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The composition of fish communities of nine Ethiopian lakes along a north-south gradient: threats and possible solutions

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Abstract

Fish populations of nine Ethiopian freshwater lakes were quantitatively sampled with a standardized protocol, using multi-mesh gill nets. In total, 27 species were identified, but only 14 species were common. Based on the common species, the fish communities showed large differences in their species composition, except for Lake Abaya and Lake Chamo which were similar. Most fish species were observed in only one or two lakes. Compared with the information reported in literature the present study generally underestimated the species richness. The empirical model of Amarasinghe and Welcomme (2002) for African lakes was used to estimate fish species richness, which was compared with species presence reported in literature. Biodiversity in the two northern highland lakes is low, but not lower than the model estimate. Lake Tana has a high biodiversity which is close to what is estimated by the model, but three Rift Valley lakes have low biodiversity, lower than estimated by the model. There are also strong indications for the Rift Valley lakes that species richness was higher in the past because the species richness reported in the older literature was generally much higher than those observed by us in the present study and those reported in the more recent literature. Threats like overfishing, high sediment load and degradation of habitats were identified. It is recommended that Ethiopia should develop guidelines for fishery legislation and implement it through an enforcement agency. Moreover, catchments management should be practiced to save the water bodies and their fish communities.

Keywords

Fish assemblages; conservation biology; habitat degradation; species abundance; community structure

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Introduction

Conservation of communities implies knowledge of the number and distribution of species of any particular area. As habitat degradation continues on a global scale, maintenance of species richness has become a central issue of conservation biology. This is particularly the case with the fish fauna of inland waters. Habitat alteration and destruction is generally the major cause of most extinctions of freshwater fishes (Thomas, 1994; Lévêque et al., 2008). Fish communities differ per water body, hence site-specific management is important in fishery biology and fish community conservation. In the past fishery biologists and managers, particularly those working in tropical countries, traditionally have tended to consider fish in isolation, as a natural renewable resource, rather than as an integral component of the aquatic ecosystem interacting with other components of the system (Lévêque, 1995). This attitude has led to various ecological disasters; therefore, a better understanding of the role of fish diversity in the functioning of ecosystems should be a precondition before manipulation of African inland waters is undertaken.

In the classical limnological approach, it was usual to regard freshwater ecosystems as operating in a physical-chemical environment which conditions the food chain from primary producers to top predators (Le Cren and Lowe-McConnel, 1980; Kalff, 2002). In this 'bottom-up' control, competition between primary producers for limited nutrients determines the state of the higher trophic levels. However, the role of fish regulating the structure and functioning of freshwater ecosystems has become generally accepted (e.g. Northcote, 1988; Hunt et al., 2003). This 'top-down' control implies that fishes have direct effects on the abundance of their resources (e.g. periphyton, macrophytes, phytoplankton, zooplankton, benthic invertebrates) and as a result also on water transparency and primary and secondary production. The number of species present or species richness, a qualitative approach, is one way of characterizing a fish community. But this approach ignores the species population abundance and size composition which are essential aspects of the community as well (Begon et al., 1996). Therefore, a quantitative approach assessing relative population densities based upon the catch per unit effort (CPUE, numbers) was used in the present study.

In Ethiopia the rate of degradation of the environment, mainly by deforestation and overgrazing of grasslands by cattle, is very high (Gebre-Mariam, 2002) and leads to approximately 1.5 billion tons of soil lost every year from the highlands (Teferra, 1994). This has already resulted in a decrease in biodiversity of the fish fauna in the different drainage basins and the Rift Valley Lakes. Getahun and Stiassny (1998) compared the number of fish species in Ethiopian drainage basins in the northern and central highlands, the eastern highlands, the Ethiopian Rift Valley and Afar lowlands and the Rift Valley Lakes during the period 1835 to 1995 on the basis of literature with the results from their own surveys in 1995-1997. They reported a reduction in species numbers for each of the drainage basins varying from 40-85% and a reduction of species numbers for the Rift Valley Lakes as a whole of ca. 65%.

Hydroelectric projects and channelling for irrigation have deleterious effects on the biota of freshwater systems (Roberts, 1993). This is brought about through reduction of water levels thereby altering, pH, nutrient regimes and sediment levels. Dams, unless carefully designed, affect most migratory fishes thereby hindering reproduction. In Ethiopia there are several major projects currently under implementation or due to take place in the future in the Omo-Gibe, Baro-Akobo and the Blue Nile (reviewed by Getahun and Stiassny, 1998). The Ethiopian Nile Irrigation and Drainage Project (ENIDP), financed by the World Bank, is engaged with several irrigation projects around Bahir Dar. One of them is the irrigation of 14 460 ha of agricultural land in the lower Ribb River watershed on the east side of Lake Tana. Furthermore, the Ministry of Water Resources of Ethiopia (MoWR) is financing the upstream Ribb Dam for irrigation, water storage and for flood management of Lake Tana (Burnside, 2008). Currently, several feasibility studies for irrigation and flood management are carried out on other feeding rivers of Lake Tana.

The potential effects of such large-scale schemes on Ethiopia's freshwater systems can only be assessed if the current biodiversity is known. Ethiopia has a large variety of freshwater lakes, but except for Lake Tana and Lake Abaya fish communities were rarely studied in a quantitative way. Nine freshwater lakes were selected for a comparative study. These lakes show large differences in size (range: 20-3000 km^2) and productivity, and are located at altitudes varying from 1233 m to 2409 m above sea level (table 1). The higher the altitude, the more temperate the climatic conditions are. Most of these lakes are currently not interconnected, but L. Chamo and L. Abaya (southern Rift Valley Lakes) were connected until a few decades ago and Lake Ziway and Lake Langano are interconnected by rivers via L. Abijata (Baxter, 2002).

