

Lake Tana: Source of the Blue Nile

Jacobus Vijverberg, Ferdinand A. Sibbing, and Eshete Dejen

Abstract At 1,830 m altitude, Lake Tana is situated on the basaltic Plateau of the north-western highlands of Ethiopia covering an area of ca 3,050 km². It is poor in nutrients and the source of the Blue Nile River (Great Abbay), with a catchment area of ca 16,500 km². The Lake has been formed by volcanic activity, blocking the course of inflowing rivers in the early Pleistocene times ca 5 million years ago. The lava also separated the Lake and its headwaters from the lower Blue Nile basin by 40 m high falls at Tissisat, 30 km downstream from the Blue Nile outflow. Terraces suggest that the Lake was originally much larger than it is today. Seven large permanent rivers feed the lake as well as ca 40 small seasonal rivers. The main tributaries to the lake are Gilgel Abbay (Little Nile River), Megech River, Gumara River and the Rib River. Together they contribute more than 95% of the total annual inflow. The Blue Nile is the only outflowing river. The shallow lake (average depth 8 m, max. depth 14 m) is Ethiopia's largest lake, containing half the country's fresh-water resources, and the third largest in the Nile Basin. In the main rainy season (July–August) the inflowing rivers carry heavy load of suspended silt into the lake, thereby increasing the turbidity of the lake water. The suspended sediments reduce the under water light intensity and as such the primary production, the basis of the food web. The fish community of the Lake is dominated by cyprinid fishes, 20 of the 27 fish species (e.g. *Labeobarbus* spp., *Barbus* spp., *Garra* spp.) are endemics

J. Vijverberg (✉)

Netherlands Institute of Ecology (NIOO-KNAW), Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands
e-mail: j.vijverberg@nioo.knaw.nl

F.A. Sibbing

Experimental Zoology Group, Wageningen Institute of Animal Sciences, Marijkeweg 40, 6709 PG Wageningen, The Netherlands
e-mail: Nand.Sibbing@wur.nl

E. Dejen

Fishery and Other Aquatic Life Research Center, P.O. Box 794, Bahir Dar, Ethiopia
e-mail: dejeneshete@yahoo.com

to the Lake catchment. This speciation was possible because the incipient Lake offered new habitats for adaptive radiation and maintained its isolation for millions of years from the lower Blue Nile. Wetlands are located all around the lake, with the exception of the Northeast. Together they are the largest in the country and integral parts of the complex Tana-ecosystem. They consist of permanent swamps, seasonal swamps, and areas subjected to regular inundation. During the raining period these wetlands are connected with the lake. They act as nurseries for most of the fish populations in the lake, and serve as breeding ground for water fowl and mammals. Around the lake and its catchment, including the town of Bahir Dar, live about 2 million people. This lake and adjacent wetlands provide directly and indirectly a livelihood for more than 500,000 people. The Blue Nile drains the NE Ethiopian Plateau (total catchment: 324,000 km²). Already in ancient Egypt civilization this river was of key importance to early agriculture and today the river is still of critical importance for the economies of Sudan and Egypt.

1 The Lake

At 12°N, 37°15'E, and 1,830m altitude, Lake Tana is situated on the basaltic plateau of the north-western highlands of Ethiopia covering an area of ca 3,050 km². It is the source of the Blue Nile River (Great Abbay), with a catchment area of ca 16,500 km² (Fig. 1). Compared to other lakes in the region, the lake has a small catchment to lake area ratio. Seven permanent rivers feed the lake as well as ca 40 small seasonal rivers. The main tributaries to the lake are Gilgel Abbay (Little Nile River), Megech River, Gumara River and the Rib River (Fig. 2). Together they contribute more than 95% of the total annual inflow (Lamb et al., 2007). The Blue Nile is the only outflowing river. The shallow lake (average depth 8 m, max. depth 14 m) is Ethiopia's largest lake, containing half the country's freshwater resources, and the third largest in the Nile Basin.

Based on chemistry, Lake Tana is mesotrophic (Teshale et al., 2001), but based on chlorophyll content and primary production it is oligotrophic (Wondie et al., 2007). Its bottom substrate is volcanic basalt mostly covered with a muddy substratum with only little organic matter (Howell & Allan, 1994). Most of the 37 islands in Lake Tana are small. Two larger islands used to be the seat of Ethiopian Emperors in the distant past. Almost all islands harbour ancient Ethiopian Orthodox Christian churches and monasteries, generally originating from 12–14th century. Daily ferry services transport goods and link major towns around the lake. Tourist traffic is increasing over the last decade offering boat tours for bird watching and visiting monasteries.

Bahir Dar (also written as Bahar Dar), located on the southern border of the lake, is a Regional capital with ca 180,000 inhabitants. Around the lake and its catchment, including the town of Bahir Dar, live about 2 million people. The area around

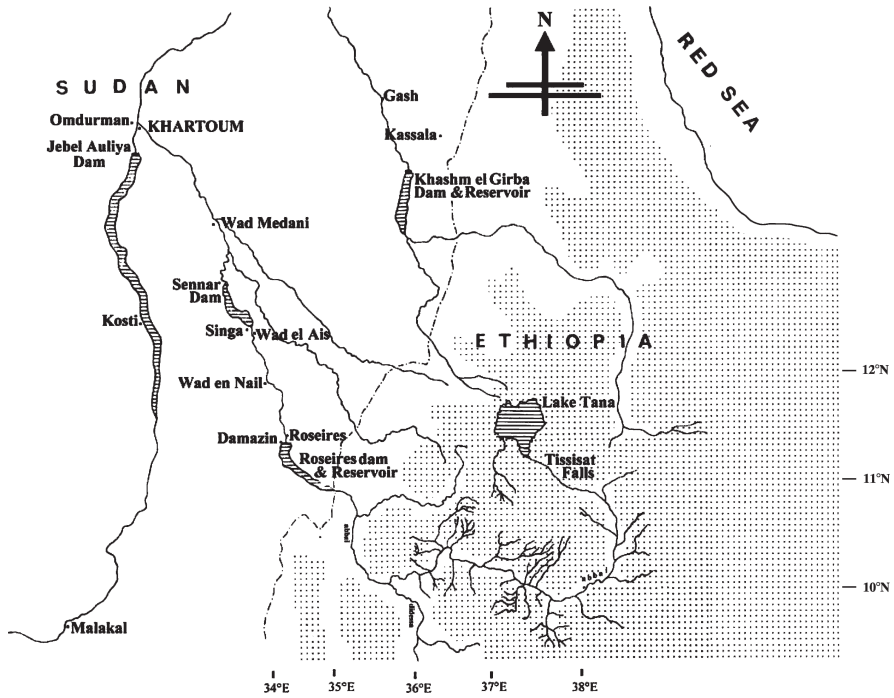


Fig. 1 Map of the Blue Nile system and the location of four large reservoirs in the Sudan of which two, Roseires and Sennar reservoirs, are in the Blue Nile River. Note Lake Tana, the source of the Blue Nile, the Tassisat Falls, 30km south of L. Tana and the numerous tributaries in the semi circular sweep of the Blue Nile Gorge on its way to the Sudan–Ethiopian border. Dotted areas are over 1,500 m asl (modified after Rzóska, 1976b)

the lake has been cultivated for centuries. This lake and adjacent wetlands provide directly and indirectly a livelihood for more than 500,000 people.

2 Wetlands

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 and by steep rocks in the west and north-west. Wetlands are located all around the lake, with the exception of the Northeast. Together they are the largest in the country and integral parts of the complex Tana-ecosystem. They consist of permanent swamps, seasonal swamps, and areas subjected to regular inundation (Kindie, 2001). During the raining period these wetlands are connected with the lake. They act as nurseries for most of the fish populations in the lake, and serve as breeding ground for water fowl and mammals. Most probably, about half of the *Labeobarbus*

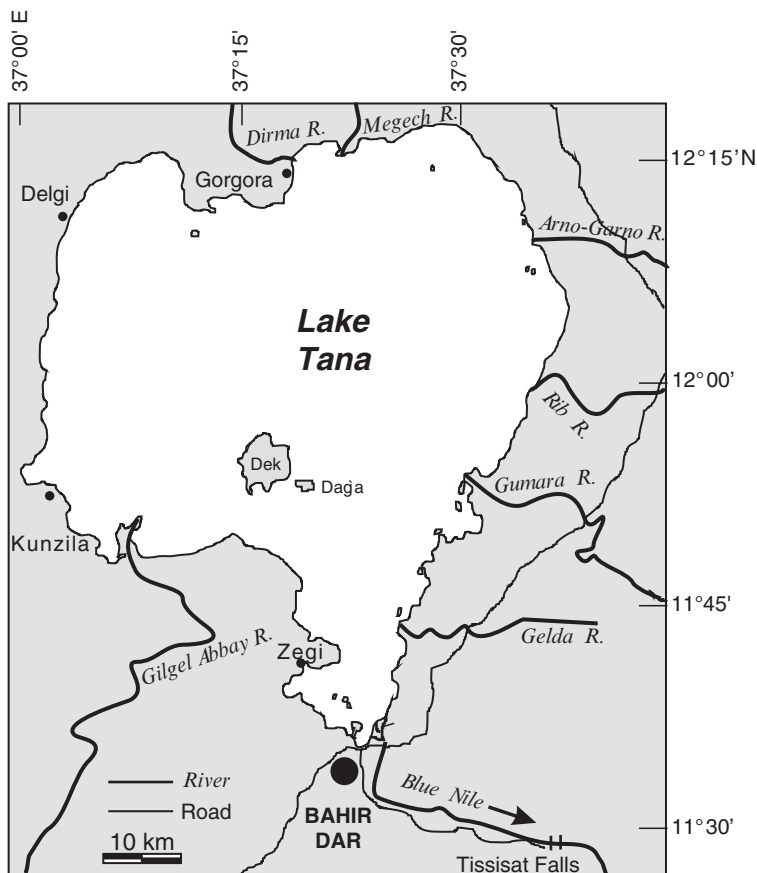


Fig. 2 Map of Lake Tana showing the Gulf of Bahir Dar, where most studies were carried out, the major tributaries and the only outflowing river: the Blue Nile (Abbay) and its falls at Tassisat (modified after Palstra et al., 2004)

species and certainly three other commercially important fish species, Nile tilapia (*Oreochromis niloticus*), African catfish (*Clarias gariepinus*) and Beso (*Varicorhinus beso*) spawn here and their juveniles feed and grow here during the first years of their life.

