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The last snapshot of natural pelagic fish assemblage in Lake Turkana, Kenya: A hydroacoustic study

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A B S T R A C T

A hydroacoustic survey and supplementary gillnet investigation were carried out in the open water of the central part of Lake Turkana in September 2009. Overall acoustic fish density and biomass were assessed as 1381 ind./ha and 30 kg/ha, respectively. The fish density estimate was lower than the results from two previous investigations in the 1970s and 1980s (long-term average 3739 ind./ha), but the biomass remained relatively unchanged (long-term average 25.4 kg/ha). A decreasing gradient in pelagic fish density from the western to eastern shore of the lake was observed. Fish were distributed unevenly within the water column. During the day, a majority of fish aggregated in the mid-water layers (10–12 m below the water surface), creating on echograms the so-called Midwater Scattering Layer. This feature dissipated completely during dusk and the majority of fish occurred in the surface layers at night. These diel vertical fish migrations influenced day and night hydroacoustic estimates of the total fish abundance. *Synodontis* spp., *Lates* spp. and *Schilbe uranoscopus* dominated the catch of both mid-water and bottom gillnets installed in open water areas. *Hydrocynus forskalii* and *Brycinus* spp. contributed significantly to the catch of mid-water gillnets while *Bagrus bayad* and the endemic *Haplochromis macconneli* occurred only in the catch of the bottom gillnets.

Introduction

Pelagic fish play important role in the ecosystem of all African Great Lakes. The extensive open water areas of African Great Lakes host rich pelagic communities dominated by small species like *Rastrineobola argentea* (Pellegriin) in Lake Victoria, *Stolothrissa tanganicae* Regan and *Limnothrissa miodon* (Boulenger) in Lake Tanganyika, *Engraulicypris sardella* (Günther) together with diverse cichlids in Lake Malawi and *Brycinus minutus* (Hopson & Hopson) plus *Brycinus ferox* (Hopson & Hopson) in Lake Turkana. These small planktivores are responsible for the relatively efficient transfer of secondary production to the higher trophic levels, as they represent an important prey to piscivorous species like native or introduced *Lates niloticus* (L.) and others (Beadle, 1974). Both small pelagic planktivores and their predators usually represent an important part of commercial fish yield in African Great Lakes. The knowledge of fish stock parameters is essential for the determination of appropriate fisheries management and definition of sustainable fish yield.

Lake Turkana is situated in the arid region of northwestern Kenya, in the eastern branch of the Great Rift Valley. With its 240 km length and 14–50 km width, it is the world's largest desert lake and also the fourth largest African lake by area (Ferguson and Harbott, 1982; Herdendorf, 1982). Since Lake Turkana was first discovered for the scientific community at the end of 19th century (von Höhnel, 1894), as the last of the African Great Lakes, only little attention was given to its environment and fish populations. The first scientific observations of Lake Turkana central sector were made by Cambridge expeditions to the East African lakes in 1930–31 (Beadle, 1932; Worthington, 1936). Later, in the 1970s, a three-year survey program (1972–75) summarized by Hopson (1982) laid the foundations of knowledge of the Lake Turkana environment. This extensive

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information was supplemented by Källqvist et al. (1988) with detailed information about its limnology and by Kolding (1989) with the characterization of its fish resources. All these studies were motivated by plans to establish a commercial fishery on the lake, which ultimately never were fulfilled.

Lake Turkana exhibits a unique combination of a closed basin situated in a desert, high seasonal and inter-annual water level fluctuations and strong unidirectional winds, which cause complete mixing of the whole water column. The water column is therefore nearly isothermal during most of the year (temperature gradient of 1–2 °C from surface to bottom in 70 m; Ferguson and Harbott, 1982), except sporadic situations during May, when the thermocline can establish between 20 and 50 m and the oxygen level can be limited for fish near the bottom (0.2 mg/l) (Källqvist et al., 1988). The water of the open lake contains a high concentration of dissolved ions (conductivity 3800 μS/m) due to their accumulation via incoming river flow and the extreme loss of lake water through evaporation (Yan et al., 2002).