Table 1.
Morphometric characteristics of the nine study lakes. Data on Rift-valley lakes from Kebede et al. (1994) and Gebre-Mariam et al. (2002); data on L. Tana from Rzoska (1976) and Dejen et al. (2004); data on L. Hayk from Baxter and Golobitsch (1970); data on L. Ashenge by Marshall (2006). For locations of water bodies see fig. 1.

Lake name	Lake abbreviation	Altitude (m)	Catchment area (km^2)	Lake area (km^2)	Mean depth (m)
Ashenge	AS	2440	82	15.4	14
Hayk	HA	2030	2700	35	23
Tana	TA	1830	16 500	3200	8
Koka	KO	1660	?	200	5
Ziway	ZW	1636	7025	434	2.5
Langano	LG	1582	1600	241	17
Awassa	AW	1680	1250	129	11
Abaya	AB	1285	17 300	1160	7.1
Chamo	CH	1233	2210	551	10

Six questions were addressed: 1) What is the catch per unit effort in each lake and is the CPUE in terms of biomass related to algal biomass? 2) What is the community structure in terms of species composition and what are the differences among lakes? 3) What is the size structure of the fish communities and what are the differences among lakes? 4) Are communities in lakes located at similar altitudes more similar to each other than fish communities in lakes located at different altitudes? 5) What are the drivers of change in biodiversity of the lake communities? 6) What management measures can be recommended to optimize the fisheries without harming the biodiversity?

Materials and methods

The survey was carried out in the dry season during four field trips in the period between 15 November 2004 and 20 January 2005. Three lakes were selected in the highlands of Ethiopia in the north and six in the Rift Valley in the south (fig. 1).

The physical parameters were measured between 09:30 and 13:30 at three sampling sites in the open water zone. Water samples were collected just below the surface at a depth of ca. 0.5 m and were pooled before filtration. All measurements were carried out in triplicate. Water temperature was measured at 1 m intervals over a vertical transect from just below the surface to 10 m depth (or less when depth was <10 m). Light penetration in the water column was determined with a standard Secchi-disk (25 cm in diameter). Ash weight was measured as an estimate of silt load. Depending on seston and silt concentrations 250-900 ml of lake water was filtered through Whatman GF/C filters. Ash weight was determined by collecting seston and silt on pre-washed and pre-weighted filters. After collection the filters were dried and weighted on a microbalance, then the contents on the filters were ashed in an oven at 550°C for 24 h and weighted again on a microbalance. Filters with chlorophyll were stored in a freezer for 5-15 days. As extraction solvent acetone was used; the absorbance of the centrifuged extract was then measured spectrophotometrically before and after acidification (ISO, 1992).

Fishes were sampled at two stations (one inshore, one in open water) during three successive days and nights. Sampling was done over substrate which was representative for each lake; it consisted usually of a rock bottom covered by a layer of fine sediment, but in Lake Hayk it was pure rock and in Lake Awassa a hard sandy bottom. Our inshore sampling was always near macrophyte fields but never within the vegetation.

Gillnets of varied mesh sizes were used: one multi-mesh monofilament gillnet with small mesh sizes (5, 8, 10, 15 and 19 mm bar mesh) and one multifilament gill net with large mesh sizes (25, 30, 38, 45 and 55 mm bar mesh). The panel length of each mesh size was 15 m and the depth 1.5 m. In the shallow inshore stations one set of two multi-mesh nets were set: one net with small meshes and one with large meshes, whereas in the deeper open water four nets were set (one set at the surface and one set at the bottom). When the water depth was more than 10 m the bottom

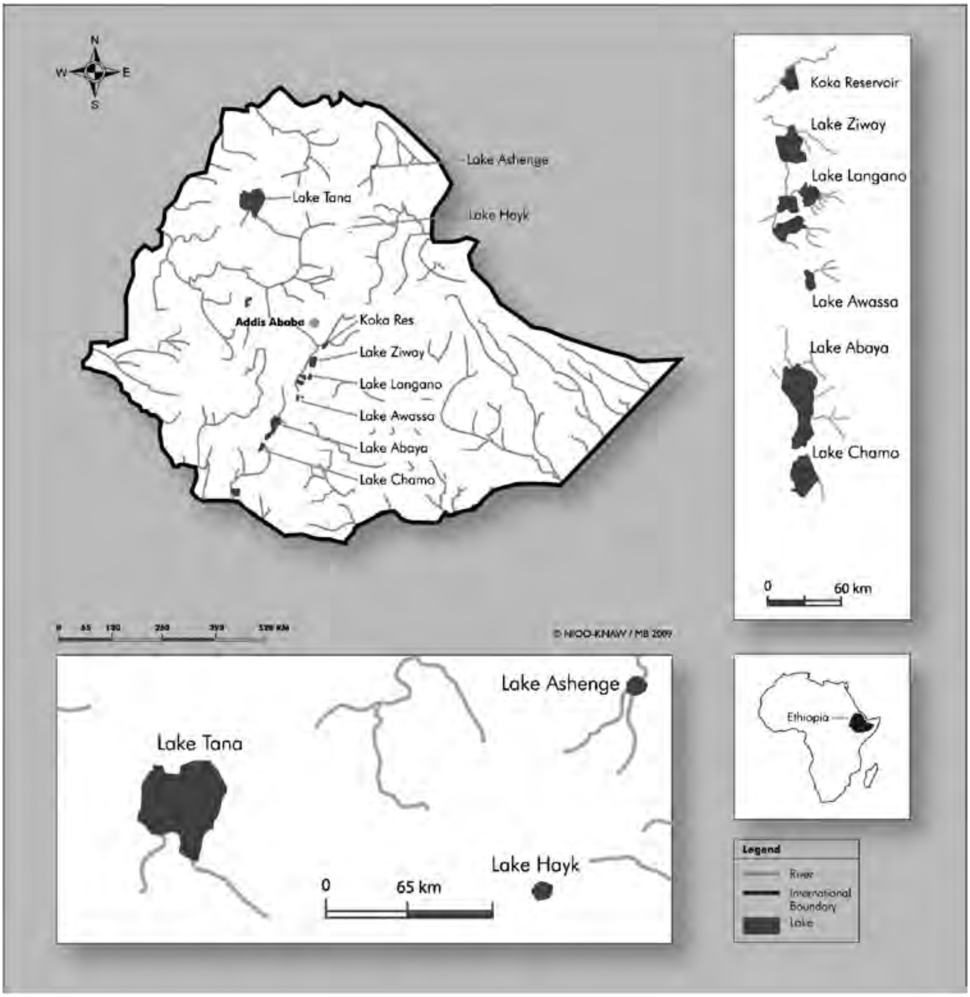

Figure 1. Map of Ethiopia showing the locations of all nine study lakes in Ethiopia and the position of Ethiopia in Africa.

