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PRIMARY RESEARCH PAPER

Growth, biomass, and production of two small barbs (*Barbus humilis* and *B. tanapelagius*, Cyprinidae) and their role in the food web of Lake Tana (Ethiopia)

**Eshete Dejen · Jacobus Vijverberg ·
Leopold A. J. Nagelkerke ·
Ferdinand A. Sibbing**

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Abstract Growth, biomass and production of two small barbs (*Barbus humilis* and *Barbus tanapelagius*) and their role in the food web of Lake Tana were investigated. From length–frequency distribution of trawl monitoring surveys growth coefficient, Φ' values were estimated at 3.71–4.17 for *B. humilis* and 3.70–4.14 for *B. tanapelagius*, respectively. Values for *B. humilis* were confirmed in pond experiments. Mean biomass of the small barbs was 13.3 kg fresh wt ha^{-1}, with *B. humilis* being most abundant in the littoral and sub-littoral zones, whereas *B. tanapelagius* was most abundant in the sub-littoral and pelagic zones. The two small barbs had a production of 53 kg fresh wt ha^{-1} year^{-1}. Although their *P*/*B* ratios of about 4.0 were relatively high for small cyprinids, both their biomass and production were low in comparison with other small fish taxa in other tropical lakes. Of the zooplankton production only about 29% was consumed by the small barbs. However, they did not utilize calanoid copepods, which were responsible for approximately 57% of the zooplankton production and it is likely that small barb production was food limited during certain periods of the year. Piscivorous labeobarbs consumed about 56% of the small barbs production annually, but additionally, *Clarias gariepinus*, and many bird species were also preying on them. Therefore, limitation of *Barbus* production by predation during certain periods in the year cannot be excluded.

Keywords Africa · Ecosystem · Fishery · Fish production · Lakes Zooplanktivory Zooplankton

Introduction

Lake Tana is the largest freshwater lake in Ethiopia and source of the Blue Nile River. Commercially important fish species in Lake Tana are an endemic flock of 15 large *Labeobarbus* spp. (Cyprinidae), *Varicorhinus beso* Rüppell (Cyprinidae), Nile tilapia, *Oreochromis*

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E. Dejen · F. A. Sibbing
Experimental Zoology Group, Wageningen University, Wageningen Institute of Animal Sciences, Marijkeweg 40, 6709, PG, Wageningen, The Netherlands
e-mail: Eshete.Dejen@fao.org

Present Address:
E. Dejen
FAO-Sub Regional Office for Eastern Africa,
P.O. Box 5536, Addis Ababa, Ethiopia

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

L. A. J. Nagelkerke
Aquaculture and Fisheries Group, Wageningen University, Wageningen Institute of Animal Sciences, Marijkeweg 40, 6709, PG, Wageningen, The Netherlands
e-mail: Leo.Nagelkerke@wur.nl

niloticus (L.) (Cichlidae) and African catfish, *Clarias gariepinus* (Burchell) (Clariidae) (Nagelkerke, 1997; de Graaf et al., 2006). In addition, three 'small barb' species (genus *Barbus*, <100 mm length, Cyprinidae), *Barbus humilis* Boulenger, *B. pleurogramma* Boulenger and *B. tanapelagius* de Graaf, Dejen and Osse, as well as three species of the genus *Garra* (Cyprinidae) have been reported from the lake.

Until recently, studies mainly focussed on the endemic species flock of *Labeobarbus* in the lake (e.g. Nagelkerke et al., 1994; Sibbing & Nagelkerke, 2001). Surprisingly, eight of these are piscivores (de Graaf et al., 2008). Studies on the three species of small barbs, *B. humilis*, *B. pleurogramma* and *B. tanapelagius* started only recently (e.g. Dejen et al., 2006a, b). *B. tanapelagius* is endemic to the L. Tana catchment and common in the large pelagic zone of the lake. *B. humilis* is a littoral species, while *B. pleurogramma* is mainly present in the wetlands around 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 (Eshete Dejen pers. observation).

Small zooplanktivorous fish, mainly cyprinid and clupeid species, are generally characterized by a high growth rate and a prolific reproduction which reduces the chance of overfishing (e.g. Duncan, 1999; Sarvala et al., 2002). Serious decline of the stocks of endemic *Labeobarbus* species in Lake Tana (de Graaf et al., 2006) raises the question if inclusion of the small zooplanktivorous barbs into the fishery would be realistic and desirable. The feasibility of such a fishery largely depends on the biomass and productivity of the stocks of the small barbs. Therefore, we addressed the following four questions: (1) What is the production of the small barbs in Lake Tana; (2) How does this production compare with other small zooplanktivorous fish in other tropical lakes; (3) Is this production limited by predation and/or food availability and (4) Is the production of the small barbs high enough to start a fishery on these species?

Materials and methods

Study area

Lake Tana is situated in the north-west of Ethiopia at an altitude of 1,800 m. The lake is turbid and shallow (average depth 8 m, maximum depth 14 m) and has a surface area of about 3,150 km^2. Based on its chlorophyll content it may be classified as mesotrophic (Dejen et al., 2004), but because of its high turbidity, gross primary production rate (annual average 2.43 g O_2 m^{-2} day^{-1}) is relatively low (Wondie et al., 2007). It is well-mixed because of wind exposure and its small depth. The shallow, littoral zone (0–4 m depth) is relatively small, about 10% (315 km^2) of the total surface area of the lake. The sub-littoral zone is intermediate in depth (4–8 m) and occupies about 20% (630 km^2) of the lake area, whereas the pelagic zone (8–14 m) covers 70% (2,205 km^2) of the lake surface area.