The ichthyofauna of Lake Turkana is derived from the Nile system and comprises 48 species with 11 endemics, which is relatively a low proportion in comparison with other African lakes (Hardman, 2008; Johnson and Malala, 2009; Seegers et al., 2003). Two of these species, the endemic characids *B. minutus* and *B. ferox* form a "midwater scattering layer" during the day (Hopson et al., 1982; Lindem, 1986).

Lake Turkana is currently the only underexploited fisheries resources in Kenya. The artisanal and small-scale commercial fisheries concentrate on littoral fish resources, while the pelagic fish community is practically unexploited (Yongo et al., 2010). Future plans for expansion of the fisheries on the lake increase the importance of fish stock assessment and appropriate management (Ojwang et al., 2010a).

The future of Lake Turkana's unique environment remains uncertain, because the second largest dam in Africa, Gibe III, is being built on the Omo River, the only perennial inlet of the lake. The dam filling and operation will probably reduce the amount of nutrient-rich water inflow into the lake or at least influence its seasonal pattern (Ojwang et al., 2010b). This may cause large-scale ecosystem changes including lake level decrease, increased salinity and eventually the total collapse of fish populations or even desiccation of the lake (ARGW, 2009).

The present study aimed to explore the fish distribution, abundance and biomass in Lake Turkana open water under natural conditions, before the impact of the Gibe III Dam manifests itself. Specifically, the objectives were to i) quantify the fish density and biomass in the central sector of the lake, ii) explore horizontal and vertical fish distributions, iii) evaluate diel changes in fish distribution and iv) compare current fish abundance and biomass with historical records.

Methods

General sampling design

The hydroacoustic assessment, supplemented by gillnet survey, was performed in the central sector of Lake Turkana (Fig. 1) during 13–19 September 2009. The central sector represents an area extending 25 km around the Central Island (CI) in all directions. This area was chosen as a representative part of the lake because it was the most studied in the past. Furthermore, limited funding along with logistical and security constraints prevented us from performing a whole-lake survey.

The position of the hydroacoustic transects (Fig. 1a; b) followed those in previous studies (Lindem, 1984, 1985, 1986). The Lake Turkana central sector was divided into 5 different localities a) south, b) north, c) west and d) east of CI as well as e) around Ferguson's Gulf (FG). To compare fish density, biomass and vertical distribution in deep pelagic regions and the relatively shallow area proximal to FG (off-FG; depths 9–22 m), all data from areas with a depth >25 m were grouped together and termed as open water (OW).

The hydroacoustic assessment was conducted during day and night. The investigation was halted when the lake waters became too rough, introducing noise into the records and causing unsafe conditions. Consequently, the surveys were performed usually during the afternoon and the first half of the night when the lake was relatively calm. A total number of eight hydroacoustic surveys represented c. 100 km in length; five of them were carried out during the day (70 km in length) the rest at night.

The historical lake level data were obtained from Kolding (1989). Current lake level is from the standard monitoring of the Kenya Marine and Fisheries Research Institute.

Acoustic device and data processing

Acoustic data were collected with a SIMRAD EK 60 echosounder at a frequency of 120 kHz. The transducer (SIMRAD ES120-7C) had a circular beam pattern (nominal beam angle 6.5°). The transducer, beaming vertically, was mounted in a 0.8 m long tow body and deployed approximately 1 m below the surface and 10 m behind the survey boat. The system was calibrated using a standard copper sphere according to Foote et al. (1987). The echosounder was driven by Simrad ER 60 software (version 2.2.0). A pulse duration of 128 μs was used throughout the study. The ping rate was kept as high as possible and ranged between 7 pings/s in shallow areas and 3 pings/s in deeper parts. The position of the survey boat was measured with a Garmin GPSMAP 60CSx GPS receiver and the geographic coordinates were embedded into the acoustic data files.