nets were set between 7 and 15 m. Nets were set just before dusk; the exposure time was 2 h for the small meshed net and 15 h for the large meshed net. The Fisheries Effort per lake was 2025 m^2 net-hours for the small meshed nets and 15 188 m^2 net-hours for the large meshed nets; Catch Per Unit Effort (CPUE) was expressed as catch per 100 m^2 net per hour. A total of 22 305 fish specimens were caught.

To test differences of chlorophyll content (μg l^{-1}) and Catch Per Unit Effort (CPUE, kg) among lakes analysis of variance (ANOVA) was performed with lake as class variable. Chl-a and CPUE values were $\log_e$-transformed to ensure normality of residuals and homogeneity of variance. Multiple pair-wise comparisons were performed using the post-hoc Tukey method to test differences between specific lakes. All statistical tests were performed with SAS 9.2.

In order to compare the fish species richness from our surveys with expectations we used the empirical model of Amarasinghe and Welcomme (2002). They concluded that species richness (S) in Africa can be best estimated by a combination of lake area (A, km^2) and altitude (Alt, m) using the equation:

$$\mathrm{Ln\,S} = 0.3813\,\mathrm{Ln\,A} - 0.0007\mathrm{Alt} + 1.4722 \quad (R^2 = 0.71,\ P < 0.001,\ N = 30)$$

Results

Physical parameters

Average water temperatures varied between 19 and 26°C, with the lowest values observed in the mountain lake Ashenge (altitude 2409 m) in the north, and the highest temperature in L. Chamo (altitude 1233 m) in the south (figs 1, 2a). Lake Tana and Koka Reservoir showed relatively low temperature values whereas the lakes in the Southern Rift Valley were warmer. The northern crater lake, L. Hayk, in the highlands showed a surprisingly high water temperature of 22°C (altitude 2030 m). There is significant correlation between altitude and water temperature ($R^2 = 0.64$, $P < 0.01$; fig. 3). After a log-log transformation of the data there is also a strong and highly significant correlation between sediment load and Secchi-disk depth ($R^2 = 0.92$, $P < 0.01$), but not between chlorophyll content and Secchi-disk depth ($R^2 = 0.30$, $P = 0.16$). Secchi-disk depth varied between 6.5 and 0.1 m (fig. 2c). Sediment load was high in Koka Reservoir and Lakes Ziway, Langano and Abaya (fig. 2b). The highest values, indicating high water transparencies, were observed in two northern lakes, L. Ashenge and L. Hayk, the lowest in some of the Rift Valley Lakes (Ziway, Langano and Abaya).

Fish communities and chlorophyll

There was a significant effect of lake on chlorophyll-a concentrations (ANOVA: $F_{8,15} = 32.8$, $P < 0.0001$) and on catch per unit of effort (CPUE, in kg) (ANOVA: $F_{8,18} = 28.9$, $P < 0.0001$). Very low chlorophyll contents and very low CPUE values were observed in L. Ashenge, L. Hayk and L. Langano. Multiple pair-wise comparisons showed that the differences in chlorophyll concentrations between L. Ashenge, L. Hayk and L. Langano were non-significant, but in each of these lakes significant lower than the concentrations in Koka Res., L. Ziway, L. Abaya and L. Chamo (fig. 4a). The chlorophyll concentrations in L. Hayk were not significant different from those in L. Tana, and L. Langano, but significantly lower than in Koka Res., L. Ziway, L. Awassa, L. Abaya and L. Chamo. Multiple pair-wise comparisons showed that the differences in CPUE between L. Ashenge, L. Hayk and L. Langano were non-significant, and in each lake significant lower than the CPUE in the remaining six lakes (fig. 4b). The CPUE of L. Chamo was significant higher than Koka Res. and L. Abaya, but not significant different from L. Tana, L. Ziway and L. Awassa. A direct correlation between chlorophyll contents and CPUE showed a sig-