Sampling procedure

Fish were sampled at 12 sampling stations in the Southern Gulf of Lake Tana from October 1999 to November 2001 (Fig. 1). The stations represented three habitat types: (a) a shallow, littoral zone with a mixture of mud and silt substratum with submerged vegetation; (b) a sub-littoral zone with mud and silt substratum and (c) a pelagic zone with predominantly inorganic silt substratum.

A bottom trawl was used during dusk and dawn. The net was kept open with a 5 m beam and was hauled at a speed of 1.0 m s^{-1} in a straight line 50 m behind a 6.8 m flat-bottomed polyester boat with a 25 HP outboard engine. The fishing width of the net was estimated to be 3 m by using thin breakable ropes. The bar mesh sizes varied from 10 to 5.5 mm from the side panels to the cod end. Hauls lasted 15 min, resulting in 2,700 m^2 swept area per haul. For each fish species, total numbers and fresh weight were recorded. A random sub-sample of at least 30 individuals (or all individuals in the sample) was taken for the measurement of fork length (nearest mm).

Growth and mortality estimates

Monthly length–frequency distributions of *B. humilis* and *B. tanapelagius* were collected for 26 consecutive months. Mean length–frequency distributions were produced for January–December. These data were used for the analysis of growth parameters in the FiSAT II computer package (Gayanilo et al., 2002). We applied both a direct analysis of length–

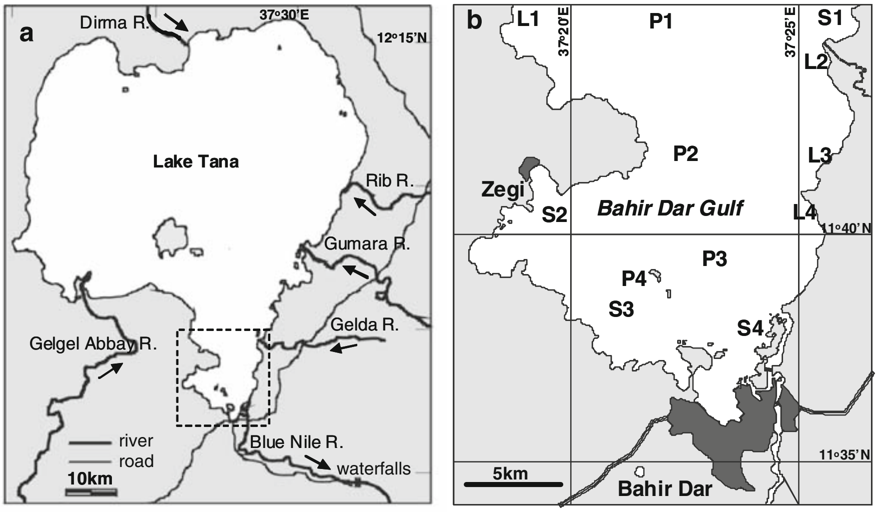

Fig. 1 Map of Lake Tana showing **a** the study area and **b** the sampling stations in three habitat zones: littoral (L1–L4), sublittoral (S1–S4) and pelagic (P1–P4)

frequency distributions, using the ELEFAN method, as well as more indirect methods based on estimated growth increments. Growth increments were estimated using an adapted version of Bhattacharya's method for the analysis of mixtures of normal distributions, which were then analysed using three methods available in the FiSAT II computer package, i.e. Munro's, Faben's and Appeldoorn's methods (Gayanilo et al., 2002). Since no significant seasonality in growth could be detected, growth was assumed to be described by the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)}\right),$$

where L_t is length at age t, L_∞ is the asymptotic size, K is the growth constant and t_0 is the hypothetical age at length zero. Estimates of L_∞ and K followed the steps, described by Amarasinghe & De Silva (1992). The value for t_0 was assumed to be zero.

The Pauly & Munro (1984) relationship was used to calculate the index of overall growth performance Φ'. This index is well suited to compare growth of closely related species (Amarasinghe, 2002).

$$\Phi' = 2 \log L_\infty + \log K.$$

In addition to catch analyses we estimated growth rate of *B. humilis* experimentally. Mean length increments of seven length classes (18–80 mm FL; $n = 99$) were measured in seven outdoor basins (diameter 300 cm, height 100 cm, water depth 50 cm) over 30 days. The basins were located in an open shed adjacent to the lake and the sides were covered by nets to prevent piscivorous birds from entering the basin area. Basins were part of an open water flow system. Water was pumped directly from the lake, distributed over the basins and flowed back to the lake. This resulted in a continuous flow of lake water with natural seston and zooplankton concentrations. No food was added. Water temperature, oxygen levels and transparency were similar to lake conditions. As all fish were from the same field population and conditions in all basins were identical, the growth of the fish in the seven basins was assumed to conform to the same pattern. The size classes of *B. humilis* used were: sc1 = 16–19 ($n = 14$), sc2 = 20–26 ($n = 14$), sc3 = 37–49 ($n = 19$), sc4 = 55–59 ($n = 15$), sc5 = 65–70 ($n = 16$), sc6 = 78–80 ($n = 17$), sc7 = 79–81 ($n = 4$). Each size class was put in a separate basin and growth increments were determined in each basin separately. Fish were measured at the start ($t = 0$) and at the end ($t = 30$ days) of the experiment.