The littoral region of the eastern and southern part of the lake is dominated by papyrus reed (*Cyperus papyrus*), common cattail (*Typha latifolia*) and common reed (*Phragmites karka*), whereas *Persicaria senegalensis*, hippo grass (*Vossia* spp.), bullrush (*Scirpus* spp.) and *Nymphaea lotus* are common (Muluneh, 2005). Common submersed macrophytes are *Ceratophyllum demersum* and *Vallisneria spiralis*. These wetlands are important resources that supply essential raw materials as fire wood, common reeds (*Typha*, *Phragmites*) and papyrus. When the lake level drops during the dry season hundreds of km² of dry lake area become available for agriculture and are used by the farmers to grow crops. The wetlands around the

southern Bay of Bahir Dar alone cover ca 1,170 km². These wetlands have water for ca 4 months and it is the country's largest rice production area. The livelihoods of ca 3,000 Negada people are totally dependent on the wetland products.

3 Origin and Geology

Lake Tana has been formed by volcanic activity, blocking the course of a number of rivers in early Pleistocene times, ca 5 million years ago (Mohr, 1962). The lava also most likely created the waterfalls at Tissisat (Figs 1 and 2), separating the Lake Tana headwaters from the lower Blue Nile basin. Terraces suggest that the Lake was originally much larger than it is today (Rzóska, 1976a).

Recently collected geophysical and core data show nearly 100 m of accumulated sediments in the lake's bottom substrates (Lamb et al., 2007). In these sediments desiccation layers indicate that the lake dried out at apparent regular intervals during the later stages of the last Ice Age 10,000–25,000 years ago. The data indicate that Lake Tana dried completely out between 18,700 and 16,700 calibrated age (cal) BP, when stiff sediments at the base of the core were deposited. Periphytic diatoms and peat at the base of a core from the deepest part of the lake overlie compacted sediments, indicating that desiccation was followed by development of shallow-water environments and papyrus swamp in the central basin between 16,700 and 15,100 cal BP. As the lake level rose, surface water evaporation from the closed lake caused it to become slightly saline, as indicated by halophytic diatoms. An abrupt return to freshwater conditions occurred at 14,750 cal BP, when the lake overflowed into the Blue Nile (Lamb et al., 2007). Since the lake dried up between 18,700 and 16,700 cal BP, the evolution of the *Labeobarbus*, *Barbus* and *Garra* species, probably took 15,000 years or less. Interestingly, the same happened around the same time in Lake Victoria, where a species flock of *Haplochromis* species evolved in a similarly short time (Johnson et al., 1996).

4 Climate and Water Levels

The climate is typical of semi-arid regions close to the Equator, with a high diurnal temperature variation between day time extremes of 30°C to night lows of 6°C. For a tropical lake, L. Tana has relatively low water temperatures (Dejen et al., 2004), varying only within small limits (range: 20.2–26.9°C) (Table 1). Rainfall may reach up to 2,000 mm per year falling in one rainy season from May to October with one peak during July–August (Fig. 3). The total annual inflow of water to the lake is $10.3 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ and the outflow as Blue Nile River is ca 36% of this, i.e. $3.7 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$. The water residence time is ca 3 years (Teshale, 2003). This large difference between inflow and outflow is caused by the high evaporation losses. During October to June evaporation exceeds input via rainfall and during this time many of the inflowing streams dry up completely (Molla & Menelik, 2004). Besides rainfall, two water resources developments have been recently constructed.

Table 1 Environmental characteristics at Southern Gulf of L. Tana from March 2000 to February 2002, annual means ± 1 SD, range and the month of minimum and maximum values. Data from Dejen et al. (2004)

Variable	Mean \pm SD	Range	Month Minimum	Month Maximum
Temperature ($^{\circ}$ C)	23.2 \pm 1.5	20.2–26.9	January	May
Conductivity (μ S cm^{-1})	132.8 \pm 11.2	115–147.9	October	February
Chlorophyll-a ($\mu\text{g l}^{-1}$)	6.4 \pm 1.1	3.4–12.9	March	January
Oxygen (mg l^{-1})	6.7 \pm 0.5	5.9–7.3	December	April
pH	7.7 \pm 0.6	6.8–8.3	August	January

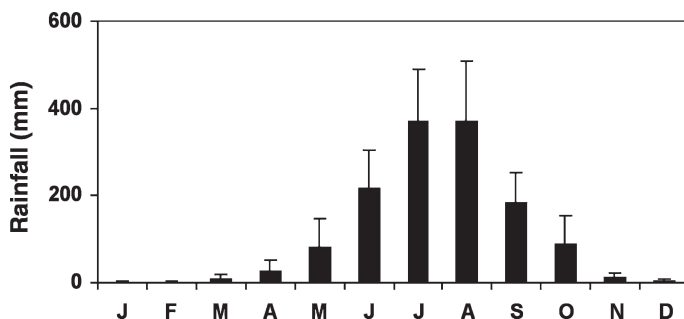


Fig. 3 Mean rainfall for the 10-year period 1992–2002. Error bars represent 1 SD (modified after Wondie et al., 2007)

Around 1995 at the mouth of the Blue Nile a water level regulation weir has been constructed and 30 km downstream of the Blue Nile outflow the Tissisat hydropower plant was built. The construction of the weir serves to increase the water supply for the hydropower plant during the dry season, which is continuously using water from the lake. The 78 MW power plant is connected to the national electricity net and provides electricity for a large part of the country. Water use for the hydroelectric power plant is especially high during the dry season (February–May) because during this time of draught this is often one of the few hydropower plants still operating in the country.

The complex pattern of water losses and inputs can cause large daily and seasonal water level fluctuations. Water levels are highest at the end of the main-rainy season and during the post-rainy period, slowly decreasing to a minimum around the end of the dry season (Fig. 4). The difference between the minimum water level in May–June and the maximum in September–October is generally 2.0–2.5 m. There is a clear trend of decreasing water levels over recent years.

Predominantly southerly winds prevail from January to July, but northerly from August until November (Gasse, 1987). The lake is well exposed to the winds since it is shallow and not protected by vegetation, except on the south-west side which is forested (Zegi Peninsula). Wind speeds show a pronounced diurnal pattern, during the night and morning wind speed is generally below 1.5 m s^{-1} , but in the afternoon starting at noon and going on until the evening (7 pm) wind speeds are generally between 3.0 and 4.8 m s^{-1} . Although a stable thermocline is lacking (Dejen et al.,

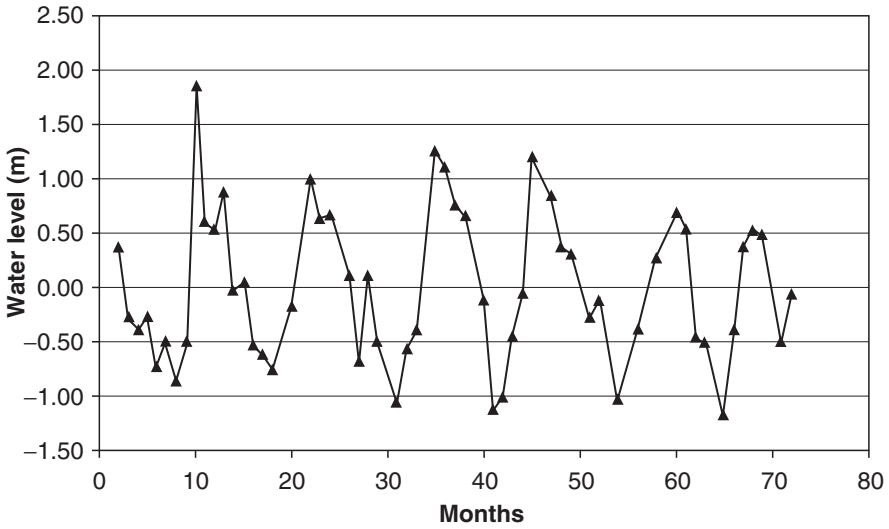


Fig. 4 Temporal variation of relative water level (meters) of Lake Tana’s surface during 1996–2002 (source: European Space Agency)

2004), a thermal stratification of short duration (i.e. several hours) may occur especially during the dry season in the morning.

5 Erosion and Silt Load

During the last 15 years deforestation became common practise in the Lake Tana catchment, facilitating conditions for soil erosion. The catchment area of the Lake (ca 16,500km²) has a dendritic type of drainage network. Due to this type of drainage, scanty vegetation and high rainfall during short periods in the main rainy season, the soil loss rate from areas around the lake is high (31–50 tons ha⁻¹ yr⁻¹) and showed a substantial increase during recent years. Soil loss rates are especially high in the eastern part of the lake, i.e. 5–250 tons ha⁻¹ yr⁻¹, and lowest on the western side of the lake (Teshale et al., 2001; Teshale, 2003).

In the main rainy season (July–August) the four major inflowing rivers carry heavy load of suspended silt into the lake, thereby increasing the turbidity of the lake water (Fig. 5) (Wondie et al., 2007). The suspended sediments reduce the under water light intensity and as such the primary production, the basis of the food web.

6 Nutrients, Water Mixing and Primary Production

The lake is characterised by low nutrient concentrations, and a low water transparency due to high silt load of the inflowing rivers during the rainy seasons (May–October) and daily resuspension of sediments in the inshore zone (Table 1, Fig. 5).

