Zrenie i blizhnyaya orientatsiya ryb*), pp. 1-175. Jerusalem: Israel Program for Scientific Translations, TT70-50065.

Reist, J.D. (1984). An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63**: 1429-1439.

Ribbink, A.J. (1987). African lakes and their fishes: conservation scenarios and suggestions. *Environmental Biology of Fishes* **19**: 3-26.

Ricklefs, R.E., & D.B. Miles (1994). Ecological and evolutionary inferences from morphology. In: *Ecological morphology, integrative organismal biology* (P.C. Wainwright & S.M. Reilly, eds), pp. 13-41. Chicago: The University of Chicago Press.

Rodriguez-Ruiz, A. & C. Granado-Lorencio (1992). Spawning period and migration of three species of cyprinids in a stream with Mediterranean regimen (SW Spain). *Journal of Fish Biology* **41**: 545-556.

Rohlf, F.J. (1993). *NTSYS-pc. Numerical taxonomy and multivariate system, version 1.80*, Setauket, New York: Exeter Software, Applied Biostatistics Inc.

Rohlf, F.J., & R.R. Sokal (1995). *Statistical tables*, 3rd edition, pp. 1-199. New York: W.H. Freeman and company.

Rosenzweig, M.L. (1978). Competitive speciation. *Biological Journal of the Linnean Society* **10**: 275-289.

Rüppell, E. (1836). (Neuer Nachtrag von) Beschreibungen und Abbildungen neuer Fische im Nil entdeckt. *Museum Senckenbergianum, Abhandlungen aus dem Gebiete der beschreibenden Naturgeschichte* **2**: 1-28.

Rzóska, J. (1976). Lake Tana, headwaters of the Blue Nile. In: *The Nile, Biology of an ancient river* (J. Rzóska, ed.), pp. 223-232. The Hague, The Netherlands: Dr W. Junk Publishers.

SAS Institute Inc. (1989). *SAS/STAT user's guide*, version 6, 4th edition, volume 2, pp. 891-1686. Cary, NC: SAS Institute Inc.

Schaefer, S.A. 1991. Morphometric investigations in cyprinid biology. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 52-82. London: Chapman & Hall.

Schliewen, U.K., D. Tautz, & Pääbo, S. (1994). Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* **368**: 629-632.

Schluter, D. (1994). Experimental evidence that competition promotes divergence in adaptive radiation. *Science* **266**: 798-801.

Schoener, Th.W. (1982). The controversy over interspecific competition. *American Scientist* **70**: 586-595.

Seyoum, S.& I. Kornfield (1992). Taxonomic notes on the *Oreochromis niloticus* subspecies-complex (Pisces: Cichlidae), with a description of a new subspecies. *Canadian Journal of Zoology* **70**: 2161-2165.

Sibbing, F.A. (1982). Pharyngeal mastication and food transport in the carp (*Cyprinus carpio* L.): a cineradiographic and electromyographic study. *Journal of Morphology* **172**: 223-58.

Sibbing, F.A. (1987). The role of taste in the feeding mechanism of the carp (Cyprinidae). *Annals of the New York Academy of Sciences* **510**: 612-15.

Sibbing, F.A. (1988). Specializations and limitations in the utilization of food resources by the carp (*Cyprinus carpio* L.): a study of oral food processing. *Environmental Biology of Fishes* **22**: 161-178.

Sibbing, F.A. (1991*a*). Food Capture and Oral Processing. In: *Cyprinid fishes: systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds.), pp. 377-412. London: Chapman & Hall.

Sibbing, F.A. (1991*b*). Food processing by mastication in cyprinid fish. In: *Feeding and the Texture of Food* (J.F.V. Vincent & P.J. Lillford, eds), SEB Seminar Series 44, pp. 57-92. Cambridge: Cambridge University Press.

Sibbing, F.A., L.A.J. Nagelkerke, & J.W.M. Osse (1994). Ecomorphology as a tool in fisheries: identification and ecotyping of Lake Tana barbs (*Barbus intermedius* complex), Ethiopia. *Netherlands Journal of Agricultural Science* **42**: 77-85

Sibbing, F.A., J.W.M. Osse & A. Terlouw (1986). Food handling in the carp (*Cyprinus carpio* L.): its movement patterns, mechanisms and limitations. *Journal of Zoology, London (A)* **210**: 161-203.

Sibbing, F.A. & R. Uribe (1985). Regional specializations in the oro-pharyngeal wall and food processing in the carp (*Cyprinus carpio* L.). *Netherlands Journal of Zoology* **35**: 377-422.

Sih, A. & R.D. Moore (1990). Interacting effects of predator and prey behaviour in determining diets. In: *Behavioural mechanisms of food selection* (R.N. Hughes, ed.), pp. 771-796. Berlin: Springer.

Simberloff, D.S. (1984). Mass extinction and the destruction of moist tropical forests. *Zhurnal Obschei Biologii* **45**: 767-778.

Simon, C.M. (1983) A new coding procedure for morphometric data with an example from periodical cicada wing veins. In: *Numerical taxonomy* (J. Felsenstein, ed.), Proceedings of the NATO Advanced Study Institute. NATO Adv. Study Institute Ser. G (Ecological Sciences), No.1, pp. 378-382. Berlin: Springer-Verlag.

Skelton, P.H., D. Tweddle, & P. Jackson (1991). Cyprinids of Africa. In *Cyprinid fishes, systematics, biology and exploitation* (I.J. Winfield & J.S. Nelson, eds), pp. 211-233. London: Chapman & Hall.

Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*, 2nd edition, pp. 1-859. New York: W. H. Freeman and company.

Sokal, R.R. & F.J. Rohlf (1995) *Biometry*, 3rd edition, pp. 1-887. New York: W.H. Freeman and company.

Stearns, S.C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience* **39**: 436-445.

Strauss, R.E. & F.L. Bookstein (1982). The truss: body form reconstructions in morphometrics. *Systematic Zoology* **31**: 113-135.

Strauss, R.E. (1987). The importance of phylogenetic constraints in comparisons of morphological structure among fish assemblages. In: *Evolutionary Ecology of North American Stream Fishes* (W.J. Mathews & D.C. Heins) pp. 136-143. University of Oklahoma Press, Norman.

Sutherland, W.J. (1996). *From individual behaviour to population ecology*, pp. 1-213. Oxford: Oxford University Press.