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

$$\ln\left(N_i \middle/ \Delta t_i'\right) = a + b t_i',$$

where N_i is the number of fish caught in a given length class i; t_i' is the relative age corresponding to length class i and $\Delta t'$ is the average time needed by the fish to grow through length class i. In this case, the estimated total mortality (Z) was equal to the natural mortality (M) since the fishery does not exploit these species.

Biomass and production estimates

Biomass (B) of the small barbs was estimated by the swept area method (Sparre & Venema, 1998) from samples taken with the bottom trawl, using:

$$B = \frac{C}{w \cdot v \cdot t} \cdot \frac{1}{q},$$

where C is the catch from the haul, w is the fishing width of the trawl net (3 m), v is the velocity of the trawl (1 m s^{-1}), t is the duration of the haul (usually 15 min), and q is the catchability coefficient, or trawling efficiency. The trawl we used had an estimated q of 50% in sampling 0+ fish in Dutch lakes (Vijverberg et al., 1990). Since the bottom trawl only fished the deepest 1 m of the water column we corrected all biomass estimates for the distribution of *Barbus humilis* and *B. tanapelagius* in the whole water column. For this purpose, we used simultaneous gillnet surveys, using benthic and pelagic multimesh, monofilament survey gillnets, composed of five randomly distributed panels with 5.0, 6.25, 8.0, 10.0 and 12.5 mm bar mesh (Dejen et al., 2006a). The abundance of fish at different depths in the gillnet was used to calculate the biomass of fish in the whole water column.

Production of small barbs (P) was estimated using Allen's (1971) assumption that in case of a constant exponential death rate and when Von Bertalanffy growth applies, the production/biomass ratio (P/B) is equal to Z, the total instantaneous mortality rate.

Potential zooplanktivorous fish production was also estimated based on the production of zooplankton, the principal food source of the small *Barbus* species. Zooplankton production was estimated by calculating biomass per species and using relevant P/B ratios given in literature. In addition, we estimated a minimum value of *Barbus* production, based on the production of their main predators, the piscivorous *Labeobarbus* species (Wudneh, 1998; de Graaf et al., 2003). We assumed 10% trophic efficiencies (see, e.g. de Angelis, 1992), and a dry:fresh weight ratio of 1:5 (see, e.g. Post & Lee, 1996).

Maximum sustainable yield

In order to evaluate the viability of a fishery on the small *Barbus* species we estimated the maximum sustainable yield (MSY) according to Sparre & Venema (1998) as $MSY = x{\cdot}M{\cdot}B_v = x{\cdot}P$, where M = natural mortality, B_v = virgin stock biomass, and x is a constant. According to the original formula of Gulland (1971) x can have a value of 0.5, but Beddington & Cooke (1983) concluded that this generally overestimates MSY by a factor 2–3, so that a value of 0.2 would result in a more realistic estimate of MSY (Sparre & Venema, 1998).

Results

Growth and mortality estimates

From the trawl survey, we monthly collected a mean number of 7,408 (SD = 4,750) and 1,887 (SD = 3,065) specimens of *B. humilis* and *B. tanapelagius*, respectively. It was found that both species are small (<100 mm FL) and that females grow to a larger size than males. The maximum length recorded was 96 and 89 mm fork length (FL) for *B. humilis* and *B. tanapelagius*, respectively. Mean length (FL) and standard deviations (±SD) from length–frequency data were 63.2 ± 8.5 mm (females, $n = 4{,}852$) and 55.6 ± 6.6 mm (males, $n = 1{,}401$) for *B. humilis* specimens and 58.6 ± 7.9 mm (females, $n = 2{,}925$) and 53.3 ± 5.5 mm (males, $n = 1{,}041$) for *B. tanapelagius*. Length–weight relationships (FL in mm; fresh weight (W) in gram) were calculated for *B. humilis* ($W = 1.97 \times 10^{-5}\ \mathrm{FL}^{2.898}$; $n = 4{,}886$; $r^2 = 0.92$), and for *B. tanapelagius* ($W = 1.54 \times 10^{-5}\ \mathrm{FL}^{2.919}$; $n = 2{,}926$; $r^2 = 0.91$).

Based on the analyses of length–frequency distributions (Fig. 2) we estimated L_∞ to range between 79 and 91 mm for *B. humilis* and between 71 and 98 mm for *B. tanapelagius*, respectively (Fig. 2). K ranged between 0.73 and 2.36 year^{-1} for *B. humilis*, and between 0.66 and 2.33 year^{-1} for *B. tanapelagius*. Values of the growth index (Φ') varied less, ranging between 3.71 and 4.17 for *B. humilis* and 3.70 and 4.14 for *B. tanapelagius*. These length-based estimates of growth parameters were confirmed by results from direct growth measurement of *B. humilis* in outdoor basins. Using the Gulland and Holt method (Sparre & Venema, 1998) we found that the growth constant K was 1.50 year^{-1} and L_∞ was 88.4 mm FL (Fig. 3), resulting in a growth index (Φ') of 4.07 which falls in the range of the estimates for the field population of this species.