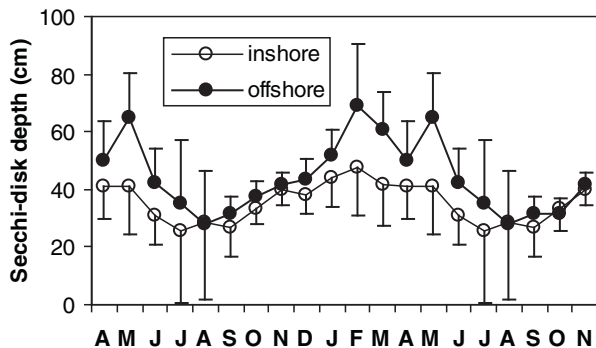


Fig. 5 Seasonal variations in water transparency at inshore (open symbols) and offshore stations (closed symbols) of Lake Tana measured as Secchi-disk depth (cm) for the period April 2003 to November 2004. Error bars represent +1 SD for the offshore and -1 SD for the inshore zone. Sampling at six sites all around the lake (with the exception of the western part), each with one sampling station inshore (ca 250 m from the shore at depth <3.5 m), and one station offshore (ca 1,500 m from the shore at depth >4 m). Six observations per sampling date for inshore and offshore zone, respectively. Note that the transparency is lowest inshore in the rainy season (modified after Wondie et al., 2007)

The phytoplankton was dominated by Cyanobacteria and Bacillariophyceae; Chlorophyta were less abundant (Wondie et al., 2007). Cyanobacteria were dominant in the post-rainy season (October–November), whereas diatoms were dominant during the dry (December–April) and the pre-rainy season (May–June). Cyanobacteria were dominated by two *Microcystis* species of which *M. flos-aquae* was the most abundant and *Anabaena flos-aquae*, *Planktolyngbya limnetica* were co-dominant. Diatoms are dominated by *Melosira varians* and five species of *Aulacoseira* (formerly named *Melosira*) *A. assizi*, *A. ambigua*, *A. granulata*, *A. muzzanensis* and *A. distans*, of which *A. granulata* is the most dominant (>50% of *Aulacoseira* spp. combined). *Staurostrum triangularis* dominated the Chlorophyta. The mean chlorophyll-a concentrations varied seasonally and ranged from 2.6–8.5 mg m⁻³ (mean: 4.5 mg m⁻³) in the offshore zone (Wondie et al., 2007). Gross primary production in the offshore zone averaged 2.43 g O₂ m⁻² d⁻¹ and ranged between 0.03 and 10.2 g O₂ m⁻² d⁻¹; production was significantly higher inshore. The highest production rates were observed in the post-rainy season (October–November) which coincided with a bloom of *Microcystis* and higher chlorophyll levels. This seasonal high production is probably caused by a relatively high nutrient availability in combination with favourable light conditions.

The gross primary production rates of L. Tana are among the lowest, compared with other tropical lakes (Wondie et al., 2007). This is primarily the result of the oligotrophic nature of the lake in combination with its relatively low water transparency. The gross primary production per unit chlorophyll in the offshore zone was in the same range as in 30 other tropical lakes and reservoirs. A large proportion of the annual primary production is realised in one of the four seasons only. This productive

post-rainy season is relatively short (2 months) and therefore efficiency of transfer of matter between the first and second trophic level of the Lake ecosystem will be poor.

7 Benthic Invertebrates

Macrobenthic invertebrates such as oligochaetes, *Chaoborus* spp. and chironomids, show low densities both inshore and offshore (Vijverberg, unpublished; Tewabe et al., 2005). Chironomid larvae showed also low densities in the zone with submersed macrophytes (*Ceratophyllum demersum*) near the shore, but because of their relative large individual size macrobenthic biomass per m² was highest in this area. However, this area is very small (<1%) compared to the surface area of the lake. In contrast the microbenthic ostracods show relatively high densities in the inshore zone (4,000–60,000 ind m⁻²), but were lacking in the offshore area of the lake. The low densities of benthic invertebrates may be caused by the low content of organic matter in the bottom substrates, which consists of volcanic basalts usually covered with a muddy substratum, transported by the inflowing rivers, which contains only little organic matter. The organic matter content in the offshore substrates is only ca 1.2%, but slightly higher values of ca 3.8% are found near to the shore at a depth of ca 0.25 m (Tewabe et al., 2005).

8 Macrofauna Associated with Macrophytes

The macrofauna associated with macrophytes of the submersed vegetation (*Ceratophyllum demersum*), the low emergent vegetation (dominated by *Persicaria senegalensis*) with submersed vegetation present, and the 100–200 cm high emergent vegetation dominated by reeds (*Phragmites karka*) and bulrush (*Typha latifolia*) with submersed vegetation present were studied by Vijverberg (unpublished) and Tewabe et al. (2005). Densities and biomass of macrofauna taxa in the macrophyte beds – sampled with a sweep net – are relatively high. Especially Ephemeroptera (mayfly larvae) and Odonata (dragonfly larvae) showed relatively high densities, whereas densities of Acari (water mites), chironomids, gastropods and Hemiptera (water bugs) were relatively low. In terms of biomass Odonata dominate the weed beds, due to their large individual weight, but Ephemeroptera showed the highest densities. Dumont (1983) reported 14 species of adult dragonflies along the shores of L. Tana at Bahir Dar (see also Dumont, 2009). Tewabe et al. (2005) observed the highest densities (1,000–1,600 ind m⁻²) of Ephemeroptera larvae in December–February, intermediate densities (200–500 ind m⁻²) in March and October–November and very low densities (0–100 ind m⁻²) in April–September. Gastropods include the endemic subspecies *Bellamaya unicolor abyssinica* and *Bulinus* spp., host to *Schistosoma haematobium*, the trematode causing bilharzia (Bacci 1951/52). Of the 15 species observed 4 are of palearctic origin, i.e. *Theodoxus africanus* (Reeve), *Radix pereger* (Müll), *Unio elongatulus dembeae* (Slowerby) and *Unio abyssinicus* Martens.

9 Crustaceans and Zooplankton

The largest crustaceans are freshwater crabs of the genus *Potamonautes*, but they are fairly rare (Nagelkerke, 1997; see also Cumberlidge, 2009). Since these species are generally associated with flowing water higher densities are expected to be present in the inflowing rivers and the Blue Nile. There have been few previous studies on zooplankton in Lake Tana. The first general account of the aquatic fauna and flora of the lake was documented by Brunelli and Cannicci (1940) and Rzóska (1976a). The freshwater medusa *Limnocyclus indica* has been cited regularly during the last 30 years (Thiel, 1973; pers. obs.), but the species living in Lake Tana may really be *L. tanganjikae* (see Dumont, 2009). The densities of littoral Cladocera are relatively low (Brunelli & Cannicci, 1940; Dumont, 1986a).

Zooplankton dynamics were recently studied by Dejen et al. (2004). Of the limnetic species, four copepods and nine cladocerans were identified, 11 of these together contributed more than 99% of all individuals collected (Table 2). Approximately half of the numbers encountered were copepods and the other half cladocerans. The calanoid copepod *Thermodiaptomus galebi lacustris*, dominated the zooplankton community, and is endemic for L. Tana. Of the three cyclopoid copepod species, *Thermocyclops ethiopiensis* was the most abundant. *Bosmina longirostris*, *Daphnia hyalina*, *Daphnia lumholtzi* and *Diaphanosoma sarsi* were the most abundant cladoceran species. Of the two rarely encountered species, *Microcyclops varicans* and *Chydorus sphaericus*, the latter species is probably predominantly littoral and associated with macrophytes. We observed it offshore in low densities, but we found high abundances in the gut

Table 2 Microcrustacean zooplankton species found in Lake Tana with their mean relative abundance (n, %). Data from Dejen et al. (2004)

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

♦ = also present in the Blue Nile River (Dumont, 1986a).

contents of littoral feeding fish. *Daphnia hyalina* was identified following Flössner (2000) and confirmed by using mitochondrial DNA sequences from the small subunit ribosomal RNA (Schwenk et al., 2000). This species was not reported before in Lake Tana, but was probably previously wrongly identified as the closely related *D. longispina* (see Dumont, 1986a).

Annual production of the calanoid *T. galebi* and total cyclopoid copepods was similar, ca 380 and 310 mg dwt m⁻³ respectively, which is low when compared to other tropical lakes (Wondie & Mengistu, 2006). The zooplankton community structure of L. Tana is unusual for tropical lakes because of its relatively high proportion of temperate species, i.e. *Daphnia hyalina*, and *Ceriodaphnia dubia*. Most probably this effect is due to its high altitude resulting in relatively low water temperatures in the lake. The addition of temperate species to its zooplankton community resulted in a relatively high biodiversity of limnetic microcrustacean zooplankton in this lake. Significant temporal differences in copepod and cladoceran abundance were observed, with highest densities during the dry season. Zooplankton abundance was negatively affected by turbidity, but not all species were affected to the same degree. *Daphnia* spp. were most strongly affected and *Diaphanosoma* spp. to the least extent. Cladocerans showed significant higher densities in the sublittoral zone, but copepods showed similar densities in littoral, sublittoral and offshore.

10 Fish Species

Twenty of the 27 fish species of Lake Tana are endemics to the Lake Tana catchment (Table 3). This speciation was possible because the incipient Lake offered new habitats for adaptive radiation and maintained its isolation since ca 5 million years from the lower Blue Nile basin by 40m high falls (Fig. 6), 30km downstream from the Blue Nile outflow (Fig. 2) (Sibbing et al., 1998). In case of the *Labeobarbus* species (15 endemic species out of 16), their niche divergence was responded by a divergence in their immune system, since molecules involved in recognizing different antigens differentiated accordingly during evolution (Dixon et al., 1996; Kruiswijk et al., 2005).

There is only one cichlid, *Oreochromis niloticus* (Nile tilapia), which is the most widespread tilapia species in Africa. This species is predominantly a herbivore, feeding on macrophytes, algae and detritus (Table 3). The catfish family (Clariidae) is also presented by a single species, *Clarias gariepinus* (African catfish), the most common member of its genus. This species is a facultative piscivore, feeding occasionally besides fish also on zooplankton, benthic invertebrates and algae. The obscure loach, *Nemacheilus abyssinicus* (Balitoridae), was only once found in the Lake itself (Nagelkerke, 1997), and was also found in small streams of the Lake Tana catchment and in large parts of the Ethiopian high plateau (Dgebuadze et al., 1994). Interestingly, this loach is the only species from this Palaeartic family known from Africa.