Teugels, G.G. (1986). A systematic revision of the African species of the genus *Clarias* (Pisces; Clariidae). *Annales de la Musée Royal de l'Afrique Central, Science Zoologique* **247**: 1-199.

Thiel, H. (1973). *Limnocnida indica* in Africa. *Publications of the Seto Marine biological laboratory, Kyoto University* **20**: 73-79.

Vincent, J.F.V. (1990). *Structural biomaterials*, revised edition, pp. 1-244. Princeton: Princeton University Press.

Vincent, J.F.V. & F.A. Sibbing (1992). How the grasscarp (*Ctenopharyngodon idella*) chooses and chews its food -some clues. *Journal of Zoology, London* **226**: 435-444.

Visser, J. de & C.D.N. Barel (1996). Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish. *Journal of Morphology* **228**: 1-18.

Wainwright, P.C. & B.A. Richard (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* **44**: 97-113.

Ward, J.H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**: 236-244.

Webb, P.W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **24**: 107-120.

Webb, P.W. (1988). Simple physical principles and vertebrate locomotion. *American Zoologist* **28**: 709-725.

Werner, E.E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* **31**: 1531-6.

West-Eberhard, M.J. (1989). Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**: 249-278.

Westneat, M.W. (1995). Phylogenetic systematics and biomechanics in ecomorphology. *Environmental Biology of Fishes* **44**: 263-283.

Wikramanayake, E.D. (1990). Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. *Ecology* **71**: 1756-1764.

Wilson, E.O. (1989). Threats to biodiversity. *Scientific American* **261**: 108-117.

Winnemiller, K.O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs* **61**: 343-365.

Witte, F. 1987. *From form to fishery. An ecological and taxonomical contribution to morphology and fishery of Lake Victoria cichlids* (F. Witte), pp. 1-83. Leiden, The Netherlands: University of Leiden, Ph.D. thesis.

Witte, F., C.D.N. Barel & R.J.C. Hoogerhoud (1990). Phenotypic plasticity of anatomical structures and its ecomorphological significance. *Netherlands Journal of Zoology* **40**: 278-298.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas & N. Bouton (1992). The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* **34**: 1-28.

Witte, F. & M.J.P. van Oijen (1990). Taxonomy, ecology and fishery of Lake Victoria haplochromine trophic groups. *Zoölogische verhandelingen,Nationaal Natuurhistorisch Museum, Leiden* **262**: 1-47.

Witte, F. & E.L.M. Witte-Maas (1981). Haplochromine cleaner fishes. A taxonomic and eco-morphological description of two new species. Revision of the haplochromine species (Teleostei, Cichlidae) from Lake Victoria. Part I. *Netherlands Journal of Zoology* **31**: 203-222.

Witte, F. & E.L.M. Witte-Maas, 1987. Implications for taxonomy and functional morphology of intraspecific variation in haplochromine cichlids of Lake Victoria. With descriptions of five zooplanktivorous species. In: *From form to fishery. An ecological and taxonomical contribution to morphology and fishery of Lake Victoria cichlids* (F. Witte), pp. 1-83. Leiden, The Netherlands: University of Leiden, Ph.D. thesis.

Wood, R.B.& J.F. Talling (1988). Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia* **158**: 29-67.

Wootton, R.J. (1990). *Ecology of teleost fishes*, pp. 1-416. London: Chapman & Hall.

Worthington, E.B. (1932). Scientific results of the Cambridge Expedition to the East African Lakes 1930-1931. 2. Fishes other than Cichlidae. *Journal of the Linnean Society of zoology* **38**: 121-134.

Wudneh, T. (1997) *Biology and management of fish stocks in Bahir Dar Gulf, Lake Tana, Ethiopia*, pp. 1-136. Wageningen, The Netherlands: Agricultural University Wageningen, Fish Culture and Fisheries Group, Wageningen Institute of Animal Sciences, manuscript draft Ph.D. thesis (April 1997).

Zander, E. 1906. Das Kiemenfilter der Teleoster. *Zeitschrift für Wissenschaftliche Zoologie* **84**: 619-713.

Zaret, T.M. (1980). *Predation and Freshwater Communities*, pp. 1-187. London: Yale University Press.

SUMMARY

The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning, and fisheries

In the highlands of northern Ethiopia, a unique species flock of carplike barbs (*Barbus* spp., Cyprinidae) was rediscovered. In this thesis the diversity of these fishes, aspects of their biology, their evolutionary origin, and the significance of these for the ecosystem and fisheries are discussed.

Aim and significance

In 1986 the Lake Tana Fisheries Resource Development Program (LTFRDP) was initiated by the Ethiopian Ministry of Agriculture, in cooperation with the development branch of the Ethiopian Orthodox Church (EOC/DICAD) the Interchurch Foundation Ethiopia (ISE, Urk, the Netherlands), and the Interchurch Coordination Commission of Development Projects (ICCO, Zeist, the Netherlands). Lake Tana is Ethiopia's largest fresh-water lake (c. 3500 km^2: approximately twice the size of the Dutch Lake IJssel), with an average depth of 8 m and a maximal depth of 14 m. It is the source of the Blue Nile river, which, at only 35 km from its outflow from the lake, drops over 40 m high waterfalls, thereby isolating the lake from other fresh-water systems. It was hoped that development of the fisheries would improve the socio-economic circumstances of the local population. However, at the moment of the start of the project hardly anything was known about the fish species that were present in the lake. Four, economically important species were distinguished: the perch-like Nile tilapia (*Oreochromis niloticus*), the African catfish (*Clarias gariepinus*), the carplike 'bezo' (*Varicorhinus beso*) and the barb (*Barbus intermedius*).

Tesfaye Wudneh, the Ethiopian fishery biologist who was assigned to monitor the fish stocks, in order to develop sustainable fisheries, quickly noticed that the barbs were very diverse. He suspected that there were several different barb populations, which would mean they had to be regarded as separate fish stocks. His suspicion was supported by the fact that local fishermen (who have fished Lake Tana on a small scale for their own consumption already for centuries), use different names for different barbs. Several researchers (of which the first, Rüppell, already published his results in 1836) have even described different Tana-barbs as separate biological species. However, these researchers have only visited a small part of the lake and have not fished from boats, limiting their knowledge of the fish. Until 1940 a maximum of 10 species with a total of 23 subspecies have been described. In 1973, Banister decided that all these species (plus a number of species from other lakes and rivers) were only morphs of one, highly variable species: *Barbus intermedius*. Our observations of the Tana-barbs indicate that this conclusion was unjustified, and that we were dealing with a unique group of fishes that is still evolving. Such a group of organisms is of great scientific interest, since processes that cause evolution can be studied on it.