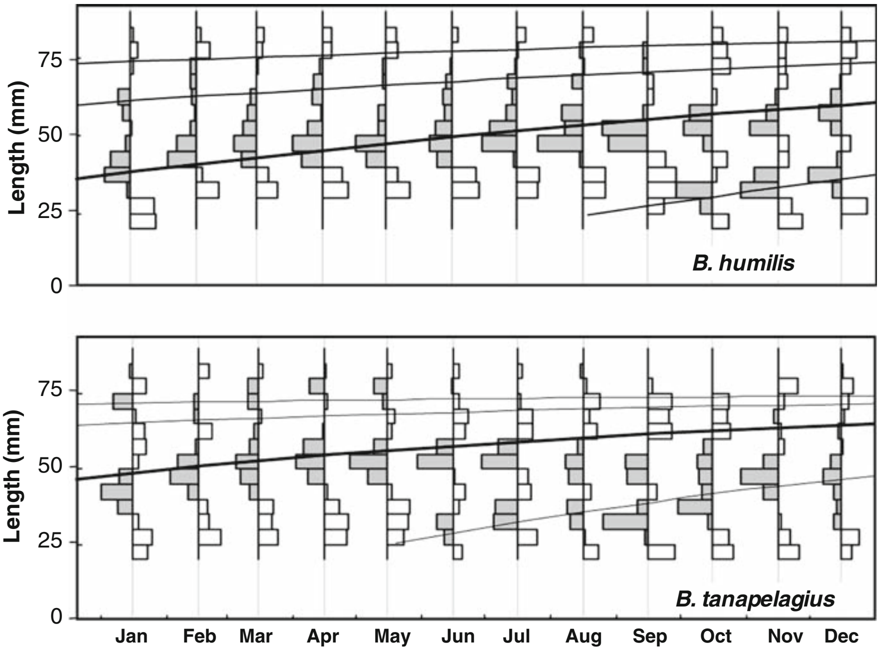

Fig. 2 Restructured length–frequency distributions of *B. humilis* (*top*) and *B. tanapelagius* (*bottom*)

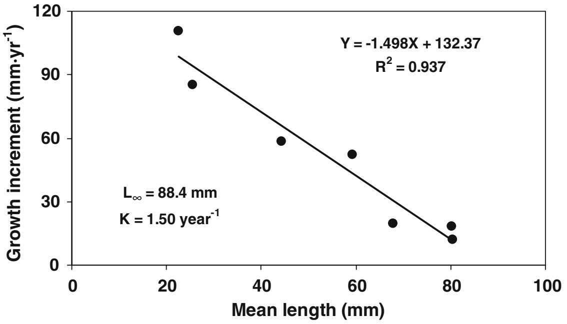

Fig. 3 Outdoor basin growth measurement on *B. humilis*. Mean length increase in mm over one year relative to the mean size per size class (($L_{t=0} + L_{t=30}$)/2). Each size class was introduced to a separate pool. The size classes and the number of fish measured were: sc1 = 16–19 (n = 14), sc2 = 20–26 (14), sc3 = 37–49 (19), sc4 = 55–59 (15), sc5 = 65–70 (16), sc6 = 78–80 (17), sc7 = 79–81 (4). Note that growth increment within 30 days (=0.0822 year) was expressed on a yearly basis in order to establish L_∞ and K from the slope and intercept

Estimated total mortality (Z) ranged between 3.9 and 4.3 year^{-1} for *B. humilis* and between 3.1 and 4.7 for *B. tanapelagius*, respectively (Fig. 4).

Biomass and production estimates

Biomass of the small barb species differed between species and habitats. *B. humilis* was most abundant in the sub-littoral zone of intermediate depth (mean value of 23.5 kg fresh wt ha^{-1}), less abundant in the littoral, shallow area (9.2 kg fresh wt ha^{-1}) and almost absent from the pelagic, deeper pelagic zone (0.2 kg fresh wt ha^{-1}; Fig. 5). When weighted for the relative area of each habitat this amounts to a mean biomass of 5.8 kg fresh wt ha^{-1} for *B. humilis* in the lake as a whole (Table 1). *B. tanapelagius* was most abundant in the deeper pelagic zone (9.2 kg fresh wt ha^{-1}), less abundant in the sub-littoral zone (5.1 kg fresh wt ha^{-1}), although in 1999 this was not the case, and virtually absent from the littoral, shallow parts of the lake (0.4 kg fresh ha^{-1}; Fig. 5). When weighted for the relative area of each habitat the biomass of *B. tanapelagius* was estimated at 7.5 kg·fresh wt ha^{-1} for the whole lake (Table 1).

Annual production of *B. humilis* was 23.7 kg fresh wt ha^{-1}·year^{-1}, based on a P/B ratio of 4.1. For *B. tanapelagius* the annual production is 29.2 kg·fresh wt ha^{-1} year^{-1} given a P/B ratio of 3.9 (Table 1). Total annual production of both small barb species in Lake Tana is estimated at 52.9 kg·fresh wt ha^{-1} year^{-1} or 16,700 t fresh wt year^{-1}.

The MSY for the whole of Lake Tana was estimated to be 4.7 kg fresh wt ha^{-1} year^{-1} (1,500 t year^{-1}) for *B. humilis* and 6.1 kg fresh wt ha^{-1} year^{-1} (1,900 t fresh wt year^{-1}) for *B. tanapelagius* (Table 1), using MSY $= 0.2\ M{\cdot}B_v = 0.2\ P$ (Sparre & Venema, 1998).