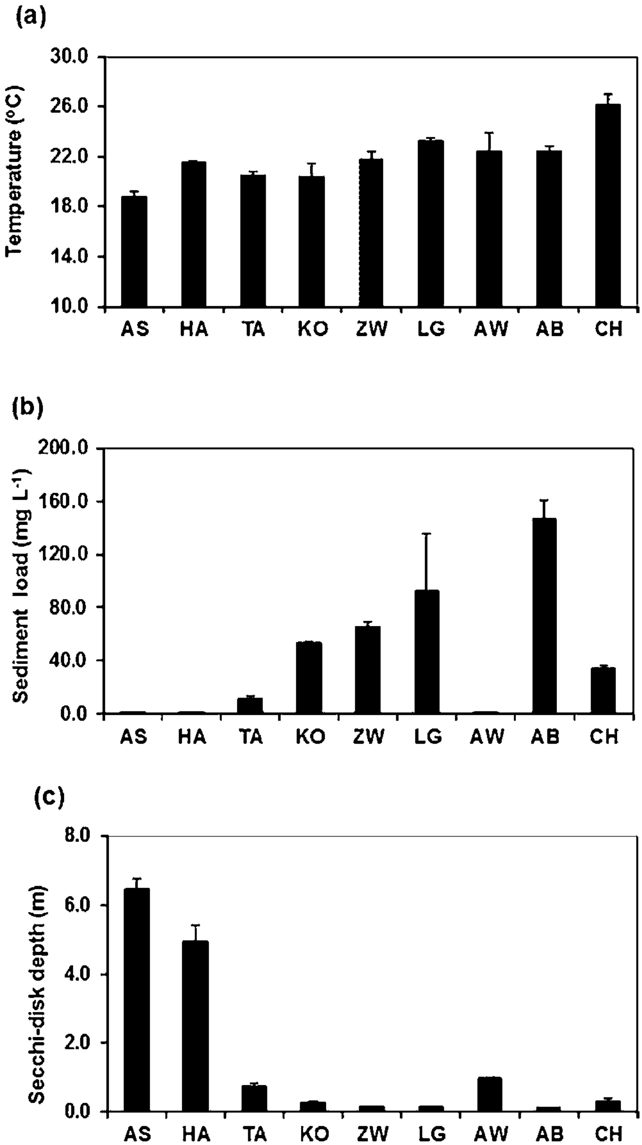

Figure 2. Environmental parameters showing (a) water temperatures (°C), (b) sediment load (mg l^{-1}), and (c) Secchi-disk depth (m) in the nine study lakes. For abbreviations of lakes see table 1. Error bars indicate +1 SD (n = 3).

nificant positive linear relationship (CPUE = 0.15 + 0.047 chlorophyll; $R^2 = 0.50$, $P < 0.05$).

In total 22 305 specimens belonging to 27 species were identified from the nine lakes, but only 12-14 species were common or abundant (i.e. relative densities or biomass $\geqslant$ 3%) (table 2, fig. 5). Based on the common and abundant species, the fish communities showed large differences in their species composition, except for

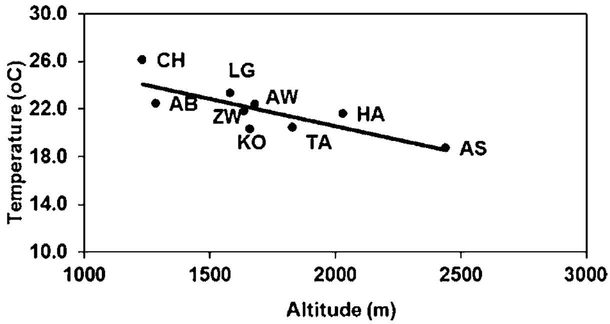

Figure 3. The relationship between mean water temperature (°C) and altitude (m) observed in the nine study lakes. The linear regression between temperature and altitude is significant ($R^2 = 0.64$, $P < 0.01$).

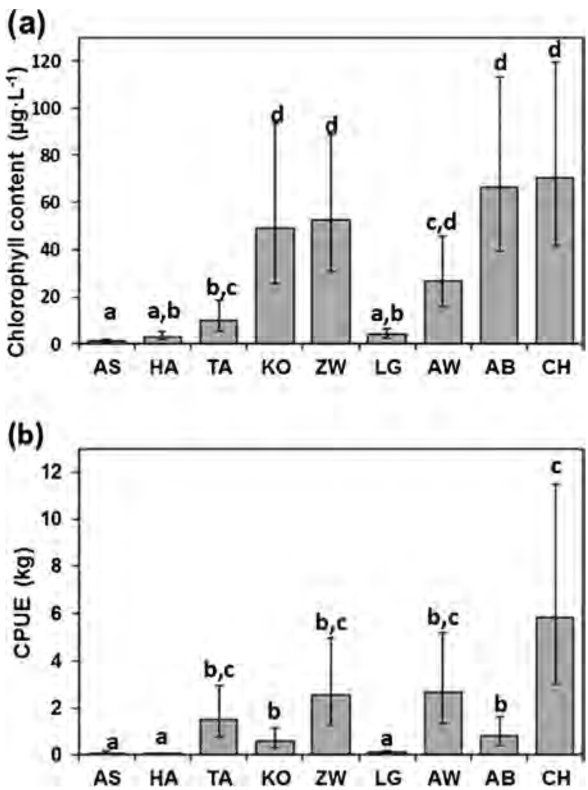

Figure 4. Multiple pair-wise comparisons (Tukey post-hoc test) of (a) chlorophyll content (μg l^{-1}), and (b) Catch Per Unit Effort (CPUE, kg) among lakes. For abbreviations of lakes see table 1. Identical letters indicate a non-significant difference ($P \geqslant 0.05$).

Table 2.
Fish species caught in the nine study lakes, with species abbreviations, number of lakes in which each species was observed, and name of these lakes. ♦: introduced exotic species, *: endemic species. AS: L. Ashenge, HA: L. Hayk, TA: L. Tana, KO: Koka Res., ZW: L. Ziway, LG: L. Langano, AW: L. Awassa, AB: L. Abaya, CH: L. Chamo.