Acoustic data files were processed with Sonar5 Pro post-processing software (version 5.9.9, Balk and Lindem, 2009). Each survey was divided into 10 min long transects, which corresponds to c. 900 m, and the transect represents elementary sampling unit in the study. An automatic algorithm was used to define the bottom line 0.3 m above the detected bottom. A surface line was added to each echogram at a distance of 2 m from the transducer to avoid the near field (1 m) and wave disturbances. Only the data between these two lines were analyzed to preclude bottom echoes and surface noise being integrated to fish backscattering measurements. To evaluate vertical fish distribution, the water column was divided into 1 m thick strata downwards from the surface line to the bottom line. These strata were grouped into layers with a characteristic acoustic picture [surface, midwater scattering, deep open-water, bottom (Hopson et al., 1982)]. The importance of a particular layer within the whole water column, in terms of the total fish density and biomass, was calculated by summing the values of all strata within a layer. The values of mean TS (dB) used in the paper are calculated from the average backscattering cross-section (σ_{bs}) of every recorded single target above a threshold (Simmonds and MacLennan, 2005). Non-fish echoes were eliminated by setting a −57 dB minimum TS threshold in order to provide the same resolution as earlier studies (Lindem, 1984, 1985, 1986) or were removed manually. Fish density (ind./ha; ind./1000 m^3) was calculated using s_v/ts scaling (Balk and Lindem, 2009) based on single echo detections (SED). SED criteria were set as follows: echo min and max. length 0.6 and 1.8 times the transmitted pulse length, respectively, max. gain compensation 3 dB (one-way), max. phase deviation 0.3. For fish biomass (kg/ha; kg/1000 m^3) estimate, detected targets were first grouped into 1 dB classes, then the TS was converted into length by Love's (1977) equation: $TS = 19.1 \log(TL) - 63.85$, where TS is in dB and TL in cm. Fish weight for each size class was calculated from the length/weight relationship of fish caught into pelagic gillnets. The same method was applied when converting the data on size structure and fish density of Lindem (1984, 1985, 1986) into a fish biomass not given in the original reports. Before the calculation of mean fish density and biomass for the year 1985, the data were weighted to adjust for the different