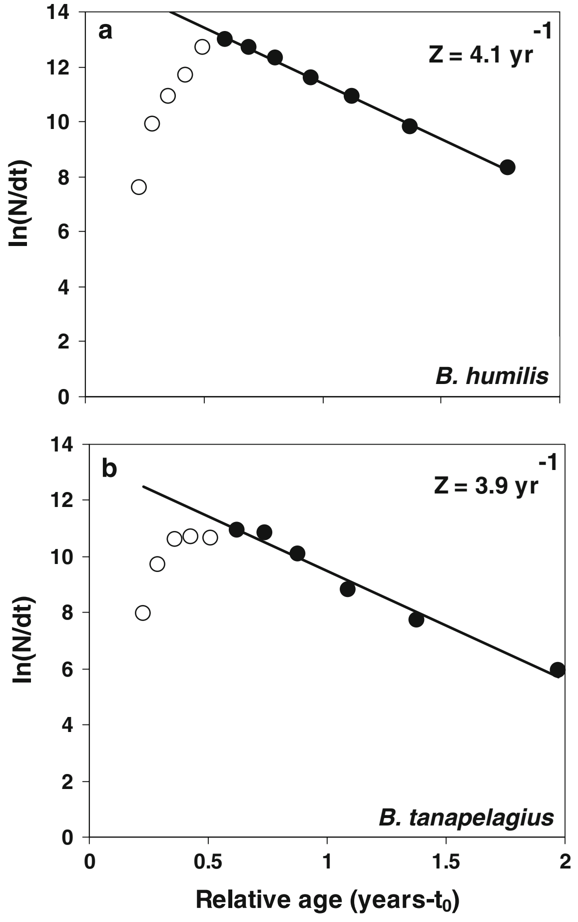

Fig. 4 Length-converted catch curve for *B. humilis* (**a**) and *B. tanapelagius* (**b**). The slope of the regression line gives the estimate for Z

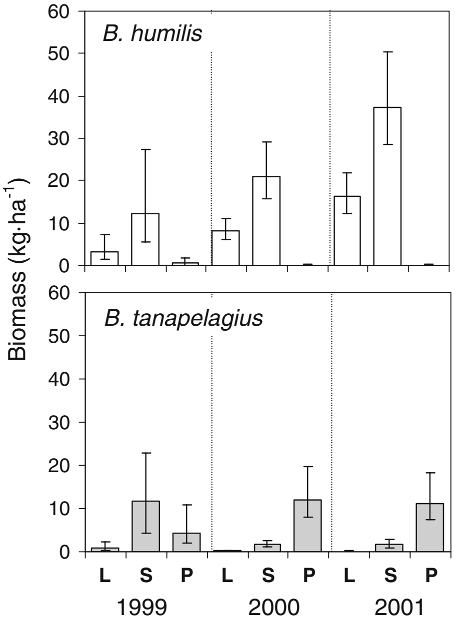

Fig. 5 Mean biomass (kg ha^{-1}) for the two small barbs (*B. humilis* and *B. tanapelagius*) at three habitats; littoral (L), sublittoral (S), and pelagic (P) in three successive years (1999–2001). *Error bars* represent 95% confidence intervals

Limiting factors for the *Barbus* production

In order to estimate potential zooplanktivorous fish production, we calculated the production of zooplankton in Lake Tana (Table 2) using densities and length–frequency distributions of the different zooplankton species given by Dejen et al. (2004) and length–weight regressions given by Amarasinghe et al. (1997). The relationships between *P*/*B* ratios and the size of the zooplankton species were taken from Amarasinghe et al. (2008). Assuming a mean water depth of 8 m, this resulted in an estimated biomass of 11.5 kg dry wt ha^{-1} and an annual zooplankton production of 370 kg dry wt ha^{-1} year^{-1} (Table 2). Assuming a 10% trophic efficiency, and a dry:fresh weight ratio of 1:5 for fish, this resulted in a potential zooplanktivorous fish production of 185 kg ha^{-1} year^{-1}. Since the total small barb production was only 52.9 kg fresh wt ha^{-1} year^{-1} (Table 1), this would mean that they only consume a small proportion (about 29%) of the total zooplankton production.

The piscivorous *Labeobarbus* species accounted for 12% (3.8 kg ha^{-1} year^{-1}) of the total annual *Labeobarbus* production (32 kg ha^{-1} year^{-1}) (Wudneh, 1998). Assuming a 10% trophic conversion efficiency, these predators would need approximately 38 kg ha^{-1} year^{-1} of prey fish production. Since the small barbs account for about 75% of their diet (de Graaf et al., 2008) this would mean that annually about 29 kg fresh wt ha^{-1} of small barbs are eaten by the piscivorous labeobarbs.

Discussion

Methodology

Length-based models are always a bit suspect and there are more modern methods available than those provided by Fisat II (see, e.g. Fournier et al., 1998). However, we decided to use the variety of techniques

Table 1 Biomass, production and maximum sustainable yield (MSY) of two small *Barbus* species from Lake Tana (fresh wt.)