Species	Abbr.	Family	No. of lakes	Lakes
Bagrus docmac	BD	Bagridae	2	CH, AB
Barbus amphigramma	BA	Cyprinidae	1	AW
Barbus humilis	BH	Cyprinidae	1	TA
Barbus paludinosus	BP	Cyprinidae	2	ZW, LG
*Barbus tanapelagius**	BT	Cyprinidae	1	TA
Clarias gariepinus	CG	Clariidae	6	HA, TA, KO, ZW, LG, AW
Cyprinus carpio♦	CC	Cyprinidae	3	HA, KO, ZW
Garra dembecha	GD	Cyprinidae	6	HA, TA, KO, AW, LG, ZW
Garra ignestii	GI	Cyprinidae	1	AS
*Garra regressus**	GR	Cyprinidae	1	TA
*Garra tana**	GT	Cyprinidae	1	TA
Hydrocynus forskahlii	HF	Characidae	2	AB, CH
*Labeobarbus acutirostris**	LA	Cyprinidae	1	TA
*Labeobarbus brevicephalus**	LB	Cyprinidae	1	TA
*Labeobarbus gorgorensis**	LG	Cyprinidae	1	TA
Labeobarbus intermedius	LI	Cyprinidae	7	TA, KO, ZW, LG, AW, AB, CH
*Labeobarbus longissimus**	LL	Cyprinidae	1	TA
*Labeobarbus macrophtalmus**	LMA	Cyprinidae	1	TA
*Labeobarbus megastoma**	LME	Cyprinidae	1	TA
*Labeobarbus nedgia**	LN	Cyprinidae	1	TA
*Labeobarbus truttiformis**	LT	Cyprinidae	1	TA
Lates niloticus	LAN	Centropomidae	1	AB
Oreochromis niloticus	ON	Cichlidae	7	AS, HA, TA, KO, ZW, LG, AW
Schilbe intermedius	SI	Schilbeidae	1	AB
Synodontis schall	SS	Mochokidae	2	CH, AB
Tilapia zillii♦	TZ	Cichlidae	1	ZW
Varicorhinus beso	VB	Cyprinidae	1	TA

L. Abaya and L. Chamo which were dominated by the same larger fish species (*Synodontis schall*, *Hydrocynus forskahlii*) (fig. 5). This high similarity is not surprising because both lakes are bordering each other and were, until recently, connected. All other lakes, with the exception of L. Langano and L. Ziway, are isolateded lakes.

The species composition based on numbers (fig. 5a) differs from the species composition based on biomass (fig. 5b) in some aspects. Especially in four of the nine lakes where small species dominate differences are relatively large. In the fish

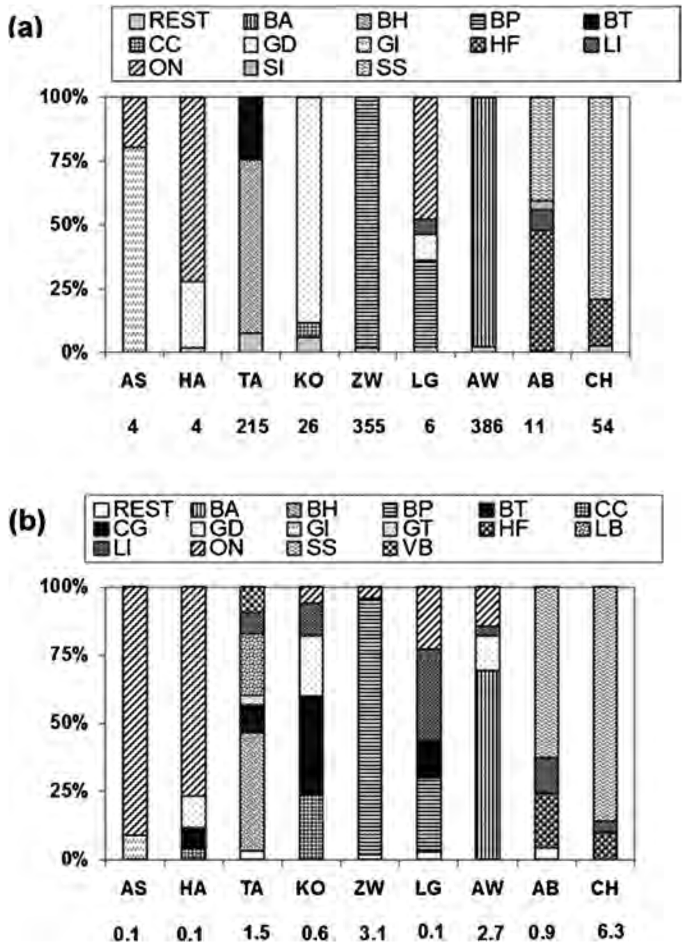

Figure 5. Community structure in terms of species composition (%) based on (a) numbers, and (b) on biomass. Numbers below columns represent CPUE in numbers (a) and biomass in kg wet weight (b). For abbreviations of lakes see table 1, for abbreviations of fish species see table 2. For clearness, the endemic *Labeobarbus* spp. (LB) in L. Tana were pooled together. Species representing a relative density or biomass $< 3\%$ were pooled in the Rest group.

communities based on biomass often the larger species dominate (fig. 5b). In L. Ashenge Nile tilapia is much more important in terms of biomass and *Garra* is almost negligible. In L. Tana the labeobarbs and *Varicorhinus beso* reach substantial proportions and the small barbs are much smaller in abundance. In Koka reservoir African catfish and common carp are abundant in terms of biomass and *Garra* is much less dominant. Finally, in L. Langano *Labeobarbus intermedius* and African catfish are much more abundant in terms of biomass than in terms of numbers, whereas the opposite holds for Nile tilapia.

Tana harboured the largest number of endemic species ($n = 11$) (table 2). The *Labeobarbus* species in L. Tana are dominated by the endemic *L. brevicephalus*,

Table 3.
Fish species richness in the nine study lakes.

Lake	All species	Species contributing ⩾1% of abundance
Ashenge	2	2
Hayk	4	3
Tana	17	3
Koka	5	5
Ziway	4	2
Langano	5	5
Awassa	5	2
Abaya	6	4
Chamo	4	3

whereas the in Ethiopia widely distributed *L. intermedius* is sub-dominant. The three *Garra* spp. (table 2), of which two endemics, were dominated by *G. tana*.