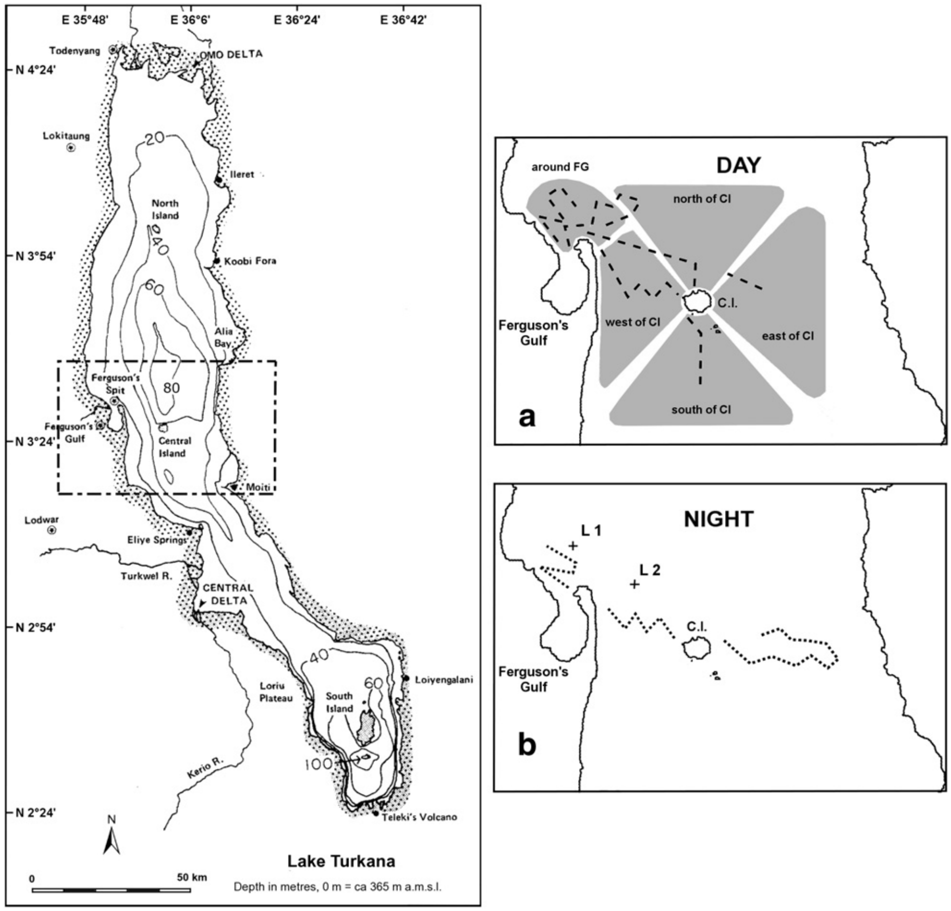

Fig. 1. Bathymetric map of Lake Turkana with 20 m depth isolines. The left rectangle indicates the central sector, where hydroacoustic and gillnet surveys were conducted in September 2009. The right rectangles show the position of a) day and b) night hydroacoustic surveys. The hydroacoustic localities are depicted together with day surveys (a) and are identical at night. The gillnet locations (L 1; L 2) are plotted together with the night hydroacoustic surveys (b).

sampling design used in 1985. Following Lindem (1986) we used a TS −43 dB to separate large from small fish.

The statistical analyses were carried out in the STATISTICA software package ver. 9.1. (StatSoft, Inc., 2010). The data were tested using the Kolmogorov–Smirnov (K–S) test (comparison of diel changes of vertical and TS distributions), *t*-test (differences in fish densities and biomasses) and regression analyses (correlation of lake level and acoustic fish biomass, density). The data were log (+1) transformed prior to the analyses when necessary.

Gillnet sampling

The gillnet catches provide valuable information that augments the hydroacoustic survey, most importantly by facilitating the species identification of the observed hydroacoustic target populations. Benthic and pelagic multi-mesh gillnets of the European standard EN 14 757 (CEN, 2005) were used to investigate the composition of the offshore fish community. The gillnets consisted of 12 panels (each 2.5 m long), having mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm (knot to knot). Pelagic gillnets were 4.5 m high and the benthic ones had a height of 1.5 or 4.5 m.

Gillnets were installed at two localities (Fig. 1b). The first locality (off-FG) was situated 6 km north of the mouth of FG (3° 35′ 55.4″ N 35° 54′ 55.6″ E), above a 25 m depth contour. Two pelagic nets were set 10 m below the water surface (i.e. they sampled the mid-water layer of 10–14.5 m) and two benthic nets 4.5 m high were installed on the bottom (i.e. they sampled the above bottom layer of 20.5–25 m). The nets were set before sunset (18:15–18:30 EAT) and stayed in the water for 23 h.

The second locality (OW), 35 m deep, was situated 10 km northwest of CI (3° 33′ 37″ N 35° 58′ 39.4″ E). Two pelagic nets were set 10 m below the water surface (i.e. they sampled the mid-water layer of 10–14.5 m) and four benthic nets (two nets were 4.5 m high and the other two were 1.5 m high) were set on the bottom. Gillnets were installed before sunset and exposed for 17 h. At both localities, the gillnet soak time was longer than the standard overnight set (12 h, CEN, 2005), because rough weather conditions on the lake precluded retrieving the gillnets at the appropriate time.