The most species-rich fish family in the lake are the cyprinids, represented by four genera: *Varicorhinus*, *Garra*, *Labeobarbus* and *Barbus*. *Varicorhinus* is represented

Table 3 The fish species of Lake Tana, their taxonomic group, maximum length (Fork Length, cm), relative abundance, food and habitat

Family	Species	Maximum Length (FL, cm)	Abundance	Food	Habitat
Balitoridae	<i>Nemacheilus abyssinicus</i>	3.6	Rare	Algae	Benthic
Cichlidae	<i>Oreochromis niloticus</i> ♦	40	Common	Macrophytes, algae-detritus	Pelagic, littoral, sublittoral
Clariidae	<i>Clarias gariepinus</i> ♦	70	Common	Fish, zooplankton, benthic invertebrates, algae	Pelagic, littoral, sublittoral
Cyprinidae	<i>Barbus tanapelagius</i> *	8.9	Common	Zooplankton	Pelagic, sublittoral, offshore
	<i>B. humilis</i>	9.6	Common	Zooplankton, benthic invertebrates	Benthic, littoral, sublittoral
	<i>B. pleurogramma</i> *	4.0	Common	Benthic invertebrates	Benthic, wetlands, flood planes
	<i>Garra dembecha</i>	17.0	Common	Algae	Benthic
	<i>Garra dembeensis</i> ♦	12.0	Rare?	Algae	Benthic
	<i>G. regressus</i> *	13.5	Common	Algae	Benthic
	<i>G. tana</i> *	12.0	Common	Algae	Benthic
	<i>Labeobarbus acutirostris</i> *	41	Common	Fish	Benthic, inshore
	<i>L. brevicephalus</i> *	32	Common	Zooplankton, adult insects	Pelagic, sublittoral, offshore
	<i>L. crassibarbus</i> *	51	Common	Detritus, benthic invertebrates	Benthic, sublittoral, offshore
	<i>L. dainellit</i> *	49	Occasional	Fish	Littoral
	<i>L. gorgorensis</i> *	62	Occasional	Benthic invertebrates, bivalves	Pelagic, littoral, sublittoral, offshore

<i>L. gorguari*</i>	53	Occasional	Fish	Littoral
<i>L. intermedius</i> ♦	49	Common	Benthic invertebrates, gastropods, macrophytes	Benthic, littoral
<i>L. longissimus*</i>	61	Occasional	Fish	Pelagic, littoral, sublittoral
<i>L. macrophthalmus*</i>	43	Common	Fish, benthic invertebrates, detritus	Pelagic, sublittoral, offshore
<i>L. megastoma*</i>	82	Common	Fish	Pelagic, littoral, sublittoral, offshore
<i>L. nedgia*</i>	71	Common	Insect larvae, benthic invertebrates	Benthic, littoral
<i>L. osseensis*</i>	29	Rare	Adult insects, macrophytes	Littoral
<i>L. platydorsus*</i>	64	Common	Fish, insect larvae, molluscs, detritus	Benthic, sublittoral, offshore
<i>L. surkis*</i>	43	Occasional	Macrophytes, algae, benthic invertebrates	Pelagic, sublittoral
<i>L. truttiformis*</i>	44	Occasional	Fish	Pelagic, sublittoral, offshore
<i>L. tsanensis*</i>	39	Common	Insect larvae, gastropods, benthic invertebrates	Benthic, sublittoral, offshore
<i>Varicorhinus beso</i> ♦	36	Common	Benthic algae	Benthic, littoral

* = endemic to Lake Tana catchment. Data from Nagelkerke and Sibbing (2000), De Graaf et al. (2006), Dejen et al. (2006a) and Vijverberg (unpublished).
 ♦ = also present in the Blue Nile River (Abu Gideiri, 1967; Banister, 1973). Habitats refer to: benthic = predominantly present near the bottom in the lower part of the water column, pelagic = predominantly present in upper part of the water column, littoral = inshore with or without macrophytes (0–4 m deep), sublittoral = inshore without macrophytes (4–8 m deep), offshore = openwater (8–14 m deep).



Fig. 6 The high (40m) Tissisat Falls ('The smoking waters falls'), 30 km downstream from the Blue Nile outflow. The falls effectively isolate the lake's fish community from the lower Nile basin. During the rainy season the waterfall is 400m wide and is the second largest of Africa (photo by F.A. Sibbing) (see *Color Plates*)

by a single species *V. beso* Rüppell which scrapes algae from substrates, and a common species in the rivers and lakes of the Ethiopian Highlands. The genus *Garra* is represented by four species in Lake Tana, *G. dembecha* Boulenger which is common and generally distributed in the Ethiopian Highlands, *G. dembeensis* Rüppell which is widely distributed all over Africa and although common in Ethiopia rare in Lake Tana, and two endemic species, *G. regressus* and *G. tana*, recently described by Stiassny and Getahun (2007). All four species are algivorous.

Fifteen large (max. 82 cm fork length, FL) hexaploid labeobarbs (*Labeobarbus* spp.) (Fig. 7, Table 3) belong to a unique species flock of endemic cyprinids as was supported by mtDNA markers (de Graaf et al., 2003c). Surprisingly eight of these are piscivores (de Graaf et al., 2003a, 2008). Many of the labeobarb species predominantly inhabit the large offshore zone as adults, whereas the juveniles probably occupy the inshore zone among macrophytes and/or in the adjacent wetlands. The only non-endemic labeobarb species present, the polymorph shore complex of *L. intermedius*, is probably most ancestral to this labeobarb species flock and a riverine generalist who feeds mainly on macrofauna associated with macrophytes and benthic invertebrates. *Labeobarbus intermedius* can be found all over Ethiopia in lakes and rivers (Banister, 1973). The fish community contains, furthermore, three diploid species of small (<11 cm FL) barbs: *Barbus humilis* Boulenger, *B. pleurogramma* Boulenger and the recently discovered *B. tanapelagi* (de Graaf et al., 2000). The latter two species are endemic to the



Fig. 7 A large *Labeobarbus megastoma* caught by commercial fishermen (photo by F.A. Sibbing) (see Color Plates)

L. Tana catchment, *Barbus pleurogramma* is mainly present in the wetlands around the lake, whereas *B. tanapelagius* is common in the large pelagic zone of the lake. *B. humilis* was assumed to be endemic to Lake Tana too, but was recently collected from the Beshilo River in the Ethiopian Plateau (Amhara Region, Wollo province). The last two named species have a long breeding period (from March to September) and the distinct bimodal size frequency distribution of eggs suggest multiple spawning for both species. The range of fecundity in both species (172–339 eggs per gram) was low compared with small lacustrine cyprinids and clupeids from other African lakes (Dejen et al., 2003).

11 Evolution of *Barbus* and *Labeobarbus* Species

Barbus humilis is a riverine species, distributed in the littoral and sublittoral of the Lake and its inflowing rivers. Most likely *B. tanapelagius* evolved out of a *B. humilis* like ancestor following the rise of large pelagic zooplankton resources after the lake filled again with water approximately 15,000 years BP. Investigations on the phylogenetic relationships of the two barbs using the mtDNA cytochrome b gene showed that the genetic divergence between the two species is very low (de Graaf et al., 2007).

The 15 large labeobarb species (*Labeobarbus*) compose a world unique concentration of endemic cyprinid fish (Nagelkerke & Sibbing, 2000). The species occupy different habitats as characterised by water depths and substratum types (Nagelkerke et al., 1994). Seven of these species do not spawn in the lake itself,

but in the permanent rivers (de Graaf et al., 2005). These seven species do not show spatial segregation among inflowing rivers but significant temporal segregation occurs in aggregating in the river mouths and in migrating towards the upstream spawning areas during the breeding season (June–October). Among the eight other species, peak gonad development occurs generally in the same period as in the riverine spawners, but they do not aggregate in the river mouths during the breeding period and are absent from the upstream spawning areas (Palstra et al., 2004). Most probably, they spawn in the wetlands where also their juveniles feed and grow, possibly extending their spawning season beyond the two rainy months.

Evolution most likely went according to the following scenario (Nagelkerke & Sibbing, 1996). After Lake Tana was formed, through volcanic blocking of the Blue Nile River, a population of riverine labeobarbs was present. This was probably a species resembling the riverine *L. intermedius*, which to day is still found all over Ethiopia both in rivers and in lakes. The *L. intermedius* populations are known to be highly variable in morphology (Mina et al., 1996). After Lake Tana was formed, an extensive new lake area, providing new lacustrine habitats with their specific resources, became available. Around this time a wave of habitat radiation probably occurred, followed by a trophic radiation (de Graaf et al., 2008). The incipient morphotypes might have radiated into different niches driven by competition for space and trophic resources. This sequential adaptive radiation probably started from the inshore areas which, because of the presence of macrophyte vegetation, look more like a riverine habitat than the offshore zone of the lake. Genetically based morphological differentiation resulting from disruptive selection became fixed by assortative mating. In the riverine spawning species this occurred by temporal segregation during the aggregating phase in the river mouths and during the migration phase towards the upstream spawning areas. How segregation occurred among the species presumably spawning in wetland areas is not known.

12 Fish Community Structure and Food Utilisation

The *Barbus* and *Labeobarbus* species dominate the fish community in terms of biomass and production (Fig. 8). The total annual *Labeobarbus* production was ca 32 kg ha⁻¹ yr⁻¹, of which the piscivorous *Labeobarbus* species account for 12% (3.8 kg ha⁻¹ yr⁻¹) (Wudneh, 1998). Annual production of *B. humilis* was ca 3.7 kg ha⁻¹ yr⁻¹, based on a P/B ratio of 3.94. For *B. tanapelagius* this amounts to 23.6 kg ha⁻¹ yr⁻¹, given a P/B ratio of 3.88. Total annual production of both small barb species in Lake Tana is estimated at 27.3 kg ha⁻¹ yr⁻¹ (Dejen et al., submitted).