It is not only of scientific importance to know whether the Tana-barbs belong to different species (and thus to different fish stocks). This knowledge is also needed to achieve rational

management towards sustainable fisheries, since different barbs play different roles in the ecosystem of Lake Tana: e.g. some eat zooplankton, others eat snails, fish, or plants. If, for example, fish-eating (piscivorous) barbs are fished intensively (which actually happens, since they are the largest and tastiest barbs), they will decrease in number. Now there are two possibilities: 1) if the piscivorous barbs are just morphs of the single species *B. intermedius*, they will be easily replaced by other young barbs that will develop into piscivores, or 2) if the piscivorous barbs are separate species, they will not be replaced and they will become rare, or even extinct.

The disappearance of the piscivorous barbs would, in itself, already be detrimental to fisheries, but it could have even more far-stretching consequences. If the piscivores are almost completely absent from the lake, more small fish will survive. These small fish predominantly eat zooplankton, which becomes rare. Zooplankters eat small algae, and because there are fewer zooplankters, algae will increase in number, which results in more turbid water. Large water plants will receive less light and will die off. Plant-eating fish will become rarer, together with these plants. Also for other animals, like fish-eating birds this will have numerous effects. Hence, overfishing of certain fish species from a community of many species can have a cascading effect in the whole ecosystem. It is therefore important to exploit the fish stock in a balanced way and to preserve the ecosystem as much as possible, to prevent undesirable effects. If there are more species this is more complicated than if there is only one barb species that can play all ecological roles.

The research

In 1990, during a 10-week field expedition at Lake Tana, we found that there were at least 13 discrete 'morphotypes, i.e. different barbs that were constant and distinct in shape. Usually we gave them descriptive names such as 'Bigmouth big-eye', 'Barbel', 'Bighead', 'White hunch', and 'Lip'. Moreover, these morphotypes had different ecological roles: they ate different things and occurred at different places (e.g. some we only caught in deep water, others only above rocks, or between plants). The fact that the morphotypes were so clear, and that we could assign almost all barbs we caught to one of the morphotypes, gradually convinced us that we were dealing with a species flock, a group of real species that evolved in isolation from one ancestral species. This would be unique, because there was only one other known species flock of carplike fishes (on the Philippines), and that disappeared because of mismanagement and overfishing. Moreover, species flocks are very vulnerable to perturbation, as became clear from Lake Victoria, from which most of more than 300 cichlid species virtually disappeared after the introduction of the Nile perch.

Since we did not have sufficient evidence yet that we were dealing with real species, and not just with morphs of one species, we searched for additional proof. In the research project that I performed from 1992 until 1996 this proof was found. The results can be summarized as follows:

1. The barbs are discrete and distinct morphotypes that widely differ in shape.
2. They use different food resources in the lake. (fish, plants, snails, insect larvae etc.).
3. They occur at different places in the lake (deep/shallow, over rocky or over sandy and muddy bottoms).
4. The barbs attain their adult morphology at a young age (if they are smaller than 10 cm, i.e. probably in their first year of life) and can be recognized as such.

5. The morphotypes reproduce at different places and/or times. Differences in this so-called spawning behaviour are very important and often decisive for species distinction.
6. Part of the genetic material (DNA) was different among barb morphotypes, but not within morphotypes, which indicates that the morphotypes do not mix reproductively. This supported the previous findings even further.

All these results have lead to the description of 14 barb species, of which seven are new to science! We have indications that the species evolved within Lake Tana itself from one common ancestral species, and we have reconstructed the following evolutionary scenario:

Lake Tana was formed at the beginning of the Pleistocene (c. 2 million years ago), by volcanic blockage of the Blue Nile. The area upstream from the blockage was flat and filled up with water. At that time, the ancestral species of the present-day Tana barbs lived in the river and the newly-formed lake. This species was probably similar to the river-barbs that are still present in the Ethiopian rivers today. The barbs in the new lake were confronted with habitats that are not found in rivers. There is e.g. no deep, stagnant water in rivers. Under the influence of these different living circumstances, in which different food resources can be found, the barbs evolved and started to occupy new ecological niches through specialisation. This resulted in the 14 species that have now been described. Because of the complete isolation of Lake Tana from other freshwater-systems, evolution could go its own way, resulting in the unique biodiversity of the Lake Tana barbs.

If the barbs have indeed evolved through adaptations to different habitats and food resources, they form an excellent chance for the study of adaptation and to gain insight in the relation between the form of an organism and its ecological role: the lake can be regarded as a natural laboratory. This is discussed in the last chapters of this thesis, since these are important biological questions.

On the basis of food properties (such as strength or toughness) and the possibilities of the fish to deal with these (if a large force is needed, e.g. to crush a snail, then the pharyngeal jaws should be larger) we have made predictions - based on functional morphological research - about the food partitioning among the Lake Tana barbs. If, e.g. species A had heavier jaws than species B, then we predicted that species A was better at crushing hard snails, than species B. The predictions were deduced from 33 measurements of the fish (from jaws to gut length), to cover all feeding actions, and because many measurements make the predictions more stable and more accurate. Consequently we have tested the predictions by collecting fish and recording their gut contents to check what they actually ate. We found that the diets of the species could be predicted fairly well, but that especially the partitioning of food types among the Tana barbs could be predicted accurately.

The significance of this 'ecomorphological method', which was elaborated at this scale for the first time, is that through understanding of the functioning of individual fish, the interactions in the whole community can be understood better. If the method works universally, it will no longer be needed to launch an extensive sampling program to catch fish at different places and times, and in different seasons, to monitor their gut contents, but it will suffice to measure a limited number of fish. If there is information on the food resources in the environment it will then be possible to predict diets and food resource utilization. The advantage is that not only the present situation can

be explained, but that the influence of changing circumstances can also be predicted, since the method is based on insights in the possibilities of the fish. The effects of large environmental perturbations, such as overfishing or the introduction of exotic species could be anticipated, or at least understood better. Shifts in the fauna could be predicted (if e.g. species A is overfished, it is possible, on the basis of the possibilities of species B to predict that the latter will take A's place, and to predict which species will take B's place).