Catches of fish species were calculated as number per unit effort (NPUE) and biomass per unit effort (BPUE), both standardized by gillnet area (100 m^2) and fishing duration (12 h).

Results

Fish density

The acoustic fish density differed among the examined localities (Table 1). During the day, the highest density (1805 ind./ha) was recorded west of CI, where only a minority (7.7%) of fish were > −43 dB TS. The second highest density (1503 ind./ha) was found around FG, with the proportion of fish >−43 dB comprising 7.1% of the sampled population. The locality south of CI had markedly lower fish density (431 ind./ha) but a population with a relatively high proportion of large fish (17.9%). Even lower fish density (232 ind./ha) was found north of CI, where fish >−43 dB comprised 7.6% of the sampled fish. The lowest day density (144 ind./ha) was recorded east of CI, although this survey was conducted mainly during twilight, which may influence the data. The proportion of fishes >−43 dB increased to 30%

Table 1
Historical (1975–1986) and current (2009) hydroacoustic estimates of fish density (ind./ha) at different localities of Lake Turkana (Hopson et al., 1982; Lindem, 1986; see Fig. 1a for localities' description). All shallow (off-FG; depth< 25 m) and open-water (OW; depth> 25 m) regions are grouped across all localities and averaged. Percentages of targets >−43 dB are given in parentheses. Data from 1975 are based on trawl catches (Hopson et al., 1982). * This part of survey east of CI was conducted during twilight instead of the day.

	1975	1984	1985	1986	2009	
	Day					Night
Around Ferguson's Gulf (FG)		5928 (7.5)	14850 (13)	4581 (6.4)	1503 (7.1)	1738 (13.1)
West of Central Island (CI)		3762 (6.9)	8586 (13.2)	3787 (6.1)	1805 (7.7)	803 (22.4)
South of CI		2241 (1.6)	3222 (4)	4352 (1.7)	431 (17.9)	
North of CI		4553 (2.0)	5098 (7.7)	3240 (0.5)	232 (7.6)	
East of CI					*144 (30)	108 (34)
Off-FG		4380	8190	4506	1424	2672
OW		1829	3595	5656	1384	360
Average	1763	2467 (5.4)	5432 (8.9)	5293 (4.6)	1381 (8.6)	774 (16.7)

at this locality. The daytime fish densities in the off-FG and OW regions were 1424 and 1384 ind./ha (Fig. 2a), respectively and did not differ significantly from each other [t(49), 0.05 = −1.3, p = 0.18].

During night, the fish density in the locality west of CI decreased to 803 ind./ha, while the proportion of fish >−43 dB increased to 22.4% of the sampled population. At the locality east of CI, the acoustic density decreased to 108 ind./ha. The density of fish >−43 dB remained nearly the same and their proportion increased to 34% of sampled fish. In general, fish density in OW decreased significantly at night [t(49), 0.01 = 6.79, p < 0.0001] (Fig. 2a). In contrast, the night density increased significantly in the off-FG locality to 2672 ind./ha [t(35), 0.01 = −3.46, p < 0.01]. Consequently, the night fish density differed significantly between the off-FG and OW regions [t(35), 0.01 = 9.79, p < 0.0001].

The size distribution of pelagic fish obtained from SED differed significantly between day and night (K–S test, D = 0.3784, p < 0.01); large fish were a higher proportion of acoustic targets during night (Fig. 3).

Fish biomass

The horizontal distribution of acoustic fish biomass resembled the pattern of fish density (Table 2). During day, the highest fish biomass was recorded west of CI (35.9 kg/ha), followed by the relatively shallow region around FG (31.1 kg/ha). The fish biomass revealed south of CI was only slightly lower (27.2 kg/ha), while the lowest biomass was found north of CI (1.9 kg/ha). Fish biomass, however, did differ significantly between the off-FG and OW regions during the day [t(49), 0.01 = 2.81, p < 0.01] (Fig. 2b).