Zooplankton is highly utilised by the fish community (Dejen et al., 2006a). The three *Barbus* spp., the juveniles of all 15 *Labeobarbus* spp. and the adults of *L. brevicephalus* feed all on zooplankton. *Barbus tanapelagius* is, however, the only obligate zooplanktivore since the other species utilise also other animal food items. *Barbus pleurogramma* maintains the most benthivorous diet, whereas *B. humilis*, juvenile labeobarbs and *L. brevicephalus* feed for ca half (by biovolume) their

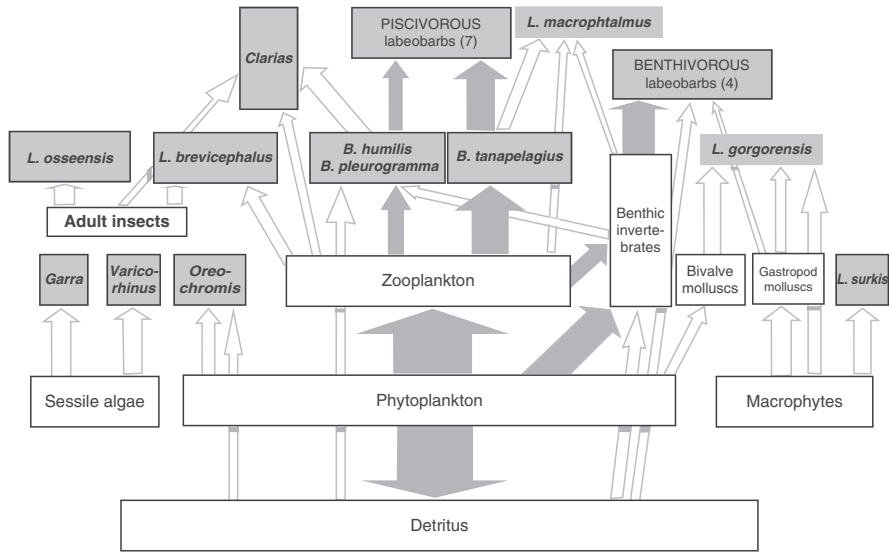


Fig. 8 Food web of L. Tana with emphasis on the fish community. Grey blocks represent fish species, white blocks food resources. Grey arrows indicate the systems main streams through zooplankton and benthos. Width of arrows reflects the contribution of a food type in the diet of a species. For benthivorous and piscivorous labeobarbs, number of species between brackets (*see Color Plates*)

diet on zooplankton and for the other half on adult floating insects, insect larvae and benthic invertebrates. *Barbus tanapelagijs* and the adults of *L. brevicephalus* occupy the same habitat, the large pelagic. They differ, however, in feeding modes and utilization of zooplankton (Dejen et al., 2006a). Both species positively select *Daphnia* as prey item. Especially *B. tanapelagijs* was infected (10%) by the cestode *Ligula intestinalis* after feeding on infected cyclopoid copepods (Dejen et al., 2006b).

Eight species of the fifteen endemic *Labeobarbus* species (more than 65% of all labeobarbs) are piscivorous, four are obligate piscivorous (>80% fish in *L. acutirostris*, *L. truttiformis*, *L. longissimus* and *L. megastoma*) and four others are facultative piscivores (>60% fish in *L. dainellii*, *L. gorguari*, *L. macrophthalmus*, *L. platydorsus*) (Sibbing & Nagelkerke, 2001). Experiments showed, however, that these piscivores are clumsy predators (de Graaf et al., 2003b) not being able to feed on fish larger than 15% of their fork length, most probably because they have a narrow pharyngeal slit and lack teeth on their oral jaws (Fig. 9). These species may only survive because specialised and more efficient non-cyprinid piscivores are lacking, whereas the abundant small barbs exactly match their potential prey size (6 cm FL barbs for a 40 cm FL labeobarb). Lake Tana is an evolutionary laboratory showing in an experiment by nature how among labeobarbs the potentials for piscivory are developed to the fullest. The piscivorous niche of these co-occurring species is segregated by habitat, diet composition and prey size (de Graaf et al., 2008). The main prey items eaten and matching their optimal prey size were *B. humilis*



Fig. 9 The 'clumsy' piscivorous labeobarbs of Lake Tana, showing lack of teeth on oral jaws and a narrow pharyngeal slit (*Labeobarbus megastoma*, photo by F.A. Sibbing) (see Color Plates)

(40% of the gut contents), *B. tanapelagi* (32%) and *Garra* species (21%). Therefore, the two small barbs form the main link between the zooplankton and the piscivorous fish in the food web of the Lake.

Besides piscivores, there are five other trophic groups of labeobarbs (Table 3, Fig. 8). One species feeds mainly on macrophytes (*L. surkis*), one upon macrophytes and molluscs (*L. gorgorensis*), one species on macrophytes and adults insects (*L. osseensis*), one species predominantly on zooplankton (*L. brevicephalus*) and four species are benthivorous feeding mainly on chironomid larvae and on macrofauna associated with macrophytes (*L. crassibarbus*, *L. intermedius*, *L. nedgia*, *L. tsanensis*).

13 Birds, Reptiles and Mammals

Lake Tana and its wetlands are rich in bird life, in total ca 215 bird species were observed of which ca 83 typical wetland species (van Perlo, 1995; Frances & Aynalem, 2007; see also Green, 2009). Piscivorous species include residents such as African spoonbill (*Platalea alba*), yellow-billed stork (*Mycteria ibis*), pied kingfisher (*Ceryle rudis*), giant kingfisher (*Megaceryle maxima*), little grebe (*Tachybaptus ruficollis*), great white pelican (*Pelecanus onocrotalus*), great and long-tailed cormorants (*Phalacrocorax carbo*, and *P. africanus*), African darter (*Anhinga rufa*), many species of herons (*Ardeola* spp., *Egretta* spp., and *Ardea* spp.), and African fish eagle (*Haliaeetus vocifer*). The density of fish eating birds is invariably higher in the shallow inshore zones of the lake and its wetlands than in the offshore region of the lake. Grey crowned crane (*Balearica regulorum*), common crane (*Grus grus*), greater flamingo (*Phoenicopterus ruber*), African open-billed stork (*Anastomus lamelligerus*), woolly-necked stork (*Ciconia episcopus*), sacred ibis (*Threskiornis aethiopicus*), glossy ibis (*Plegadis falcinellus*), Hadada ibis (*Bostrychia rara*), hamerkop (*Scopus umbretta*), Egyptian

goose (*Alopochen aegypticus*), spur-winged goose (*Plectropterus gambensis*) and the African pygmy goose (*Nettapus auritus*) are the most conspicuous non-piscivorous aquatic birds. Palaearctic migrants include osprey (*Pandion haliaetus*), great black-headed, lesser black-backed and herring gulls (*Larus ichthyaetus*, *L. fuscus*, and *L. argentatus*), and whiskered and white-winged black terns (*Chlidonias hybridus* and *C. leucopterus*) (Nagelkerke, 1997).

The largest reptiles are the Nile monitor (*Varanus niloticus*) and a python (*Python sebae*) of which the latter is rare. There are few aquatic mammals. The Hippopotami are mainly restricted to the river mouth of the Blue Nile. Otters are caught sometimes in the nets of the fishermen. Amphibians, especially Anurans are mainly present in the marshy shore-areas.

14 Fisheries

The maximum sustainable yield for Lake Tana fishery is only ca 4 kg ha⁻¹ (10,000–15,000 tons for the whole lake), which is low compared with the Ethiopian Rift valley Lakes (ca 10 kg ha⁻¹) and other tropical African lakes physically similar to Lake Tana (10–100 kg ha⁻¹) (Pitcher, 1995). There are fish processing and marketing enterprises in Bahir Dar. Traditionally, Lake Tana fisheries consisted of mainly artisanal predominantly subsistence fishery conducted from papyrus reed boats (tankwa's, Fig. 10), which resemble those of ancient Egypt. The fishermen, who are using mainly fish traps and small gill nets, are almost exclusively members of the Negede Woito tribe.



Fig. 10 A traditional fisherman of L. Tana using a papyrus reed boat (tankwa) and a fish trap made from reeds (photo by F.A. Sibbing) (see *Color Plates*)

Since 1986 a motorized commercial gillnet fishery was developed by the Ethiopian Orthodox Church in cooperation with an interchurch NGO and fishermen from Urk (Netherlands). Commercial catches of large barbs in Lake Tana initially (1987–1997) increased six fold (Wudneh, 1998). However, over the last decade they have sharply decreased, due to overfishing during fish migration to their spawning rivers (de Graaf et al., 2004; see also Chapter on Fisheries by Witte et al., 2009).

The three main species groups targeted by this fishery are a species flock of endemic, large *Labeobarbus* spp., African catfish (*Clarias gariepinus*) and Nile tilapia (*Oreochromis niloticus*) (Table 4). The commercial gillnet fisheries was monitored during 1991–1993 and in 2001 in conjunction with an experimental trawling program (de Graaf et al., 2006). In the experimental fishery large specimens of African catfish (>50 cm) and Nile tilapia (>20 cm) decreased significantly over ca 10 years time, but recruitment of young fish to the adult populations was not negatively affected. During the same period the commercial catch of riverine spawning *Labeobarbus* spp. declined with 75%. In the experimental fishery a similar decrease was observed and the populations of juvenile labeobarbs in the littoral (length range: 5–18 cm) decreased even by more than 85% (de Graaf et al., 2006). The major reason for the collapse of these fish species is due to destructive fishing during their spawning season. These species form aggregations in the river mouths in August–September, during which period they are targeted by the commercial gillnet fishery. Overfishing of labeobarbs near and in rivermouths and upstream in the rivers on and near the spawning grounds by traditional fishermen and opportunistic farmers reduced their densities to a very low level. Additionally destruction

Table 4 Lake Tana: Fish ecology and susceptibility to fisheries. Based on information from de Graaf et al. (2006)

	Labeobarbs	African Catfish	Nile Tilapia
Reproductive Biology			
Spawning period	2 months August–September	4 months June–September	All year
Spawning aggregations	River mouths	None	None
Spawning areas	Floodplains, upstream rivers	Floodplains	Floodplains
Ecology			
Diet	Specialists	Generalist with broad diet spectrum	Generalist feeding mainly on algae and detritus
Habitat	Specialists	Bottom-dwelling All over the lake	Water column Inshore zone
Growth			
Age at maturity	3–5 years	2–3 years	1–2 years Highly flexible
Susceptibility to Fisheries			
	High Vulnerable	Moderate Resilient	Low Most resilient

of spawning grounds by farmers who build small scale irrigation channels for their agricultural lands contributes to the reduced recruitment. It is clear that in case of the migrating labeobarbs recruitment-overfishing is taking place and that the seven species of this unique species flock are in danger of becoming extinct.

Fisheries on the small barbs is no common practise in Lake Tana, although small fish are caught and dried especially on the island Dek. *Barbus tanapelagius* would be the most safe target for fisheries since it is spatially segregated from the juvenile large barbs (Dejen et al., 2006a). However, night fishing using strong lights, as applied in Lake Victoria for catching *Rastrineobola*, only yields small catches in Lake Tana, probably because of its lower fish densities and its high turbidity (Eshete Dejen, pers. comm.).