Understanding and predicting of shifts of the fish fauna within an ecosystem will therefore help to develop better strategies towards sustainable fisheries and simultaneous protection of biodiversity.

SAMENVATTING

De barbelen van het Tana-meer, Ethiopië: vormdiversiteit en haar betekenis voor taxonomie, benutting van voedselbronnen en visserij

In de hooglanden van Noord-Ethiopië is een unieke soortenzwerm van karperachtige barbelen (*Barbus* spp., Cyprinidae) herontdekt. In dit proefschrift worden hun diversiteit, aspecten van hun biologie, hun evolutionair ontstaan en het belang daarvan voor het ecosysteem (levens-gemeenschap) en de visserij beschreven.

Doel en belang

In 1986 werd door het Ethiopische Ministerie van Landbouw in samenwerking met het ontwikkelingsdepartement van de Ethiopisch Orthodoxe Kerk (EOC/DICAD), de Interkerkelijke Stichting Ethiopië (ISE) uit Urk, en de Interkerkelijke Coördinatie-commissie Ontwikkelingsprojecten (ICCO) uit Zeist, het Tana-meer Visserij-Ontwikkelingsprogramma (LTFRDP) gestart. Het Tana-meer is het grootste zoetwatermeer van Ethiopië (ca. 3500 km^2: ongeveer twee keer zo groot als het IJsselmeer), met een gemiddelde diepte van 8 en een maximale diepte van 14 m. Het is de bron van de Blauwe Nijl, die op slechts 30 km vanaf de uitstroom uit het meer over 40 m hoge watervallen naar beneden stort, waardoor het meer afgesloten is van andere zoetwatersystemen. Men hoopte dat de ontwikkeling van de visserij in het meer zou bijdragen aan de sociaal-economische ontwikkeling van de lokale bevolking. Op het moment dat het project startte was er echter nauwelijks iets bekend over de aanwezige vissoorten. Er werden vier, commercieel interessante, soorten onderscheiden: de baarsachtige Nijltilapia (*Oreochromis niloticus*), de Afrikaanse meerval (*Clarias gariepinus*), de karperachtige 'bezo' (*Varicorhinus beso*) en de barbeel (*Barbus intermedius*).

Tesfaye Wudneh, de Ethiopische visserijbioloog die aangesteld was om de visbestanden in kaart te brengen om zo tot management van een duurzame visserij te komen, merkte echter al snel op dat de barbelen zeer divers waren. Hij vermoedde dat er verschillende populaties van barbelen aanwezig zouden kunnen zijn en dat zou betekenen dat die als verschillende visbestanden beschouwd moeten worden. Hij werd gesterkt in zijn vermoeden door het feit dat de lokale vissers, die al eeuwenlang op zeer kleine schaal voor hun eigen consumptie vis vangen, verschillende namen hebben voor de verschillende barbelen. Verscheidene onderzoekers (waarvan de eerste, Rüppell, al

in 1836 zijn bevindingen publiceerde) hebben verschillende van de Tana-barbelen ook als aparte biologische soorten beschreven. Deze onderzoekers hebben echter slechts een klein deel van het meer bezocht en hebben meestal niet vanaf boten gevist, waardoor hun kennis van vooral de vissen van het open water, beperkt bleef. Tot 1940 zijn er maximaal 10 soorten met een totaal van 23 ondersoorten beschreven. In 1973 besloot Banister dat al deze soorten (en nog een aantal soorten uit andere meren en rivieren) slechts vormen van één zeer variabele soort waren: *Barbus intermedius*. Onze waarnemingen aan de Tana-barbelen deden vermoeden dat deze conclusie onjuist was en dat we te maken hadden met een unieke groep vissen, die nog steeds aan het evolueren is. Zo'n diergroep is wetenschappelijk van groot belang omdat daaraan processen die de evolutie veroorzaken bestudeerd kunnen worden.

Het is niet alleen van wetenschappelijk belang om te weten of de Tana-barbelen tot verschillende vissoorten (en daarmee tot verschillende visbestanden) behoren. Ook om tot een verstandig beheer te komen, zodat een duurzame visserij ontwikkeld kan worden is die kennis vereist. De verschillende barbelen vervullen namelijk verschillende rollen in de levensgemeenschap van het Tana-meer: sommige eten watervlooien, sommige slakjes, andere weer visjes of planten. Als er bijvoorbeeld intensief wordt gevist op vis-etende barbelen, wat in de praktijk gebeurt, omdat ze het grootst en smakelijkst zijn, dan nemen die in aantal af. Er zijn dan twee mogelijkheden: 1) als de vis-etende barbelen slechts een van de vormen zijn van de variabele *B. intermedius*, dan zullen de weggevangen vis-eters makkelijk vervangen kunnen worden door andere jonge barbelen die zich dan tot viseters zullen ontwikkelen, of 2) als de vis-etende barbelen andere soorten zijn dan de andere barbelen, dan zullen ze niet vervangen kunnen worden en zullen ze zeldzaam worden of zelfs uitsterven.

Het wegvallen van de vis-etende barbelen is op zichzelf al slecht voor de visserij, maar het kan nog verstrekkender gevolgen hebben. Doordat er nu vrijwel geen viseters meer zijn in het meer zullen er meer kleine visjes overblijven. Deze eten vooral watervlooien die daardoor zeldzaam worden. De watervlooien eten algjes, en aangezien er minder watervlooien zijn zullen de algen in aantal toenemen, waardoor het water troebeler wordt en grote planten minder licht zullen krijgen en afsterven. Plantenetende vissen zullen samen met de waterplanten zeldzamer worden. Ook voor andere dieren, zoals visetende vogels zal dat allerlei effecten hebben. Overbevissing van bepaalde vissoorten uit een gemeenschap van vele soorten kan dus een sneeuwbaleffect veroorzaken in de hele levensgemeenschap. Het is dus belangrijk om de visstand evenwichtig te exploiteren en de levensgemeenschap (ecosysteem) zoveel mogelijk in stand te houden om ongewenste effecten te voorkomen. Als er meerdere soorten zijn is dat ingewikkelder dan als er slechts één soort barbeel is die alle ecologische rollen kan vervullen.