During night, the highest biomass of 42 kg/ha was found at around the FG locality. West of CI, the biomass reached 31.3 kg/ha. Very low fish biomass (7.4 kg/ha) was recorded at the locality east of CI. Night acoustic biomass differed significantly between the off-FG and OW regions [t(35), 0.01 = 7.85, p < 0.0001] (Table 2). In general, the biomass in OW decreased significantly from the daytime 19.5 kg/ha to nighttime 9.1 kg/ha [t(49), 0.01 = 3.75, p < 0.01] (Fig. 2b).

No relationship was found when the historical and current data on the density and biomass of pelagic fish were plotted against the mean lake level in the preceding year (density: F(1; 3) = 2.01, p = 0.25, r^2 = 0.40; biomass: F(1; 3) = 0.12, p = 0.75, r^2 = 0.04) (Fig. 4).

Vertical distribution

The distribution of pelagic fish within the water column was not homogeneous. During day, fish typically avoided the upper 7 and 9 m of the water column in the OW and off-FG regions, respectively (Fig. 5). Within these surface layers, the fish densities reached only 0.61 and 1.54 ind./1000 m^3 on average, which represent 2.1 and 4.9% of the whole water column fish density in the OW and off-FG regions, respectively.

The peak of fish density was found 10 m below the surface in OW, where the density reached 22 ind./1000 m^3, and 12 m below the surface in the off-FG area, with a maximum density of 47 ind./1000 m^3. The fish density in the surrounding strata was also higher than in the rest of the water column and an approximately 7 m thick clear layer of higher fish densities was observed in the echograms, representing MWSL. The average fish density within the MWSL, was 13 and 23 ind./1000 m^3 in the OW and off-FG localities, respectively. This represents 62 and 71% of the total fish density in the whole water column. The deep pelagic layer (i.e. 15–51 m in OW and 17–20 m in off-FG)

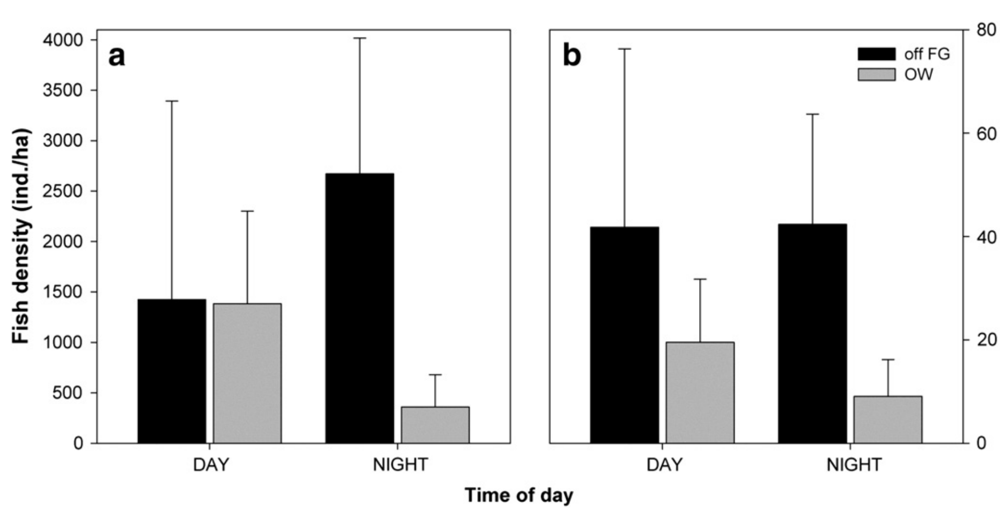

Fig. 2. Mean (+SD) day and night acoustic fish density (ind./ha) in the off FG and OW regions (a) and mean (+SD) day and night acoustic fish biomass in the off FG and OW regions (b).