15 Blue Nile

Lake Tana is the source of the Blue Nile (Great Abbay), and not as most Ethiopians believe the Little Nile (Gilgel Abbay, Fig. 2) which is the most important tributary. It springs lie ca 100km south of the lake. The Blue Nile drains the NE Ethiopian Plateau (total catchment: 324,000km²) (Fig. 1). The name 'Blue Nile' is misleading and an incorrect translation of the Arabic name 'Al Bahr al Azraq' meaning 'dark' Nile. The latter name is very appropriate because in the rainy season when the river flow rate is highest, the water has a dark reddish-brown muddy colour because of all the sediments it contains. Already in ancient Egypt civilization this river was of key importance to early agriculture and today the river is still of critical importance for the economies of Sudan and Egypt. Since L. Tana was dry between 18,700 and 16,700cal BP and did not reach overflow until 14,750cal BP, when base flow was re-established, the Blue Nile must have been reduced to an intermittent seasonal flow during 18,700–14,750cal BP. During that period without base flow, it must have been totally dependent on intermittent inflows from tributary streams in a rainfall regime that was significant drier than that of today (Lamb et al., 2007).

The source of the Blue Nile was first discovered by a Portuguese Jesuit, Fr. Pedro Paez, in 1613. The Blue Nile descends from the Ethiopian high plateau (Fig. 11). The mean annual outflow is about 3.7km³ per year, which is only ca 8% of the total flow of the Blue Nile (Teshale et al., 2001). It receives a great number of tributaries in its upper course in the Ethiopian Highlands and two more tributaries in its lower course in Sudan. Although the Blue Nile flows for fewer miles than its sister the White Nile and has a relative small drainage area, it carries 60–69% of the total discharge and a vastly greater proportion of its transported sediment (Dumont, 1986b). Most of the water flows during the rainy season from May to October each year. Annual river flow is on average ca 46km³, but there are strong annual variations associated with variations in rainfall (Conway, 2000).

After leaving the lake the Blue Nile flows to the south-east before descending over the high (ca 40m) Tissisat Falls ('Smoking waters' falls), 30km downstream from its outflow (Figs 1 and 2). The falls effectively isolate the lake's fish community

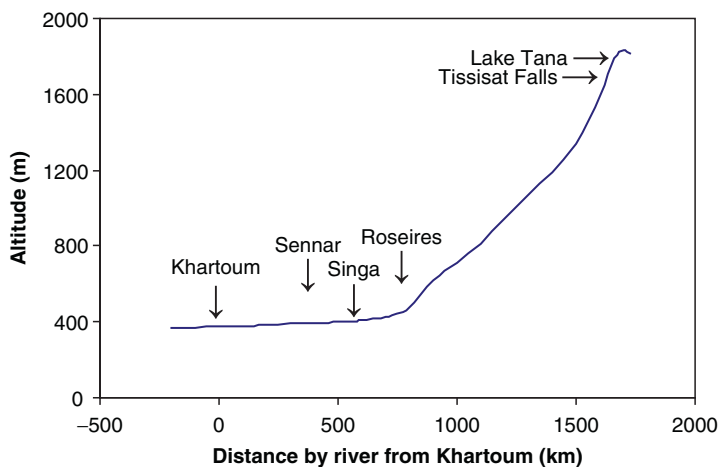


Fig. 11 Longitudinal altitude-profile of the Blue Nile. Note the location of Lake Tana and the Tassisat Falls in the right hand upper corner (modified after Rzóska, 1976b)

from the lower Nile basin. During the rainy season the waterfall is 400m wide and is the second largest of Africa (Fig. 6).

From Lake Tana to the Sudan border at Roseires the river drops ca 1,300 m in about 860 km (Figs 1 and 11). The river cuts deep through the Ethiopian Highlands and flows only a short distance through the arid lowlands of Eastern Ethiopia, before it reaches the Sudan. The Blue Nile Gorge stretch is ca 500 km long, this region has provided the sediment which has built up the Gezira in Sudan, the alluvial Nile valley and the Delta. Most of the Gorge has very steep slopes which rise immediately from the river banks. Not much is known about the hydrobiology of the Gorge region. Most information comes from the Great Abbay Expedition (August–September 1968) (Morris et al., 1976). The Gorge is sometimes several kilometres wide, the sides descending in steps. At the bottom of this chasm the river flows for a considerable distance in a narrow ‘inner Gorge’. Sand banks and a narrow fringe of forest or dense undergrowth occur at the river’s edges. In relative few places the river is calm enough to allow growth of aquatic vegetation. The Gorge generates its own climate. Large quantities of bare rock store up heat during the day so that the Gorge is warmer at night than the plateau 1,000 m or more above it. This special area supports its own fauna, quite separate and distinct from that of the adjacent plateau. Through the Nile and its Gorge, many riverine animals have penetrated from lower, warmer areas of the Sudan, eastwards deep into Central Ethiopia from whose high grounds they are otherwise absent. Most obvious examples are the hippopotamus (*H. amphibius*), Nile monitor (*Varanus niloticus*), Nile crocodile (*Crocodylus niloticus*), leathery turtle (*Trionyx triunguis*) and the side necked terrapin (*Pelomedusa subrufa*), but it also applies to the fish species.

During the main rainy season (July–August) the river is very turbulent and often broad (sometimes >100 m) and full of suspended mud, but during the dry

season the river almost ceases to flow and meanders between broad banks. In the wet season the river constitutes an inhospitable environment for aquatic life. This is no doubt the reason of the scarcity of fish, zooplankton and phytoplankton in the Gorge (Morris et al., 1976; Talling, 1976). A large majority of the fishes in the river in the Gorge are not visual predators. Catfish (*Bagrus docmak*, *Synodontis schall*, *Heterobranchus*) predominate whereas electric fishes (*Malapterurus electricus*, *Mormyrops anguilloides*) are also found. Four other species, *Garra blanfordii*, *Garra dembeensis*, *Labeobarbus intermedius* and *Varicorhinus beso* are restricted to the Blue Nile River in the Ethiopian Plateau (Banister, 1973; Berie, 2007; Stiassny & Getahun, 2007). The three last named species also occur in Lake Tana. *Oreochromis niloticus* (Nile tilapia) has also recently been found in the upper reaches of the Blue Nile below the falls (Dr Abebe Getahun pers. comm.). Furthermore, *Clarias gariepinus* (African catfish) and *Labeobarbus nedgia*, both also present in Lake Tana, have been also reported from tributaries of the Blue Nile in Ethiopia that join it downstream of the Tisisat Falls and hence their presence in the Blue Nile proper is likely (Anonymous, 2003; Berie, 2007). Therefore, most likely L. Tana and the Ethiopian part of the Blue Nile below the Tisisat Falls share only 6 fish species (Table 3). This large difference in species composition is no doubt the result of the 40 m high falls in the Blue Nile, only 30 km downstream of the river mouth in Lake Tana.

From the Sudan–Ethiopian border the Blue-Nile flows north under humid to increasingly arid conditions, and there is usually little additional runoff north of Roseires. The exceptions are two tributaries, the Dinder and the Rahad. They join the main flow downstream of the Sennar Dam and have their headwaters in the Ethiopian Highlands. By Roseires the slope has nearly levelled out and the river begins to meander through the Sudan plains, an Acacia-grass savannah, and finally merges with the White Nile at Khartoum (Figs 1 and 11). This section has undergone great changes in water regime and its biology due to the construction of two reservoirs, at Sennar in 1925 and at Roseires in 1966 (Rzóska, 1976b). Besides supplying water for irrigation and hydroelectric power these reservoirs support important fisheries.

Phytoplankton and zooplankton densities were closely linked to water flow rates (Talling & Rzóska, 1967). The low densities observed during the flood increased rapidly after the flood period ended and reached two maxima one in January–February and one in May. In May the White Nile at Khartoum slows down the weak discharge of the Blue Nile. This creates almost lake-like conditions, with almost stagnant water and high temperatures which together favour plankton increases in the Blue Nile in its final stretch (Hammerton, 1972). Generally cladocerans dominated over copepods (Talling & Rzóska, 1967). After the Roseires Reservoir has been completed phytoplankton composition in the Blue Nile was similar to that of Lake Tana with the diatom *Aulacoseira* (formerly named *Melosira*) *granulata* dominating immediately after the flood and blue green algae (mainly *Microcystis flos-aqual*) dominating in February–May.

Primary production was measured at four stations from the Ethiopian border to Khartoum during May 1968 (Hammerton, 1976). In the river, gross primary

production was much lower at Diem ($1 \text{ g C m}^{-2} \text{ d}^{-1}$) than at the final stretch at Khartoum ($6 \text{ g C m}^{-2} \text{ d}^{-1}$), whereas both reservoirs also showed a high productivity ($5.5\text{--}6.6 \text{ g C m}^{-2} \text{ d}^{-1}$) and much higher densities of zooplankton. The depth of the photosynthetic zone increased from 2.5 m at Diem to 4.0 m at the Blue Nile near Khartoum; the photosynthetic depth was much deeper in the two reservoirs (6–7.6 m).

The cladoceran species composition showed a high similarity with that of Lake Tana (Table 2). Of the 9 cladoceran species reported for Lake Tana, 8 species were also reported for the Blue Nile (Dumont, 1986a). It is likely that the only cladoceran species present in the Lake and so far not reported for the Blue Nile, *Daphnia hyalina*, is also present in this river. This species is easily mistaken for the closely related *D. longispina* reported earlier from Lake Tana and the Blue Nile (see Dumont, 1986a). Of all cladoceran species reported for the Blue Nile, only *D. longispina*, *D. barbata* and *Ceriodaphnia reticulata* were not observed in Lake Tana. *Daphnia hyalina* and *D. longispina* belong to the *D. longispina* temperate species complex, common in Europe and Central Asia and favoured by low temperatures. In contrast, *D. barbata* and *D. lumholtzi* are tropical-subtropical species favoured by high temperatures. The copepod species composition showed less similarity: of the 4 species observed in Lake Tana only 2 species are in common, viz. *Mesocyclops aequatorialis* and *Thermodiaptomus galebi* (Dumont, 1986a). Furthermore, 4 cyclopoid and 3 calanoid species reported for the Blue Nile are lacking in Lake Tana.

Information about the benthic fauna is scarce; no systematic quantitative studies were carried out. The inshore benthic fauna is poor, probably because of drastic changes of water level (Rzóska, 1976c). Hammerton (1976) reported the presence of large numbers of the giant bivalve mussel *Etheria elliptica* attached to rock outcrops in the river between Diem and Roseires.

To date the fish fauna between Roseires and Khartoum contains 50 species belonging to 14 families (Abu Gideiri, 1967; Mishrigi, 1970). Most species were found downstream of Roseires, probably because these reaches were more intensively sampled than the upper reaches. There are large differences between the fish fauna of the Blue Nile and Lake Tana (Table 3). Of the 50 species reported between Roseires and Khartoum only two species, *Oreochromis niloticus* (Nile tilapia) and *Clarias gariepinus* (African catfish), are also occurring in Lake Tana.