Het onderzoek

In 1990 werd op een 10-weekse veldexpeditie aan het Tana-meer vastgesteld dat er minstens 13 verschillende discrete 'morfotypen' waren, d.w.z. verschillende barbelen die herkenbaar zijn in hun constante vorm. Meestal gaven we die beschrijvende namen, zoals 'Grootbek groot-oog', 'Baarddraad', 'Grootkop', 'Bochel' en 'Diklip'. Deze morfotypen hadden bovendien een verschillende ecologische rol: ze aten verschillende dingen en ze kwamen voor op verschillende plaatsen (sommige vingen we bijvoorbeeld alleen in diep water, andere alleen boven rotsen, of tussen de planten).

Het feit dat de morfotypen zo duidelijk waren en we bijna alle barbelen die we vingen tot een van die morfotypen konden benoemen overtuigde ons geleidelijk dat we te maken hadden met een soortenzwerm, een groep echte soorten die in afzondering is ontstaan uit één vooroudersoort. Dit zou uniek zijn, aangezien er maar één andere soortenzwerm van karperachtige vissen bekend was (nl. op de Filippijnen) en die is verdwenen door wanbeheer en overbevissing. Soortenzwermen zijn bovendien erg kwetsbaar voor verstoring, zoals gebleken is in het Victoria-meer, waar een soortenzwerm van meer dan 300 soorten cichliden (bonte baarzen) grotendeels verdwenen is na de invoering van de Nijlbaars.

Aangezien we nog niet voldoende bewijs hadden dat we met echte soorten en niet slechts met vormen van één soort te maken hadden, zochten we naar aanvullend bewijs. In het onderzoeksproject dat ik van 1992 t/m 1996 uitvoerde werd dat ook gevonden. De resultaten kunnen als volgt worden samengevat:

1. De barbelen vormen discrete en consistente morfotypen die sterk in vorm verschillen.
2. Ze benutten verschillende voedselbronnen in het meer (vis, planten, slakken, insektenlarven enz.).
3. Ze komen op verschillende plaatsen in het meer voor (diep/ondiep, boven rots of boven zand en modder).
4. De barbelen krijgen al jong (als ze kleiner dan 10 cm zijn, d.w.z. waarschijnlijk in hun eerste levensjaar) al het uiterlijk van volwassen vissen en zijn dan ook al te onderscheiden.
5. De morfotypen planten zich op verschillende plaatsen en/of tijdstippen voort. Verschillen in dit z.g. paaigedrag zijn heel belangrijk en vaak doorslaggevend voor het onderscheid tussen soorten.
6. Een deel van het erfelijk materiaal (DNA) bleek verschillend te zijn tussen barbeel-morfotypen, maar niet binnen de morfotypen, wat erop wijst dat de verschillende morfotypen zich niet vermengen. Dit versterkte de vorige argumenten nog verder.

Al deze argumenten samen hebben ons ertoe gebracht 14 barbelensoorten te beschrijven, waarvan zeven nieuw zijn voor de wetenschap! We hebben aanwijzingen dat de soorten in het Tana-meer zelf zijn ontstaan uit één gemeenschappelijke vooroudersoort en hebben het volgende evolutionaire scenario gereconstrueerd:

Het Tana-meer is ontstaan aan het begin van het Pleistoceen (ongeveer 2 miljoen jaar geleden), doordat de Blauwe Nijl afgedamd werd door vulkanische uitbarstingen. Het gebied stroomopwaarts van de afdamming was vlak en stroomde vol water. Op dat moment leefde daar de vooroudersoort van de huidige Tana-barbelen in de rivier en in het nieuwgevormde meer. Deze soort leek waarschijnlijk erg veel op de rivier-barbelen die ook tegenwoordig nog talrijk in Ethiopische rivieren voorkomen. De barbelen in het zich vormende meer werden geconfronteerd met een leefomgeving (habitat) die niet in rivieren wordt gevonden. Zo is er in rivieren geen diep, stilstaand open water. Onder invloed van de verschillende leefomstandigheden, waarin verschillende voedselsoorten te vinden zijn evolueerden de barbelen en begonnen door specialisatie nieuwe ecologische 'niches' in te nemen. Dit resulteerde in de 14 soorten die we nu beschreven hebben. Door de volledige isolatie van het Tana-meer van andere zoetwatersystemen kon de evolutie hier ongestoord zijn eigen weg gaan, hetgeen de unieke biodiversiteit van de Tana-barbelen heeft opgeleverd.

Als de barbelen inderdaad door hun aanpassingen aan verschillende omgevingen en voedsel zijn geëvolueerd, vormen ze een buitenkans om de evolutie van aanpassingen (adaptatie) te bestuderen en om inzicht te krijgen in het verband tussen vorm van een organisme en zijn ecologische rol; het meer is a.h.w. een natuurlijk laboratorium. In de laatste hoofdstukken van het proefschrift wordt hier aandacht aan besteed, aangezien dit belangrijke biologische vragen zijn.

We hebben op basis van de eigenschappen van voedsel (zoals de sterkte of de taaiheid) en de mogelijkheden van de vis om daar mee om te gaan (als er veel kracht nodig is om bijv. een slak te kraken, dan moeten de kaken zwaarder zijn) voorspellingen gedaan - gebaseerd op functioneel morfologisch onderzoek - over het voedselgebruik van de Tana-barbelen. Als bijvoorbeeld soort A zwaardere kaken had dan soort B dan voorspelden we dat soort A beter stevige slakken kon kraken dan soort B. De voorspellingen zijn opgesteld door meting van 33 verschillende kenmerken aan de vissen (vanaf de kaken tot aan de darmlengte), om alle voedingsfuncties hierin te betrekken en omdat met veel metingen de voorspelde voorspellingen stabieler en preciezer worden. Vervolgens hebben we de voorspellingen getest door vissen te verzamelen en in hun darmen te kijken wat ze daadwerkelijk gegeten hebben. Het bleek dat de diëten van de soorten redelijk goed te voorspellen waren, maar dat vooral de manier waarop bepaalde voedseltypen tussen de verschillende Tana-barbelen wordt verdeeld nauwkeurig voorspeld kon worden.