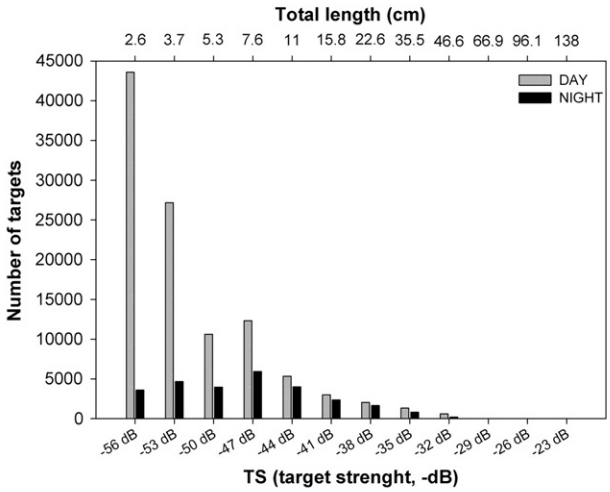

Fig. 3. The size distribution histograms of target strength (TS; -dB) and total length (TL; cm) of pelagic fish recorded during day and night surveys. TS and TL values refer to the middle of each interval.

contributed to the whole fish density by 31%, with the average of 1.2 ind./1000 m^3 in OW, and by 13% with the average fish density of 7.24 ind./1000 m^3 in the off-FG region. The bottom layer, defined as the two 1 m thick strata closest to the bottom, represented 4.8% of the total fish abundance in the OW (8.5 ind./1000 m^3) and 11.7% in off-FG region (30 ind./1000 m^3).

The vertical distribution of fish biomass did not resemble the pattern of fish density. In the OW area, the peak of fish biomass (0.3 kg/1000 m^3) was recorded close to the bottom at depth 51 m and significant fish biomass occurred also at a 9 m depth (Fig. 5a). In the off-FG region, the highest biomass (0.9 kg/1000 m^3) was found 5 m below the surface and also in the bottom layer (Fig. 5b).

The surface layer above MWSL represented 13 and 42% of the total fish biomass, with an average of 0.07 and 0.3 kg/1000 m^3 in the OW and off-FG regions, respectively. The MWSL comprised 20% of total biomass in OW and 33% in off-FG, as exhibited by the respective average biomass of 0.08 and 0.22 kg/1000 m^3. In the deep mid-water layers, we found an average fish biomass of 0.04 and 0.11 kg/1000 m^3 in the OW and off-FG regions, respectively, which represented 55 and 9% of the whole biomass. The bottom layer contained only 12 and 16% of the total biomass in the OW and off-FG regions, respectively. However, these strata hosted the highest average biomass in both regions, 0.2 (OW) and 0.7 (off-FG) kg/1000 m^3.

The above mentioned layers were also occupied by characteristic fish assemblages. The fish that dwell in the surface layer in OW and off-FG during day (Fig. 5a and b) had a TS between −40 and −37 dB (18–26 cm TL) and −43 and −34 dB (12–37 cm), respectively. The fish in the MWSL reached an extent of −53 and −40 dB (4–18 cm) in OW and −51 and −41 dB (5–16 cm) in the off-FG area. Fish in the densest part of the MWSL were smaller in both the OW (−53 dB or 3.7 cm) and in the off-FG regions (−51 dB or 4.7 cm). The TS of fish throughout the rest of the water column down to the bottom fluctuated around −42 dB (14 cm) in both OW and off-FG. The biggest fish (−34 dB; 37 cm) occurred near the bottom or in the surface layer (−36 dB; 29 cm) in OW and off-FG, respectively.

The night vertical distribution of fish density in OW, as well as the off-FG region, was different from the day distribution (Fig. 5). The surface layer (3–7 m in OW, 3–9 m in off-FG) that was nearly abandoned during day contained the majority of fish at night with a peak in fish density occurring in the uppermost layer (3–5 m). Fish density gradually decreased toward the bottom and increased again directly above the bottom. The diurnal and nocturnal vertical distributions of fish density differed significantly in OW (K–S test, $D=0.63$, $p<0.001$) but did not differ significantly in the off-FG region (K–S test, $D=0.42$, $p=0.056$).