Most fish species were observed in only one or two lakes. However, five species occurred in three or more lakes (table 2). These were *Oreochromis niloticus* (Nile tilapia), *Labeobarbus intermedius* (common large barb), *Clarias gariepinus* (African catfish), *Garra dembecha*, and *Cyprinus carpio* (common carp) (table 2). With the exception of L. Tana all fish communities showed a low species richness (maximum of 6 species). The biodiversity was much influenced by rare (i.e. relative densities (numbers) $< 1\%$) species. If we exclude these rare species, all lakes including L. Tana showed a low fish species richness (maximum of 5 species: table 3, fig. 5). Especially small barbs (*Barbus amphigramma*, *B. humilis*, *B. paludinosus*, *B. tanapelagius*) reached very high relative densities in L. Tana, L. Awassa and L. Ziway (92-98% of the total catch) and substantial relative densities in L. Langano (ca. 35% of the total catch) (fig. 5). The small *Garra* from L. Ashenge and Koka Reservoir also reached relatively high densities (80-88% of the total catch), whereas L. Hayk contained substantial densities of *Garra* (ca. 25%). The size composition of the Nile tilapia (*O. niloticus*) was very different in L. Ashenge as compared to L. Hayk. In L. Ashenge predominantly large tilapias (average weight 150 g) were caught, whereas in L. Hayk the catch was dominated by small ones (average weight 15 g). L. Langano was characterised by a relatively high abundance of small Nile tilapia (*O. niloticus*) and small *Garra* spp. The catfish *Synodontis schall* which is dominant in L. Chamo (80% of the total catch) is a relatively large fish (average weight 125 g) and present in substantial numbers in Lake Abaya. In both lakes the tiger fish (*Hydrocyon forskalii*) is also abundant.

On basis of the size composition two different categories of fish communities can be distinguished: 1) fish communities which are dominated in numbers by small *Barbus* spp. (maximum length 10 cm) as in L. Tana, L. Ziway and L. Awassa, and 2) fish communities where the relatively large (maximum length 28 cm) *Synodontis* *schall* is present in relatively large numbers (i.e. L. Abaya and L. Chamo). All other lake fish communities are intermediate in their size composition.

Species richness

Much qualitative information is available about the biodiversity of the fish fauna in the Ethiopian lakes surveyed, except for the two northern lakes, L. Ashenge and L. Hayk. Compared with the information reported in the literature the present study generally underestimated the species richness by 20-60% (fig. 6). Our best estimates were for Koka Res. and L. Awassa, where only one species (*Aplocheilichthys antinorii*) was missed, followed by Lakes Langano and Ziway where two species were missed. The highest proportion of fish species missed was in Lakes Abaya and Chamo, which have the most diverse fish fauna of the studied Rift Valley Lakes.

The question remains whether the species richness of these lakes is higher or lower than may be expected from an African lake. The empirical model of Amarasinghe and Welcomme (2002) was used to estimate fish species richness of the nine study lakes on the basis of their area and altitude. In this model, which is based on information from 30 African lakes, species richness is positively correlated with lake area and negatively with altitude. For all the three northern lakes (L. Ashenge, L. Hayk and L. Tana) the model estimated accurately the observed biodiversity and in the two other cases (L. Abaya, L. Awassa) the estimate was close to the observations based on literature data (fig. 6). In three Rift Valley Lakes (L. Ziway, L.

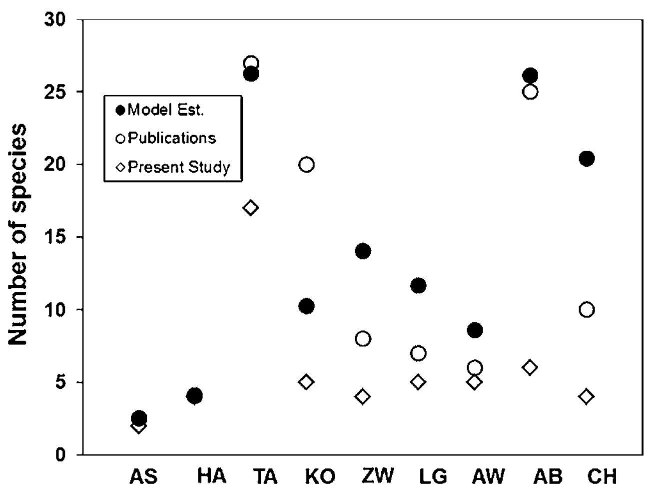

Figure 6. Number of fish species observed in the nine study lakes according to recently published studies, according to estimates based on the empirical model for African lakes (Amarasinghe and Welcomme, 2002) and according to the present study. Literature used: L. Tana (Nagelkerke and Sibbing, 2000; De Graaf et al., 2006), Koka Res. (Vanden Bossche and Bernacsek, 1991), L. Ziway (Vanden Bossche and Bernacsek, 1991), L. Langano (Seyoum, 1990; Golubtsov et al., 2002), L. Awassa (Golubtsov et al., 2002; Bjørkli, 2004); L. Abaya (Vanden Bossche and Bernacsek, 1991) and L. Chamo (Golubtsov et al., 2002).

Langano and L. Chamo) the estimated species richness was distinctly higher than the reported species number per lake.

Discussion

Environmental conditions

The northern crater lake, L. Hayk, showed in spite of its high altitude (i.e. 2030 m) a surprisingly high water temperature. This may have been the result of volcanic activity. In this lake clear water conditions were observed (Secchi-disk depth ca. 5 m), low chlorophyll content (<5 μg l^{-1}) and relative high densities of cladoceran zooplankton densities (numbers $\pm$ 1 SD) of *Daphnia magna* were 15.3 $\pm$ 1.6 and of *Diaphanosoma lacustris* 27.2 $\pm$ 1.6 per litre (Vijverberg, unpublished). In 1989 the lake appeared much more eutrophic and around that time massive fish kills occurred regularly (Kebede et al., 1992). Furthermore, cladocerans were lacking and only small copepodites were present. The average chlorophyll content over a vertical transect of 20 m was ca. 17 μg l^{-1} and the Secchi-disk depth 1.2 m. The authors suggest that this eutrophication had been caused by the introduction of the Nile tilapia (*O. niloticus*) in 1978. The conditions observed now were similar to the situation before 1970 when the lake was extremely clear, with a Secchi disk-depth of 9 m and a chlorophyll content of <1 μg l^{-1} (Baxter and Golobitsch, 1970) and the presence of large cladocerans like *Diaphanosoma* spp. and *Daphnia magna* (Cannicci and Almagia, 1947). The reason for this temporary eutrophication is unclear, but the increased water temperature suggests that the bottom layer of this lake is still showing geothermal activity, which may enhance the vertical mixing during periods of volcanic activity. This could have occasionally released nutrients from the volcanic bottom layers which are generally rich in nutrients.