Het belang van deze voor het eerst op deze schaal uitgewerkte 'ecomorfologische methode' is dat door het begrijpen van het functioneren van individuele vissen de interacties in de levensgemeenschap beter begrepen kunnen worden. Als de methode universeel werkt dan is het niet meer nodig om een zeer uitgebreid monsterprogramma op te zetten om op verschillende plaatsen, over de seizoenen heen, vissen te vangen om naar hun darminhouden te kijken, maar volstaat het om een aantal metingen te doen aan een beperkt aantal vissen. Als er informatie is over de voedselbronnen in het milieu dan zal het mogelijk zijn om de diëten en voedselbronbenutting te voorspellen. Het voordeel is dat niet alleen de bestaande situatie verklaard kan worden, maar dat de invloed van veranderende omstandigheden ook voorspeld kan worden. De methode is immers gebaseerd op inzicht in de mogelijkheden van de vis. De gevolgen van grote ingrepen in het milieu, zoals overbevissing of de invoering van nieuwe soorten zouden voorzien kunnen worden, of op zijn minst beter begrepen. Verschuivingen in de fauna zouden kunnen worden voorspeld (als bijvoorbeeld soort A wordt overbevist is het mogelijk op grond van de mogelijkheden van soort B te voorspellen dat deze soort de plaats van A inneemt, en wie dan weer soort B vervangt).

Het begrijpen en voorspellen van verschuivingen van de visfauna in een levensgemeenschap kan dan ook helpen tot betere strategieën te komen om duurzame visserij en gelijktijdige bescherming van de biodiversiteit te waarborgen.

DANKWOORD EN EPILOOG

Aangezien dit waarschijnlijk een van de beter gelezen gedeelten van mijn proefschrift wordt en de kans dat mijn geheugen me in de steek laat niet denkbeeldig is, is het schrijven van dit onderdeel niet van risico's gespeend. Het zou echter te makkelijk zijn om het daarom maar achterwege te laten. Mocht ik je vergeten zijn, bedenk dan dat dat slechts door mijn beperkte vermogen tot het herinneren van namen is, en niets met een gebrek aan waardering te maken heeft.

De afgelopen jaren heb ik veel geleerd: niet alleen over vissen en biologie, maar ook (en soms vooral) over mezelf. Ik bleek bepaalde zaken beter te kunnen dan ik zelf in eerste instantie had verwacht. Ik begon zelfs genoegen te scheppen in het werken onder lastige omstandigheden in een ver en afgelegen land, in het onderhandelen met autoriteiten, het opzetten en leiden van een monsterprogramma en in het improviseren. Er waren echter ook negatieve verrassingen: mijn leerproces omvatte ook een nogal harde confrontatie met eigen zwakheden en de duistere kanten van mijn geest. Dat was niet altijd een even aangename ervaring, maar ik hoop dat ik van die kennismaking per saldo beter en sterker geworden ben. De belangrijkste steun gedurende het project en in mijn persoonlijk leven heb ik dan ook ondervonden van mensen die mij ondanks die minder plezierige kanten zijn blijven waarderen. Ik weet dat jullie zelf weten wie ik bedoel: dank daarvoor. Dank ook aan de vrienden met wie ik naar de kroeg kon gaan en die me, na ettelijke glazen kostelijk bier, geregeld hebben verteld dat het volkomen idioot is dat een volwassen kerel zich full time met vissen bezig houdt. Soms had ik die botte relativeringen en de erop volgende bevrijdende lach buitengewoon nodig.

Iets anders dat me zeer gesteund heeft in de afgelopen jaren is een hobby die wellicht voor velen volkomen belachelijk lijkt, maar beschikt over rustgevende en helende krachten voor wie daar gevoelig voor is. Ik heb het over vogelen. De zeldzame momenten dat je door het veld struint en plots oog in oog staat met een ander wezen dat zo anders is dan wijzelf, kunnen voor een groot geluksgevoel zorgen.

Als je Ethiopië en Tana-meer zegt, dan zeg je de laatste jaren ook Nand Sibbing. Nand, zonder jouw onophoudelijke steun, inzet, inspanningen en ideeën was het project niet van de grond gekomen en was dit boekje er zeker niet geweest. De samenwerking kon wat mij betreft, nauwelijks beter. Jan Osse, dank voor de discussies, de originele wetenschappelijke en andere invallen ("We kunnen toch wel gaan onderhandelen met die rebellenleider?") en de hilarische momenten (is die foto van die neushoornvogel nog gelukt?). De studenten die bij me in het veld zijn geweest nemen eveneens een bijzondere plaats in. Terwijl ik probeerde diesel te kopen, een auto te regelen of een vergunning voor export te krijgen deden jullie het meeste praktische werk. Geert, Michiel, Hans, Sander en Arnold, zeer bedankt daarvoor en voor de vriendschap die ik van jullie mocht ondervinden. Micha en Ingrid zijn weliswaar in Nederland gebleven, maar hun nuttige bijdragen mogen zeker niet onvermeld blijven.

Ik wil verder Albert Otten en Marcel Machiels bedanken voor de hulp bij wiskundige analyses. Heleen Zwennes wil ik bedanken voor de prachtige tekeningen van de barbelen. Wim Valen, dank voor de vele foto's die je voor me hebt afgedrukt en de collages die je hebt gemaakt. Dank ook aan de andere collega's die voor me klaarstonden met een praatje en een kop koffie: ik vond Zodiac een

fijne plek om te werken. Één van mijn paranimfen deelt die ervaring met me, hoewel dat al weer even geleden is: Kees Meyboom heeft ook zijn tijd op EDC doorgebracht. Mijn andere paranimf is mijn jongste broer Ko. Ik verheug me erg op hun bijstand gedurende de plechtigheid.

I would also like to express my thanks towards Anni Rask and Preben Holler, who were stationed in Bahar Dar during 1995. Their door was always open, and I have spent many pleasant hours in their company. Tesfaye Wudneh and his family have been dear friends during our whole stay in Ethiopia. Fishing together, going to Dek, and drinking *tej* were some of the best experiences I had. Thanks very much. Negist Addis has taken care of the house-keeping during our stay in Ethiopia and she was also a great friend. Special thanks go to Asfaw Berhe and his family, who helped us greatly in all sorts of matters. Unfortunately Asfaw is not here anymore, as he died in December 1995.

Mijn grootste dank gaat uit naar Suzanne, met wie ik al meer dan 11 jaar samen ben. Suzanne heeft het niet gemakkelijk gehad in Ethiopië en ook niet met mij. Ondanks alles is ze me blijven steunen en heeft me geholpen op het persoonlijk vlak en met heel veel praktische zaken. Toen ik dysenterie kreeg heeft ze me vanaf het lab naar huis gestuurd, het monsterprogramma van die dag afgemaakt, me gerustgesteld dat mijn koorts (die op dat moment boven de 40°C was) niet zou blijven stijgen en ik er niet aan zou doodgaan, en me verzorgd tot ik weer beter was. Suzanne, ik heb geen woorden voor de dankbaarheid en liefde die ik voor je voel.