	B. humilis Mean (low–high)	*B. tanapelagius* Mean (low–high)	Total Mean (low–high)
Biomass (kg·ha^{-1})	5.8 (4.0–9.0)	7.5 (4.5–13.4)	13.3 (8.5–22.4)
Biomass (×1,000 t)	1.8 (1.3–2.8)	2.4 (1.4–4.2)	4.2 (2.7–7.0)
Z (year^{-1}) ≈ *P*/*B*	3.9–4.3	3.1–4.7	
Production (kg ha^{-1} year^{-1})	23.7 (15.6–38.8)	29.2 (13.9–62.7)	52.9 (29.5–101.5)
Production (×1,000 t year^{-1})	7.5 (4.9–12.2)	9.2 (4.4–19.8)	16.7 (9.3–32.0)
MSY (kg ha^{-1} year^{-1})	4.7 (3.3–7.4)	6.1 (3.7–10.9)	10.9 (7.0–18.3)
MSY (×1,000 t year^{-1})	1.5 (1.0–2.3)	1.9 (1.2–3.4)	3.4 (2.2–5.8)

Indicated are mean estimates and lower (*low*) and upper (*high*) 95% confidence limits

Table 2 Biomass (*B*, kg dry wt ha^{-1}) and production (*P*, kg·dry wt ha^{-1} year^{-1}) of the crustacean zooplankton of Lake Tana

Species	Average density (n l^{-1})	Average size (L in mm)	*B* (kg ha^{-1})	*P* (kg ha^{-1} year^{-1})	*P*/*B* (year^{-1})
Bosmina longirostris	7.9	0.38	0.9	67.7	78
Ceriodaphnia cornuta	0.2	0.31	0.0	0.7	113
Ceriodaphnia dubia	0.8	0.42	0.0	2.7	65
Diaphanosoma spp	8.0	0.77	0.6	14.5	23
Daphnia hyalina	5.2	1.24	1.1	10.6	10
Daphnia lumholtzi	4.6	0.90	0.5	8.2	16
Moina micrura	1.4	0.50	0.1	7.8	155
Mesocyclops aequatorialis	2.4	0.79	0.4	12.4	31
Thermocyclops ethiopiensis	8.6	0.59	0.8	33.5	40
Thermodiaptomus galebi	17.7	0.79	7.0	212.3	30
Total	56.8		11.5	370	32.2

Annual *P*/*B* ratios were estimated from the relationship between zooplankton length and *P*/*B* given by Amarasinghe et al. (2008)

provided by this computer package in order to allow direct comparisons with studies on other tropical systems, which mostly used similar methods. Moreover, the quality of the data would most probably not lead to much better estimates using more sophisticated methods.

The concepts of MSY and biomass estimates by swept area using a trawl are generally not very accurate and represent only rough approximations for potential yield and standing stock biomass and this is also true for our study. The constant '*x*' which determines the MSY is quite arbitrary. Although by using $x = 0.2$ our estimates for MSY are conservative, this figure should be regarded with caution. However, we are confident that in this study the use of MSY and biomass estimated by swept area are useful concepts because we apply a four-pronged approach to estimate the sustainability of a fishery on the small barbs: First, the MSY estimate of the small barbs; second, the production estimate of the two barbs and their consumption of zooplankton; third, a production estimate of food organisms of the small barbs and fourth, an estimate of the consumption of small barbs by piscivores.

Biomass and productivity of small fish taxa in tropical lakes

The biomass of the two small *Barbus* species in Lake Tana (# TA-6, TA-7 in Fig. 6) of 5.8 and 7.5 kg ha^{-1} is low in comparison with the biomass of most other small, predominantly planktivorous, fish taxa in other tropical lakes and reservoirs (Table 3; Fig. 6a). Of the 19 fish taxa reviewed, only five had a similar low biomass: three feeding guilds of haplochromines in Lake Victoria (# 8, 9, 10), a small cyprinid in Lake

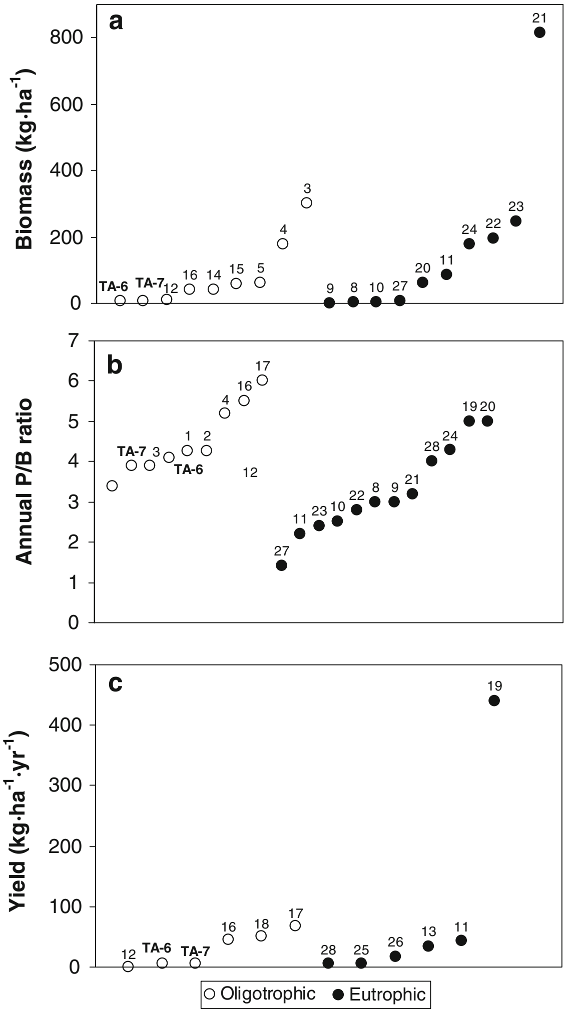

Fig. 6 Overview of **a** biomass, **b** annual *P*/*B* ratios, and **c** yield of small planktivorous fish taxa of 17 tropical lakes and reservoirs varying in trophic status (oligotrophic/mesotrophic, eutrophic). For each lake only the taxon with the highest yield is given; the estimated maximum sustainable yield for the two barbs of Lake Tana is given for comparison. Fish taxa of each lake/reservoir are indicated by a reference number. For names of fish taxa, names of reservoirs and lakes and authorities see Table 3. Barbs of Lake Tana are indicated by TA