In Lake Awassa, in comparison to the other Rift Valley Lakes, a relative high water transparency and low sediment load was observed. The silt content in the water is relatively low because the large swampy area to the east on the Tikur Wuha River acts as an efficient settling area for silt coming from the higher hills and mountains of the eastern escarpment of the Rift Valley (Kibret and Harrison, 1989).

The lake water of most Rift Valley Lakes contained considerable amounts of ash weight. Part of this weight will be ash residuals of phytoplankton since most algae contain 4-10% ash on the basis of total dry weight (Winberg et al., 1971). The water of L. Chamo, a lake with a relative high algal biomass (measured as chlorophyll content), contained only a moderately high ash weight, meaning that less eutrophic lakes with much higher ash weights per litre lake water contained higher sediment loads. It is striking that of the four Rift Valley lakes with high sediment loads three (Koka Res., L. Langano and L. Abaya) are characterised by low CPUEs.

The low chlorophyll content observed in L. Langano is confirmed by Taylor et al. (2002) who reported similar values (range: 2-7 μg l^{-1}). This low chlorophyll content in L. Langano is difficult to explain since this lake is not phosphorus- or nitrogen-limited (Kebede et al., 1994) and other Rift Valley Lakes like Koka, Ziway and Abaya have similar low water transparencies, but much higher chlorophyll contents. As a result of this low productivity, L. Langano has the lowest CPUE (biomass) of all the Rift Valley Lakes included in our study.

Community structure

Although there were a few exceptions, the community structure in terms of relative population densities varied much among lakes. Altitude was not a strong determinant of fish community structure, but had some effect. The two lakes located at the highest altitude range, L. Ashenge and L. Hayk (altitude: 2030-2409 m) were somewhat similar since in both lake communities were dominated by Nile tilapia and one *Garra* sp., but both were very different from L. Tana (altitude: 1830 m). Furthermore, the two lakes located at the lowest altitude range, Lakes Abaya and Chamo (altitude: 1233-1285 m) were much alike, and they differed much from the other more northern Rift Valley Lakes (altitude range: 1582-1680 m). Their similar fish community is probably the result of being until recently connected.

Quantitative assessments of fish species composition based on experimental fisheries are scarce for Ethiopian lakes. The best quantitative information is from L. Tana (e.g. Dejen et al., 2003, 2006, 2009; de Graaf et al., 2006, 2008) and from L. Abaya (Schröder, 1984). Our estimates for L. Tana agree with recent studies, although we overestimated to some degree the abundance of *B. humilis* and underestimated the importance of *B. tanapelagius*. This difference can be explained by our sampling strategy. Our fisheries effort in the offshore zone was twice the effort in the inshore zone, since the offshore zone in this large lake is ca. 9 times larger than the inshore zone (Dejen et al., 2006), this will lead automatically to an underestimation of the pelagic fish species like *B. tanapelagius*. Taking into account the relative low fisheries effort we employed for this large lake it is not surprising that in the present study ten rare fish species were not caught.

Schröder (1984) quantified the relative densities of the fish species of L. Abaya by intensive trawling during 1982. Of the ten species he caught, there were four common and six occasional or rare species. Although in the present study several of the less abundant fish species were missed our relative density estimates of the more common fish species agreed with the previous density estimates. Similar to our findings, Schröder (1984) reported that the fish community was dominated by the cat fish *Synodontis schall* (52% of the total catch, numbers) and that the Tiger fish (*Hydrocynus forskahlii*) and *Schilbe intermedius* were common. There was only one distinct difference, *Mormyrus caschive* (Mormyridae) which was common (13%, numbers) in the catch of Schröder (1984) was not caught at all in our survey.

Fish introductions

There are about ten exotic fish species introduced from abroad into Ethiopian freshwaters, and the Rift Valley is the region of Ethiopia with highest number of introduced fish species (Getahun and Stiassny, 1998; Golubtsov et al., 2002; Froese and Pauly, 2008). In only one of the nine water bodies studied (Koka Res.) an exotic fish species was abundantly present (*Cyprinus carpio*, common carp). This species was introduced in 1936-1940 in the Awash River system (Golubtsov et al., 2002). Of the other introduced fish species, in the present study only *T. zillii* was found in Lake Ziway (density $< 0.1\%$). Hence, it seems that exotic species do not play an important role in Ethiopian lake communities.

Habitat degradation due to irrigation

In Ethiopia there has been a great increase in the extent of irrigation schemes in recent years (Getahun and Stiassny, 1998; Getahun et al., 2008; Alemayehu et al., 2009). Water is being removed directly from the lakes and/or diverted from rivers that feed the lakes. This has created considerable water level declines in several Rift Valley Lakes (e.g. L. Ziway, L. Abijata) which damaged the breeding grounds of fish species that spawn in shallow parts of the lakes, such as Nile tilapia (*O. niloticus*) (Gebre-Mariam and Dadebo, 1989) and this has caused reduced tilapia stocks in L. Ziway (Gebre-Mariam, 2002).

The up river spawning migrations of seven endemic *Labeobarbus* species of Lake Tana are also affected by development activities such as small-scale irrigation and dam construction at the inflowing rivers (Anteneh et al., 2008; Getahun et al., 2008; Alemayehu et al., 2009; McCartney et al., 2010). Increased soil erosion brings excess sediment load and causes low oxygen content and mud cover on the gravel beds in the inflowing rivers and wetlands and flood plains are converted to agriculture (Mohammed et al., in press). This habitat degradation seriously affects the recruitment of these endemic species and threatens the biodiversity of L. Tana (Dejen, 2008).