Het zit erop; het ei is gelegd: op naar nieuwe avonturen!

CURRICULUM VITAE

Leopold (Leo) Adrianus Jacobus Nagelkerke werd op 25 april 1966 in Breda geboren. Tot zijn derde jaar woonde hij in Prinsenbeek om na een kort verblijf in Oosterhout (N.B.) zijn schooltijd in Roosendaal te beginnen. In 1982 verhuisde hij naar Oudenbosch. In 1984 deed hij *cum laude* eindexamen aan het Gertrudislyceum te Roosendaal en begon in datzelfde jaar aan een studie Biologie aan de toenmalige Landbouwhogeschool (spoedig omgedoopt tot Landbouwuniversiteit) in Wageningen. Tijdens zijn studie heeft hij geprobeerd een breed zicht op de gehele biologie te houden, door vakken te volgen die het cellulaire tot het populatie integratieniveau besloegen en heeft hij met veel plezier verschillende praktika begeleid. Als eerste doctoraalvak werd Functionele Diermorfologie gekozen aan de vakgroep Experimentele Diermorfologie en Celbiologie (EDC). Hij werkte daar o.l.v. Nand Sibbing aan de efficiëntie van het eten van driehoeksmosseltjes (*Dreissena polymorpha*) door brasem, kolblei en blankvoorn. Vervolgens werd aan dezelfde vakgroep een doctoraalvak Celbiologie/Immunologie verricht met Lidy Verburg als begeleidster. De 'respiratory burst' van karper-fagocyten, een belangrijk aspect van het aspecifieke afweersysteem, vormde het onderwerp. Een ERASMUS-beurs stelde hem in staat in 1989 zes maanden in Aberdeen door te brengen, waar in het Fish Lab onder begeleiding van Chris Secombes aan de zuurstofconsumptie van macrofagen van de regenboogforel werd gewerkt. Dit onderzoek leidde tot een eerste wetenschappelijke publicatie. In augustus 1990 studeerde hij *cum laude* af, om anderhalve maand later, als toegevoegd onderzoeker bij de vakgroep EDC, op een tienweekse veldexpeditie mee te gaan naar het Tana-meer in Ethiopië. De eerste vijf weken was hij daar onderdeel van een team van vier mensen, de laatste periode werd alleen in Bahar Dar toegebracht. Dit was de eerste keer dat hij geconfronteerd werd met isolement, een oorlogssituatie en dysenterie, zodat aanzienlijk minder van hem terug naar Nederland vloog dan oorspronkelijk in Ethiopië was gearriveerd. Tot maart 1992 was hij werkzaam als toegevoegd onderzoeker. Gedurende die tijd werd het project: "Food, feeding abilities and niche differentiation in the *Barbus intermedius* complex of Lake Tana, Ethiopia", door de Stichting voor wetenschappelijk onderzoek van de tropen (WOTRO) goedgekeurd (projectnummer W 88-176), waarna hij in oktober 1992 als assistent-in-opleiding samen met zijn echtgenote Suzanne van Gaans voor vijftien maanden naar het Tana-meer vertrok. Het jaar 1994 werd in Nederland doorgebracht, 1995 weer in het veld. Tussen het reizen, vissen, in- en uitklaren en bakkeleien met autoriteiten door werd het onderzoek verricht dat in dit proefschrift is beschreven, en dat tot op heden resulteerde in vier publicaties in internationale vakbladen. Verder is nog een manuscript geaccepteerd door een vakblad en worden de laatste twee hoofdstukken nog daarvoor bewerkt.

LIST OF PUBLICATIONS

Research articles (refereed)

Dixon, B., L.A.J. Nagelkerke, F.A. Sibbing, E. Egberts & R.J.M. Stet (1996). Evolution of MHC class II β chain-encoding genes in the Lake Tana barbel species flock (*Barbus intermedius* complex). *Immunogenetics* **44**: 419-431.

Dixon, B., L.A.J. Nagelkerke, F.A. Sibbing, E. Egberts & R.J.M. Stet (1996). Isolation of major histocompatibility complex class II beta sequences from Lake Tana barbel (*Barbus intermedius* complex). *Folia Zoologica* **45**(sup. 1): 47-54.

Nagelkerke, L.A.J., M.V. Mina, T. Wudneh, F.A. Sibbing & J.W.M. Osse (1995). In Lake Tana, a unique fish fauna needs protection. *Bioscience* **45**: 772-775.

Nagelkerke, L.A.J., M.C. Pannevis, D.F. Houlihan & C.J. Secombes (1990). Oxygen uptake of rainbow trout *Oncorhynchus mykiss* phagocytes following stimulation of the respiratory burst. *Journal of experimental Biology* **154**: 339-353.

Nagelkerke, L.A.J. & F.A. Sibbing (1996). Reproductive segregation among the *Barbus intermedius* complex of Lake Tana, Ethiopia. An example of intralacustrine speciation? *Journal of Fish Biology* **49**: 1244-1266.

Nagelkerke, L.A.J. & F.A. Sibbing (1996). Efficiency of feeding on zebra mussel (*Dreissena polymorpha*) by common bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*): the effects of morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences*: **53**: 2847-2861.

Nagelkerke, L.A.J. & F.A. Sibbing (accepted). A revision of the large barbs (*Barbus* spp., Cyprinidae, Teleostei) of Lake Tana, Ethiopia, with a description of seven new species. *Zoölogische Verhandelingen Leiden*

Nagelkerke, L.A.J. & F.A. Sibbing (in preparation). Trophic segregation within the *Barbus* species flock of Lake Tana, Ethiopia: 2. Test of diet predictions and food partitioning.

Nagelkerke, L.A.J., F.A. Sibbing, J.G.M. van den Boogaart, E.H.R.R. Lammens & J.W.M. Osse (1994). The barbs (*Barbus spp.*) of Lake Tana: a forgotten species flock? *Environmental Biology of Fishes* **39**: 1-22.

Nagelkerke, L.A.J., F.A. Sibbing & J.W.M. Osse (1995). Morphological divergence during growth in the large barbs (*Barbus* spp.) of Lake Tana, Ethiopia. *Netherlands Journal of Zoology* **45**: 431-454.

Sibbing, F.A. & L.A.J. Nagelkerke (in preparation).Trophic segregation within the *Barbus* species flock of Lake Tana, Ethiopia: 1. Diets predicted from food properties and fish morphology.