16 Major Threats and Conservation Measures Needed

This account is largely based on the recommendations from the workshop 'Management and Conservation of Lake Tana' (Dejen et al., 2006c).

1. Despite the limited direct human influences on Lake Tana, both wetlands and surrounding catchment area have already been seriously damaged by man and most of the original forest has disappeared. A number of factors are responsible for the degradation of the catchment, of which population pressure and associated deforestation, cultivation of marginal lands and soil erosion by heavy rains

are the most important. The indiscriminate forest clearing, complete removal of crop residue, overgrazing, poor soil management and land use practices further aggravate the situation. Overgrazing of grasslands by livestock and continuing deforestation are on the moment the most important direct causes for the further degradation of the catchment area. Several soil conservation and reforestation programs are currently carried out by the Government.

2. The littoral region and wetlands of the lake are currently under severe degradation by the local inhabitants. Especially the area covered by papyrus has been decreasing recently (Teshale et al., 2001) by the ever growing human population in the wetlands around the lake and the need to increase the food and firewood production for their livelihoods. The local community is harvesting papyrus reed roots during low water level to use it as fuel wood. Farmers are cultivating the wetlands when the water is residing.
3. In the outflow of the Blue Nile from the lake, a large dam has been constructed, resulting in increased silt load and turbidity of lake water and reduced water levels (Fig. 4) Local fishermen in the Gulf of Bahir Dar observed that since the dam was constructed more sediment has accumulated on the lake bottom. The withdrawal of lake water for generating hydroelectric power in combination with the predicted increased variations and progressive decrease of rainfall over the years (Global Change) is expected to cause severe water level fluctuations and reduced water levels in the coming decade. Both will have a negative effect on the wetland functions such as, duration of the inundation period, sediment transport and biological production. Furthermore, the construction of five more major dams for irrigation, and power generation by diverting water from Lake Tana through a canal in the western part around Kunzila (Fig. 2) and connected to Beles river are foreseen for the near future (Tana-Beles Hydro-power Project for the Electric Power Corporation).
4. The increasing silt inflow and, due to the dam, its sedimentation in Lake Tana will raise the floor of this basin and eventually flood adjacent areas, even threatening the city of Bahir Dar.
5. The abundance of endemic *Labeobarbus* species in Lake Tana decreased dramatically with ca 75% in 10 years time (1991–2001). The destructive fishing operations during the spawning season (August–September) in rivermouths and upstream on the spawning grounds in combination with alteration and destruction of spawning habitats may lead to extinction of 7 of the 15 endemic labeobarbs. Recently the Amhara Regional State approved regional fisheries legislation, which is the first positive development for the proper utilization of the fish resource which was recognized as an important commodity by the government.
6. Introduction of specialized piscivorous fish (e.g. Nile perch) from other waterbodies in Ethiopia or from outside the country would certainly lead to the extinction of at least the 8 piscivorous *Labeobarbus* species. They are clumsy predators, being cyprinids, and will be out competed by more specialist piscivores from other fish taxa.
7. Bahir Dar is a rapidly growing town, a six times population increase up to 1,800,000 inhabitants is expected in the next 50 years (Teshale, 2003).

The current practice of discharging untreated industrial and domestic waste into the lake will have adverse effects on the quality of the lake water. Therefore, the construction of sewerage with waste water treatment plant is urgently needed. Furthermore, pollution from agricultural sources as fertilizers, insecticides and herbicides are recently increasing.

8. The Lake catchment lacks a proper institutional arrangement for the wise use of the resource. The lake resource use is not regulated and there is open access for any body who want to use it. There is no responsible organization which monitors, controls and plans integrated utilization of the resource.

17 The Call for an Integrated Water Management

As we have shown, Lake Tana is a multipurpose lake which has become a source of conflict for the different stakeholders such as: farmers, fishermen, local inhabitants, authorities, community based organizations and NGO's. Currently, there is no platform that brings those different stakeholders together. All the development activities are not integrated. Therefore, there is a strong need to establish a Lake Tana Basin Authority that will bring the different stakeholders together, to enhance a more harmonious development and a sustainable utilization of the resources and protecting the people around the lake area from human caused flooding.

18 Conflicts over Water Use

Ethiopia, Sudan and Egypt, the three countries depending on the water of the Blue Nile, traditionally depend on rain-fed agriculture for their food supply. Because of their fast growing population, water demands are expected to increase in the coming years in order to meet the food requirements of these additional people. Egypt and Sudan have little water supply of their own and are strongly dependent on water from Ethiopia. A large potential for conflict over water use is therefore evident, which is why achieving an integrated regional development of water resources on a sustainable basis is critical to the socioeconomic development of the Nile countries. Currently, efforts are under way to promote a water agreement between all Nile Basin countries through the Nile Basin Initiative (see also Allan, 2009).

References

- Abu Gideiri, Y. B., 1967. Fishes of the Blue Nile between Khartoum and Roseires. *Revue de Zoologie et Botanique Africaine* 76: 345–348.
- Allan, J. A., 2009. Nile Basin asymmetries: a closed freshwater resource, soil water potential, the political economy and Nile transboundary hydrogeopolitics. In H. J. Dumont (ed.), *The Nile. Origin environments, limnology and human use. Monographiae Biologicae*, Springer. Heidelberg, Germany.

- Anonymous, 2003. Reconnaissance survey on the river fisheries of Benishangul–Gumuz regional state. Report National Fisheries and Other Living Aquatic Resources Research Center (NFLARR/EARO), Addis Ababa, Ethiopia.
- Bacci, G., 1951–1952. Components of the malacofauna of Abyssinia and Somalia (in Italian). *Annali di Museo Civico di Storia Naturale Giacomo Doria* 65: 1–44.
- 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.
- Berie, Z., 2007. Diversity, abundance and biology of fishes from Beles and Gilgel Beles Rivers, Abbay basin Ethiopia. Unpublished M.Sc. thesis, Department of Biology, Addis Ababa University.
- Brunelli, G. & G. Cannicci, 1940. The biological characteristics of Lake Tana. *Missione di studio al Lago Tana* (in Italian). *Ricerche limnologiche B. Chimica e Biologia. Reale Accademia d'Italia* 3: 71–116.
- Conway, D., 2000. The climate and hydrology of the upper Blue Nile River. *The Geographical Journal* 166: 49–62.
- Cumberlidge, N., 2009. Freshwater crabs and shrimps (Crustacea: Decapoda) of the Nile Basin. In H. J. Dumont (ed.), *The Nile. Origin environments limnology and human ure. Monographiae Biologicae*, Springer, Heidelberg, Germany.
- de Graaf, M., E. Dejen, F. A. Sibbing & J. W. M. Osse, 2000. *Barbus tanapelagijs*, a new species from Lake Tana (Ethiopia): its morphology and ecology. *Environmental Biology of Fishes* 59: 1–9.
- de Graaf, M., E. Dejen, J. W. M. Osse & F. A. Sibbing, 2003a. Ecological differentiation among the eight piscivores within the *Barbus* species flock (Pisces, Cyprinidae) of Lake Tana, Ethiopia. In M. de Graaf, *Lake Tana's piscivorous Barbus (Cyprinidae, Ethiopia); ecology – evolution – exploitation*. Ph. D. thesis, Wageningen University, The Netherlands, pp. 51–81.
- de Graaf, M., G. H. van de Weerd, J. W. M. Osse & F. A. Sibbing, 2003b. Feeding performance and predation techniques among segregating piscivores in Lake Tana's *Barbus* species flock (Cyprinidae; East-Africa). In M. de Graaf, *Lake Tana's piscivorous Barbus (Cyprinidae, Ethiopia); ecology – evolution – exploitation*. Ph. D. thesis, Wageningen University, The Netherlands, pp. 83–107.
- de Graaf, M., J. Samallo & H. J. Megens, 2003c. Rapid speciation of Lake Tana's *Barbus* (Cyprinidae; East-Africa) as inferred from mtDNA markers. In M. de Graaf, *Lake Tana's piscivorous Barbus (Cyprinidae, Ethiopia); ecology – evolution – exploitation*. Ph. D. thesis, Wageningen Institute of Animal Sciences, Wageningen University, The Netherlands, pp. 167–179.
- de Graaf, M., M. A. M. Machiels, T. Wudneh & F. A. Sibbing, 2004. Declining stocks of Lake Tana's endemic *Barbus* species flock (Pisces; Cyprinidae): natural variation or human impact? *Biological Conservation* 116: 277–287.
- de Graaf, M., E. D. Nentwich, J. W. M. Osse & F. A. Sibbing, 2005. Lacustrine spawning: is this a new reproductive strategy among 'large' African cyprinid fishes? *Journal of Fish Biology* 66: 1214–1236.
- de Graaf, M., P. A. M. van Zwieten, M. A. M. Machiels, E. Lemma, T. Wudneh, E. Dejen & F. A. Sibbing, 2006. Vulnerability to a small-scale commercial fishery of Lake Tana's (Ethiopia) endemic *Labeobarbus* compared with African catfish and Nile tilapia: An example of recruitment-overfishing? *Fisheries Research* 82: 304–318.
- de Graaf, M., H.-J. Megens, J. Samallo & F. A. Sibbing, 2007. Evolutionary origin of Lake Tana's (Ethiopia) small *Barbus* species: indications of rapid ecological divergence and speciation. *Animal Biology* 57: 39–48.
- de Graaf, M., E. Dejen, J. W. M. Osse & F. A. Sibbing, 2008. Adaptive radiation of Lake Tana's (Ethiopia) *Labeobarbus* species flock (Pisces, Cyprinidae). *Marine and Freshwater research* 59: 391–407.
- Dejen, E., F. A. Sibbing & J. Vijverberg, 2003. The reproductive biology of two 'small barbs' (*Barbus humilis* and *B. tanapelagijs*: Cyprinidae) in Lake Tana, Ethiopia. *Netherlands Journal of Zoology* 52: 281–299.