Malawi (# 12), and the Indian glassfish in Lake Veli in S. India (# 27). The highest biomass observed (approximately 800 kg ha^{-1}) was a phytoplanktivorous cyprinid in the eutrophic reservoir Tissawewa in Sri Lanka (# 21). For all other fish taxa ($n = 13$) biomass values ranged between 40 and 300 kg ha^{-1}. Within this range, trophic state seemed to have no effect on the biomass of the fish taxa (Fig. 6a).

Productivity (annual *P*/*B* ratio) of small fish taxa ($n = 20$) varied from 1.4 for the Indian glassfish in the S. Indian Lake Veli (#27) to 6.0 for the clupeid *Limnothrissa miodon* in Kariba reservoir (# 17) (Table 3; Fig. 6b). The estimated *P*/*B* ratios of the small *Barbus* species from Lake Tana (# TA-6, TA-7) of 3.1–4.7 fall within the range of values of other small cyprinids (# 12, 21, 22, 23 and 24) and are relatively high in comparison with most other cyprinid taxa. Most often the clupeids (# 1, 2, 3, 16, 17 19, 20, 28) and the characid *Alestes* spp. (# 4) have a higher productivity than the cyprinid taxa. Hence, productivity seems to depend predominantly on the taxonomic position of the fish and less on the trophic status of the waterbody the fish inhabits.

Limiting factors for the Barbus production in lake Tana

Since several oligotrophic/mesotrophic lakes are able to support much higher biomass stocks of small fish taxa than Lake Tana (Fig. 6a), it seems plausible that *Barbus* stocks in Lake Tana are either bottom-up limited by their resources or top-down limited by predation. At first glance it seems unlikely that the *Barbus* spp. are limited by the zooplankton production because only about 29% of the zooplankton production is consumed by them. Apart from the two *Barbus* spp. only juvenile labeobarbs of all species, and adult *Labeobarbus brevicephalus*, are zooplanktivores (Nagelkerke & Sibbing, 2000). The latter species represents approximately one-third of the *Labeobarbus* stock in the lake (Palstra et al., 2004) and consumes only about 1% of the zooplankton production annually.

This poor zooplankton utilisation can be caused by morphological restrictions of the zooplanktivore, or because of characteristic of the zooplankton individuals (e.g. small size, escape behaviour). The size of the zooplankton in Lake Tana is relatively large for a tropical lake, which is favourable for small zooplanktivores (Ariyaratne et al., 2008). The main reason for the poor zooplankton utilisation would then not be size, but probably the escape behaviour of especially the calanoid copepods (*Thermodiaptomus galebi*). Calanoid copepods represent on average 57% of the total zooplankton production in Lake Tana (Table 2), but in the barb's diets they only represent 2.7 and 9.6% of the zooplankton for *B. tanapelagius*

Table 3 Overview of small predominantly planktivorous fish taxa of 17 tropical lakes and reservoirs in Africa and Asia of which biomass, yield, and/or productivity (*P*/*B*) are known

#	Water body	Taxon	References
1	L. Tanganyika	*Limnothrissa miodon*	Pearce (1988)
2		*Stolothrissa tanganicae*	Roest (1978)
3		Clupeids	Marshall (1995), Sarvala et al. (1999)
4	L. Turkana	Alestes spp.	Kolding (1993)
5	L. Kivu	Clupeids	Marshall (1995)
6	L. Tana	*Barbus humilis*	This study
7		*Barbus tanapelagius*	This study
8	L. Victoria	Benthivorous haplochromines	Moreau (1995)
9		Planktivorous haplochromines	Moreau (1995)
10		Predatory haplochromines	Moreau (1995)
11		*Rastrineobola argentea*	Moreau (1995), Pitcher et al. (1996)
12	L. Malawi	*Engraulicypris sardella*	Degnbol (1993)
13	L. Chilwa	*Barbus paludinosus*	Furse et al. (1979)
14	Cahora Bassa reservoir	Clupeids	Marshall (1995)
15	Kariba reservoir	Clupeids	Marshall (1995)
16		*Limnothrissa miodon*	Moreau et al. (1997)
17		*Limnothrissa miodon*	Marshall (1995), Machena et al. (1993)
18	Nam Ngum Reservoir	*Clupeichthys aesarnensis*	Mattson et al. (2001)
19	L. Taal	*Sardinella tawilis*	Baluyut (1999)
20	Parakrama Samudra Res.	*Ehirava fluviatilis*	Duncan (1999)
21	Tissawewa reservoir	*Amblypharyngodon melettinus*	Pet et al. (1996)
22		*Barbus chola*	Pet et al. (1996)
23		*Barbus dorsalis*	Pet et al. (1996)
24		*Rasbora daniconius*	Pet et al. (1996)
25	Sirikit reservoir	*Clupeichthys aesarnensis*	EGAT (1991)
26	Sirindhorn reservoir	*Clupeichthys aesarnensis*	EGAT (1991)
27	L. Veli	*Chanda ranga*	Aravindan (1993)
28	Ubolratana reservoir	*Clupeichthys aesarnensis*	Chookajorn et al. (1994)