Sibbing, F.A., L.A.J. Nagelkerke & J.W.M. Osse (1994). Ecomorphology as a tool in fisheries: identification and ecotyping of Lake Tana barbs (*Barbus intermedius* complex), Ethiopia. *Netherlands Journal of Agricultural Science* **42**: 77-85.

Abstracts and other small publications

Dixon, B., L.A.J. Nagelkerke, F.A. Sibbing, E. Egberts & R.J.M. Stet (1994). Evolution of MHC class II beta chain polymorphism in the *Barbus* species flock of Lake Tana. *Developmental and Comparative Immunology* **18** (Sup. 1): 49.

Nagelkerke, L.A.J. (1992). De onbekende barbelen van het Tana-meer. *Missing Link* **9**: 16-22.

Nagelkerke, L.A.J. (1995). The unique barbs (*Barbus* spp., Cyprinidae) of Lake Tana, Ethiopia: present status and possible threats. *SILnews* **15**: 4-5.

Nagelkerke, L.A.J., F.A. Sibbing & C. van den Berg (1991). Efficiency of molluscivory in bream, white bream and roach. *Abstracts of presentations of the Seventh International Ichthyological Congress of the European Ichthyological Union. Bulletin of the Zoological Museum, University of Amsterdam*: 54.

Nagelkerke, L.A.J., F.A. Sibbing & J.W.M. Osse (1993). Morphological and ecological differentiation among the large barbs (*Barbus intermedius* complex) of Lake Tana, Ethiopia. *Abstracts of the International Symposium on Biological Diversity in African Fresh and Brackish Water Fishes, Dakar, Senegal*: 45.

Nagelkerke, L.A.J., F.A. Sibbing & R.J.M. Stet (1996). Intralacustrine speciation of the unique *Barbus* species flock of Lake Tana, Ethiopia. *Abstracts of the 76th annual meeting of the American Society of Ichthyologists and Herpetologists at New Orleans, 13-19 June 1996*: 228-229.

Osse, J.W.M., F.A. Sibbing & L.A.J. Nagelkerke (1993). Diversité morphologique et écologique au sein des *Barbus intermedius* du lac Tana. *Cahiers d'Éthologie* **13**: 217.

Sibbing, F.A. & L.A.J. Nagelkerke (1996). Trophic segregation within the *Barbus intermedius* species flock of Lake Tana. *Abstracts of the 76th annual meeting of the American Society of Ichthyologists and Herpetologists at New Orleans, 13-19 June 1996*: 281.

Sibbing, F.A., L.A.J. Nagelkerke & J.W.M. Osse (1993). Typing of Lake Tana *Barbus* a must for fisheries development. *Abstracts of the International Symposium on Biological Diversity in African Fresh and Brackish Water Fishes, Dakar, Senegal*: 59.

Stellingen

1. Trofische segregatie van vissoorten in laag-produktieve systemen is te voorspellen door bestudering van hun morfologie.
dit proefschrift (hoofdstuk 7)

2. Zonder veldobservaties blijven soortbeschrijvingen dode categorieën.
dit proefschrift

3. Traditionele visserijmethoden zijn niet per definitie duurzaam, zeker niet bij toenemende bevolkingsdruk.
dit proefschrift (hoofdstuk 4, over het vissen met vergif)

4. Het bestuderen en gebruiken van lokale talen levert niet alleen goodwill en sociale interacties op, maar kan tevens een bron van belangrijke biologische informatie zijn.
dit proefschrift (hoofdstuk 4,5)

5. De opmerking van majoor Cheesman dat de nijlpaarden in het Tana-meer uitgestorven zijn is een typisch voorbeeld van een stelling waaraan vele malen klakkeloos is gerefereerd, zonder te pogen nieuwe informatie in te winnen. Tussen 1990 en 1995 heb ik vele malen een kleine populatie waargenomen.
R.E. Cheesman, in: "Lake Tana and the Blue Nile." (1936)

6. Taxonomie is te belangrijk om alleen aan taxonomen over te laten.

7. Niet alleen de Klasse en de Orde, maar ook de Species is een kunstmatige categorie en geen natuurlijke entiteit.
contra Linnaeus: "Classis et Ordo est sapientiae, Species naturae opus."

8. Soortenzwermen ("species flocks") zijn geen uitzonderlijk verschijnsel maar zullen binnen afzienbare tijd in uiteenlopende diergroepen worden onderkend.

9. Zelfs indien het bewijs ontbreekt dat ecosystemen met een grote biodiversiteit produktiever zijn dan die met een lage biodiversiteit en ook als er bewijs is voor het omgekeerde, dan nog hebben we de ethische plicht zorgvuldig met die biodiversiteit om te gaan.

10. Yet the importance of a discovery lies in the impact and reforming power of ideas expressed and theories thereby altered, not in the "modernity" of methodology employed.
S.J. Gould in: "Dinosaur in a haystack." (1996)

11. Het uitbreiden van de veestapel met soorten die aan lokale omstandigheden zijn aangepast (zoals hertenzwijn, waterschildpad, of leguaan), kan niet alleen de effectiviteit van de vleesproduktie verhogen zonder ingrijpende aantasting van de leefomgeving (zoals bij het invoeren van runderen of geiten), maar levert ook interessante culinaire mogelijkheden op.
vrij naar E.O. Wilson in: "The diversity of life." (1992)

12. Het argument dat proefboringen naar olie in de Waddenzee slechts een "marginaal effect" hebben op het milieu is juist een reden dergelijke ondernemingen te weren, aangezien de ene marginale aantasting na de andere een sluipend en oncontroleerbaar afbrokkelen van de natuurwaarden ten gevolge heeft.

13. De onzorgvuldigheid en ongeïnteresseerdheid waarmee onze taal behandeld wordt versnelt het historische slinken van het Nederlands taalgebied (Duinkerken, Rijssel, Robeke).

14. In West-Europa is de levensverwachting het hoogst, maar worden ouderen hoe langer hoe meer uit het maatschappelijk leven geweerd.

15. Zeer grote verdraagzaamheid is vaker het gevolg van desinteresse dan van betrokkenheid.

16. Het kijken naar vogels heeft zijn wortels in een weemoedig verlangen om zelf te kunnen vliegen.

Stellingen bij het proefschrift:
"The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning, and fisheries." van Leo Nagelkerke.

7 oktober 1997