Overfishing

Published records on landings are scarce from Ethiopian lakes. Among the given estimates few distinguish between the species composition or take into account species-specific differences in size composition. For most lakes catch and effort data are not available.

In all study lakes, fisheries is predominantly focussed on Nile tilapia (e.g. Abebe and Getachew, 1992; Bjørkli, 2004). It is only in L. Tana that *Labeobarbus* spp. are also heavily fished during a seasonal fishery (de Graaf et al., 2006). Before 15-20 years Nile perch used to contribute about 20% of the total fish landings from Lakes Abaya and Chamo, however, at this moment this is reduced to a very small proportion due to overfishing and the lack of proper fisheries management (Reyntjens et al., 1998).

In Lake Tana Nile tilapia was not overfished in 2001, but several migrating *Labeobarbus* species are probably seriously overfished by a seasonal fishery (de Graaf et al., 2004, 2006). Half of the labeobarb species seasonally migrate into inflowing rivers for spawning; others developed a lake spawning strategy (Nagelkerke and Sibbing, 1996; Palstra et al., 2004; de Graaf et al., 2005).

Recently, overfishing of tilapia was probably taking place in Lakes Chamo, Abaya, Awassa, Langano and Ziway (Reyntjes and Wudneh, 1998). There is a large variation in length at first maturity in different populations of Nile tilapia within the Rift Valley Lakes (Bjørkli, 2004). Maturation at a relative small size, i.e. 'dwarfing', is considered to be an adaptation to high fisheries mortality at the adult size. In L. Awassa and L. Ziway females matured at a small size (ca. 14 cm) indicating overfishing, whereas size at fist maturity in L. Chamo was much larger at about 42.0 cm indicating that overfishing is unlikely (Abebe and Getachew, 1992; Teferi and Admassu, 2002; Bjørkli, 2004).

In three out of nine lakes (L. Tana, L. Ziway and L. Awassa) the fish community was numerically dominated by small fish species (i.e. *Barbus* spp.) which represent a low economical value for fisheries. In marine fisheries a similar phenomenon has been observed. Due to overfishing of large-bodied fish species, there has been a gradual shift in fish capture from large and valuable carnivorous species to smaller, less valuable species that feed at lower trophic levels (Pauly et al., 1998). This trend has also been observed in freshwater fisheries where increasing fishing effort lead to a dramatic increase of the small ($<$8 cm) zooplanktivorous clupeid *Clupeichthys aesarnensis* and a decrease in the densities of its main predator *Hampala macrolepidota* (Mattson et al., 2001).

Species richness

Compared with the information reported in the literature we generally underestimated the species richness (fig. 6). Apparently most rare species were missed in our survey, most probably because our fishing effort was too low. This was especially true for the large lakes. However, there is also a strong indication for the Rift Valley lakes that species richness was higher in the past because the species richness reported by Vanden Bossche and Bernacsek (1991: table 1) and based on papers published between 1972 and 1987 was generally much higher than those observed by us and those reported in the more recent literature (Abebe and Getachew, 1992; Getahun and Stiassny, 1998; Golubtsov et al., 2002; Bjørkli, 2004).

For all the three northern lakes and two water bodies in the Rift Valley (L. Awassa, L. Abaya) the model of Amarasinghe and Welcomme (2002) estimated correctly the assessed or reported biodiversity. In only one Rift Valley water body (Koka Reservoir) the estimated species number was distinctly lower than the reported number in the literature (Vanden Bossche and Bernacsek, 1991). In three Rift Valley Lakes (L. Ziway, L. Langano, and L. Chamo) the estimated species richness was distinctly higher than the reported species numbers per lake. Hence, at present fish species diversity in the Rift Valley lakes is lower than would be expected on the basis of lake area and altitude. Low biodiversity was also observed in the present study and recent literature. Most probably species were lost during the last decades as a result of overfishing, habitat degradation and increased sediment load. This is corroborated by Getahun and Stiassny (1998) who compared species richness of different drainage basins in Ethiopia in the period 1835 to 1995 on the basis of literature with the results from their own surveys in 1995-1997. They reported a reduction in species numbers for each of the drainage basins varying from 40-85% and a reduction of species numbers for the Rift Valley Lakes as a whole of ca. 65%.

Resource management

Recognizing the danger posed on most water bodies of the country, a National Fisheries Proclamation was ratified by the Federal Parliament in 2003. It provides broad guidelines related to resource conservation, food safety and aquaculture. This document puts considerable emphasis on regulation, permits and the role of the fishery inspector. It is intended that the regional administration should then use this as a broad framework within which respective regions develop their own proclamations. Until now, Amhara Region was the first and the only region to develop its Regional Fisheries Proclamation in 2003. It covers the same area as the national policy, but has an additional objective relating to the creation of employment opportunities in fishing communities. It also states that information, including research findings, should be made available to the fishing communities. As with the National Proclamation it relies heavily on regulatory measures (command and control) and on the role of the fishery inspector. Although the proclamation is there, it still is not implemented because there are no guidelines and enforcement strategies. The current social and economic conditions in Ethiopia, that is high population growth rates and sparse job opportunities coupled with the absence of an effective fisheries management, tend to lead rapidly to overfishing (Reyntjens et al., 1998).

The water of most lakes in the Rift Valley contains a high sediment load (see fig. 2b) which reduces light transparency and is expected to reduce primary productivity and the carrying capacity for the fish community. This is the direct result of the deforestation of the surrounding mountains in the catchments of these lakes (Getahun and Stiassny, 1998). It is, therefore, important for the government to exercise watershed management approach to arrest this alarming degradation of the catchments of the water bodies. Afforestation, soil conservation, controlled grazing and prohibiting of hill side crop farming are some of the measures that should be exercised urgently.

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