See also Fig. 6

and *B. humilis*, respectively (Dejen et al., 2006a). Catching calanoids is challenging for small planktivorous fish since these copepods are fast swimmers and therefore have better chances to escape predation than cyclopoid copepods and cladocerans (Drenner & McComas, 1984). Apparently, both *Barbus* spp. are not well suited to prey on these fast-moving zooplankton species, in contrast to many freshwater clupeids that successfully feed on calanoid copepods (Ariyaratne et al., 2008). An evolutionary reason for this might be that the planktivory of the small *Barbus* species is a relatively novel evolutionary development, since they originate from riverine ancestors, which were not specialised zooplanktivores. In contrast, freshwater clupeids have ancestors of marine origin, which probably already were specialised zooplanktivores (Ariyaratne et al., 2008). This means that the food available for the small barbs is predominantly limited to cladocerans and cyclopoid copepods, amounting to 43% of the zooplankton production and resulting in a potential production of zooplanktivorous fish of 79 kg ha^{-1} year^{-1}. This number is much closer to the estimated 52.9 kg ha^{-1} year^{-1} (Table 1), than the 185 kg ha^{-1} year^{-1} of potential zooplanktivore production when calanoids are included in the equation. The densities of cladocerans and cyclopoid copepods showed large fluctuations during the year (Dejen et al., 2004). It is therefore likely that food was limiting growth and production of the two *Barbus* spp. during relatively short periods when cyclopoid copepod and cladoceran densities were low.

Annually the piscivorous labeobarbs consume about 29 kg fresh wt ha^{-1} of small barbs, which corresponds to 56% of the small barb production. This seems a low predation pressure, but there are also other predators of the small *Barbus* species in the lake, such as the common *C. gariepinus* and an array of bird species, such as terns (*Chlidonias* spp.), gulls (mainly *Larus* spp.), African darter (*Anhinga rufa*), long-tailed cormorant (*Phalacrocorax africanus*) and several heron species (mainly *Egretta* spp.; Nagelkerke, 1997). The piscivorous birds will be especially effective during the period of low water levels at the end of the dry season in May–June when water levels are 2.0–2.5 m lower than during the rainy season (Wondie et al., 2007). This could lead to increased mortality during the dry season. It therefore seems likely that at certain times in the year *Barbus* production was limited by either the availability of cladocerans and cyclopoid copepods, or by increased predation by birds.

Fisheries management aspects

We compared the estimated MSY of the small barbs of Lake Tana (TA) with 10 fisheries on small fish taxa from other tropical lakes and reservoirs (Table 3; Fig. 6c). The highest recorded yield was for a clupeid species (*Sardinella tawilis*) in a eutrophic crater lake in Philippines (# 19), all other values were much lower, ranging between 0.1 and 68 kg fresh wt ha^{-1} year^{-1}. The small cyprinid *Rastrineobola argentea* from eutrophic L. Victoria (# 11) showed similar yields as clupeids from oligotrophic/mesotrophic lakes in Africa and Asia (# 16, 17, 18) and was much higher than the predicted yield of the two small barbs from the oligotrophic/mesotrophic Lake Tana. The predicted yield for the two small barbs of Lake Tana falls within the same range as the realised yields of the small cyprinid *Engraulicypris sardella* in oligotrophic L. Malawi (# 12) and of the small clupeid *Clupeichthys aesarnensis* in three Thai reservoirs (# 25, 26, 28). This suggests that also in Lake Tana such a fishery on small barbs could be feasible if the existing fisheries, which focuses on Nile tilapia, African catfish and labeobarbs (de Graaf et al., 2006), are not endangered.

Conservation of the existing fisheries resources is the primary concern for managers of the Lake Tana fishery (Zikre Hig, 2003). One of the major problems at the moment is over-exploitation of the large *Labeobarbus* species (de Graaf et al., 2006). The exploitation of small cyprinids, low in the food web might alleviate this problem, although care should be taken not to over-exploit the food base of the piscivorous species of Lake Tana. In order to evaluate the viability of a fishery on the small *Barbus* species a first estimate of the MSY is important. We estimated for the whole of Lake Tana an MSY of 1,000–2,300 t fresh wt year^{-1} for *B. humilis*, and 1,200–3,400 t fresh wt year^{-1} for *B. tanapelagius.*

Since the biomass of small barbs is relatively high in the sublittoral (mean 28.6 kg fresh wt ha^{-1}), which is easily accessible for artisanal fishermen in unmotorised boats, a marginal fishery on small barbs may be possible here. The sub-littoral accounts for 20% of the lake surface, resulting in an estimated MSY of both species of about 1,800 t fresh wt year^{-1}. Despite the biological potential for a subsidiary fishery for small barbs in the sub-littoral zone in Lake Tana, we advise to be cautious in promoting this fishery, because the sub-littoral area is also the main habitat of juvenile *Labeobarbus* species (Dejen et al., 2006a), and because the small barb species form the main food base for the piscivorous *Labeobarbus* species. We therefore recommend first an experimental fishery under strict control of fisheries managers of the Amhara Region Agricultural Research Institute (ARARI) in close cooperation with the Bureau of Agriculture and Rural Development (BoARD) and evaluation of these results before a decision is made on granting permission for a fishery on small barbs in Lake Tana.

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