- Dejen, E., J. Vijverberg, L. A. J. Nagelkerke & F. A. Sibbing, 2004. Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (L. Tana, Ethiopia). *Hydrobiologia* 513: 39–49.
- Dejen, E., J. Vijverberg, M. de Graaf & F. A. Sibbing, 2006a. Predicting and testing resource partitioning in a tropical fish assemblage of zooplanktivorous ‘barbs’: an ecomorphological approach. *Journal of Fish Biology* 69: 1356–1378.
- Dejen, E., J. Vijverberg & F. A. Sibbing, 2006b. Spatial and temporal variation of cestode infection and its effects on two small barbs (*Barbus humilis* and *B. tanapelagijs*) in Lake Tana, Ethiopia. *Hydrobiologia* 556: 109–117.
- Dejen, E. (ed.), M. de Graaf, L. A. L. Nagelkerke, T. Wudneh, J. W. M. Osse & F. A. Sibbing, 2006c. Lake Tana fishery and its sustainable development (in Amharic). Amhara Region Agricultural Research Institute & Department of Animal Sciences and Wageningen University. Tis Abay Printing Press, Bahir Dar, Ethiopia: 84 pp.
- Dejen, E., J. Vijverberg, L. A. J. Nagelkerke & F. A. Sibbing, submitted. Growth, biomass and production of two small barbs (*Barbus humilis* and *B. tanapelagijs*, Cyprinidae, and their role in the food web of Lake Tana) (Ethiopia).
- Dgebuadze, Y. Y., 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., 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 barb species flock (*Barbus intermedius* complex). *Immunogenetics* 44: 419–431.
- Dumont, H. J., 1983. Dragonflies from the Ethiopian Plateau and from Lake Tana. *Notulae odonatologicae* 2: 10–11.
- Dumont, H. J., 1986a. Zooplankton of the Nile system. In B. R. Davies & K. F. Walker (eds), *The Ecology of River Systems*. Kluwer, Dordrecht, pp. 75–88.
- Dumont, H. J., 1986b. The Nile River system. In B. R. Davies & K. F. Walker (eds), *The Ecology of River Systems*. Kluwer, Dordrecht, pp. 61–74.
- Dumont, H. J., 2009. The Cnidaria of the Nile Basin. In H. J. Dumont (ed.), *The Nile. Origin environments, limnology and human ure*, Monographiae Biologicae, Springer, Dordrecht. Vol. 89: 495–498.
- Flössner, D., 2000. *Daphnia hyalina* Leydig 1860. In D. Flössner, *Die Haplopoda und Cladocera (Ohne Bosminidae) Mitteleuropas*. Backhuys, Leiden, pp. 177–182.
- Frances, I. & S. Aynalem, 2007. Bird surveys around Bahir Dar-Lake Tana IBA. Filed Report, RSPB International Division, UK, 91 pp.
- Gasse, F., 1987. Ethiopie and Djibouti (in French). In *African wetlands and shallow water bodies*. In M. J. Burgis & J. J. Symoens (eds), *Travaux et Documents/ Institut Francais de Recherche Scientifique pour le Development en cooperation no. 211* Paris, ORSTOM, 300–311.
- Green, J., 2009. Birds of the Nile. In H. J. Dumont (ed.), *The Nile. Origin environments, limnology and human ure*, Monographiae Biologicae, Springer, Dordrecht. Vol. 89: 705–720.
- Hammerton, D., 1972. The River Nile, a case history. In R. T. Oglesby, C. A. Carlson & J. A. McCann (eds), *River Ecology and Man*. Academic, New York, London, pp. 171–214.
- Hammerton, D., 1976. The Blue Nile in the plains. In J. Rzóska (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 243–256.
- Howell, P. P. & P. Allan, 1994. *The Nile: Sharing a Scarce Resource*. Cambridge University Press, Cambridge, UK.
- Johnson, T. C., C. A. Scholz, M. R. Talbot, K. Kelts, R. D. Ricketts, G. Ngobi, K. Beuning, I. Semmanda & J. W. McGill, 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273: 1091–1093.
- Kindie, A., 2001. Wetlandss distribution in Amhara region, their importance and current threats. In A. B. Dixon, A. Hailu & A. P. Wood (eds), *Proceedings of the Wetland Awareness Creation and Activity Identification Workshop in Amhara National Regional State*. January 23rd 2001 Bahir Dar, Ethiopia, pp. 14–17.

- Kruiswijk, C. P., T. Hermsen, J. van Heerwaarden, B. Dixon, H. F. J. Savelkoul & R. J. M. Stet, 2005. Major histocompatibility genes in the Lake Tana African large barb species flock: evidence for complete partitioning of class II *B*, but not class I, genes among different species. *Immunogenetics* 56: 894–908.
- Lamb, H. F., C. R. Bates, P. V. Coombes, M. H. Marschall, M. Umer, S. J. Davies & E. Dejen, 2007. Late Pleistocene dessication of Lake Tana, source of the Blue Nile. *Quaternary Research* 26: 287–299.
- 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.
- Mishrigi, S. Y., 1970. Fishes of Lake Roseires on the Blue Nile. *Revue de Zoologie et Botanique Africaine* 82: 193–197.
- Mohr, P. A., 1962. *The Geology of Ethiopia*. Addis Ababa, Ethiopia. University College of Addis Ababa Press.
- Molla, M. & T. Menelik, 2004. Environmental impact assessment for unusual reduced water level of Lake Tana. In *Proceedings of the Symposium on Lake Tana Watershed Management*. Lake Net, USA: 35–48.
- Morris, P., M. J. Largen & D. W. Yalden, 1976. Notes on the biogeography of the Blue Nile (Great Abbai) Gorge in Ethiopia. In J. Rzóška (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 233–242.
- Mulneh, A. A., 2005. Ecological importance of aquatic macrophytes in the Southern part of Lake Tana. Report of the Amhara National Region Rehabilitation Development Organisation (TIRET).
- Nagelkerke, L. A. J., 1997. The barbs of Lake Tana, Ethiopia: morphological diversity and its implications for taxonomy, trophic resource partitioning and fisheries. Ph. D. thesis, Wageningen University, The Netherlands, 296 pp.
- 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, 2000. The large barbs (*Barbus* spp., Cyprinidae, Teleostei) of Lake Tana (Ethiopia), with a description of a new species, *Barbus osseensis*. *Netherlands Journal of Zoology* 50: 179–214.
- 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.
- Palstra, A. P., M. de Graaf & F. A. Sibbing, 2004. Riverine spawning and reproductive segregation in a lacustrine cyprinid species flock, facilitated by homing? *Animal Biology* 54: 393–415.
- Pitcher, T. J., 1995. Thinking the unthinkable: a candidate model for predicting sustainable yields of introduced fish species in African lakes. In T. J. Pitcher & P. J. B. Hart (eds), *The Impact of Species Changes in African Lakes*. Chapman & Hall, London, pp. 495–525.
- Rzóška, J., 1976a. Lake Tana, headwaters of the Blue Nile. In J. Rzóška (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 223–232.
- Rzóška, J., 1976b. The Blue Nile System. In J. Rzóška (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 219–221.
- Rzóška, J., 1976c. Notes on the benthos of the Nile system. In J. Rzóška (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 345–351.
- Schwenk, K., D. Posada & P. D. N. Hebert, 2000. Molecular systematics of European *Hyalodaphnia*: the role of contemporary hybridisation in ancient species. *Proceedings of the Royal Society of London B* 267: 1833–1842.
- Sibbing, F. A. & L. A. J. Nagelkerke, 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries* 10: 393–437.
- Sibbing, F. A., L. A. J. Nagelkerke, R. J. M. Stet & J. W. M. Osse, 1998. Speciation of endemic Lake Tana barbs (*Cyprinidae*, Ethiopia) driven by trophic resource partitioning: a molecular and ecomorphological approach. *Aquatic Ecology* 32: 217–227.

- Stiassny, M. L. J. & A. Getahun, 2007. An overview of labeonin relationships and the phylogenetic placement of the Afro-Asian genus *Garra* Hamilton, 1922 (Teleostei: Cyprinidae), with the description of five new species of *Garra* from Ethiopia, and a key to all African species. *Zoological Journal of the Linnean Society* 150: 41–83.
- Talling, J. F., 1976. Phytoplankton: composition, development and productivity. In J. Rzóska (ed.), *The Nile, Biology of an Ancient River*. Junk, The Hague, pp. 385–402. (see also this volume pp. 431–463)
- Talling, J. F. & J. Rzóska, 1967. The development of plankton in relation to the hydrological regime in the Blue Nile. *Journal of Ecology* 55: 637–662.
- Teshale, B., 2003. Influence of sediment on physico-chemical properties of Lake Tana. Workshop 'Fish and Fisheries of Lake Tana: Management and Conservation'. 6–8 October 2003, Bahir Dar, Ethiopia.
- Teshale, B., R. Lee & G. Zawdie, 2001. Development initiatives and challenges for sustainable resource management and livelihood in the Lake Tana region of Northern Ethiopia. In A. B. Dixon, A. Hailu & A. P. Wood (eds), *Proceedings of the Wetland Awareness Creation and Activity Identification Workshop in Amhara National Regional State*. January 23rd 2001, Bahar Dar, Ethiopia, 33–43.
- Tewabe, D., S. Muhammed & B. Abdissa, 2005. Distribution and abundance of macro-benthic and weed-based faunas in the northern part of Lake Tana. Internal Report ARARI, Bahir Dar, Ethiopia, 14 pp.
- Thiel, H., 1973. *Limnocyclus indica* in Africa. *Publications Seto marine Biology Laboratory* 20: 73–79.
- van Perlo, B., 1995. *Birds of Eastern Africa*. Collins' Illustrated Checklist. Harper & Collins, London, 301 pp.
- Witte, F., M. de Graaf, O. Mkumbo, A.I. El-Moghraby & F.A. Sibbing, 2009. Fisheries in the Nile system. In H. J. Dumont (ed.), *The Nile: Monographiae Biologicae* Springer, Dordrecht. Vol. 89: 723–747.
- Wondie, A. & S. Mengistu, 2006. Duration of development, biomass and rate of production of the dominant copepods (Calanoid and cyclopoida) in Lake Tana, Ethiopia. *SINET: Ethiopian Journal of Science* 29: 107–122.
- Wondie, A., S. Mengistu, J. Vijverberg & E. Dejen, 2007. Seasonal variation in primary production of a large high altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency. *Aquatic Ecology* 41: 195–207.
- Wudneh, T., 1998. *Biology and management of fish stocks in Bahir Dar Gulf, Ethiopia*. Ph. D. thesis, Wageningen University, The Netherlands, 143 pp.