During night, the fish biomass in the OW region accumulated in the bottom layer, with mid-water layers nearly devoid of fish (Fig. 5a). The vertical fish biomass distribution in OW differed significantly between day and night (K–S test, $D=0.57$, $p<0.001$). The distribution of biomass within the water column in the off-FG region was nearly homogenous at night (Fig. 5b), except for the somewhat lower values in the upper 6 m, and did not differ from the day biomass distribution (K–S test, $D=2.44$, $p=0.5$).

The vertical distribution of the average TS (TL) changed dramatically between day and night (Fig. 5). At night, the surface layer was occupied by small fish between −48 and −47 dB (7–8 cm) in both regions. The rest of the water column was homogenously populated by fish having an average TS between −44 and −43 dB (11–12 cm), with exception of the bottom layer in deeper areas (OW), where larger fish of −40 dB (18 cm) occurred.

Gillnet catches

A total number of 229 fish individuals representing 10 species were caught with multimesh gillnets. Two species of the genus *Lates* (*Lates longispinis* and *L. niloticus*) that occur in Lake Turkana are morphologically very similar, and consequently were not distinguished to the species level (labeled as *Lates* spp.). The same applies to *Synodontis schall* and *Synodontis formosa* (labeled as *Synodontis* spp.). At the off-FG locality (25 m deep), *Synodontis* spp. and *Lates* spp. dominated the catch of the bottom gillnets, both in terms of numbers and biomass (Fig. 6a). *Hydrocynus forskalii* was the second most abundant species in the catch of mid-water gillnets, which was dominated by *Synodontis* spp., both in numbers and biomass (Fig. 6a). Small planktivorous characid *B. ferox* comprised only a minor part of the total numerical catch of the mid-water gillnets.

Table 2
Historical (1974–1986) and current (2009) hydroacoustic estimates of fish biomass (kg/ha) at Lake Turkana. Results from 1974 to 75 are based on trawl catches (Hopson et al., 1982; Table 8.19) and the values for years 1984–1986 were computed from fish density estimates and size composition given by Lindem (1984, 1985, 1986). The data were grouped according to transect depth to the off-FG locality with a max. depth 25 m and OW with a depth >25 m.

	Day			Night		
	Off-FG	OW	Average day	Off-FG	OW	Average night
1974–75			26.4			
1984	14.7	6.6	8.6			
1985	74.1	18.0	40.4			
1986	31.0	24.1	26.3			
2009	41.8	19.5	30.0	42.3	9.1	21.2

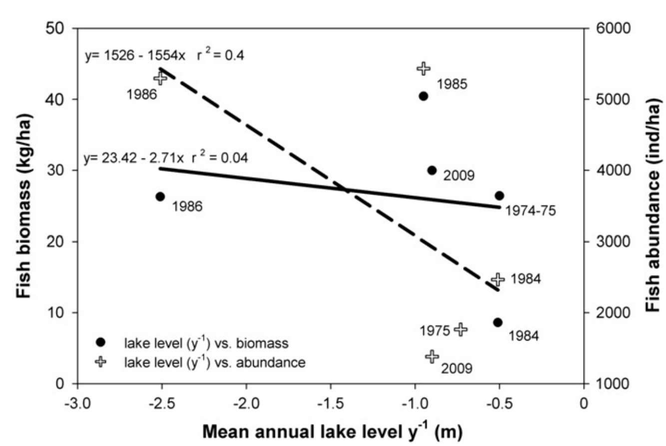

Fig. 4. Acoustic fish density (dashed line; ind./ha) and biomass (full line; kg/ha) plotted against the mean annual lake level of the preceding year. Historical data are from Hopson (1982), Lindem (1986) and Kolding (1989).

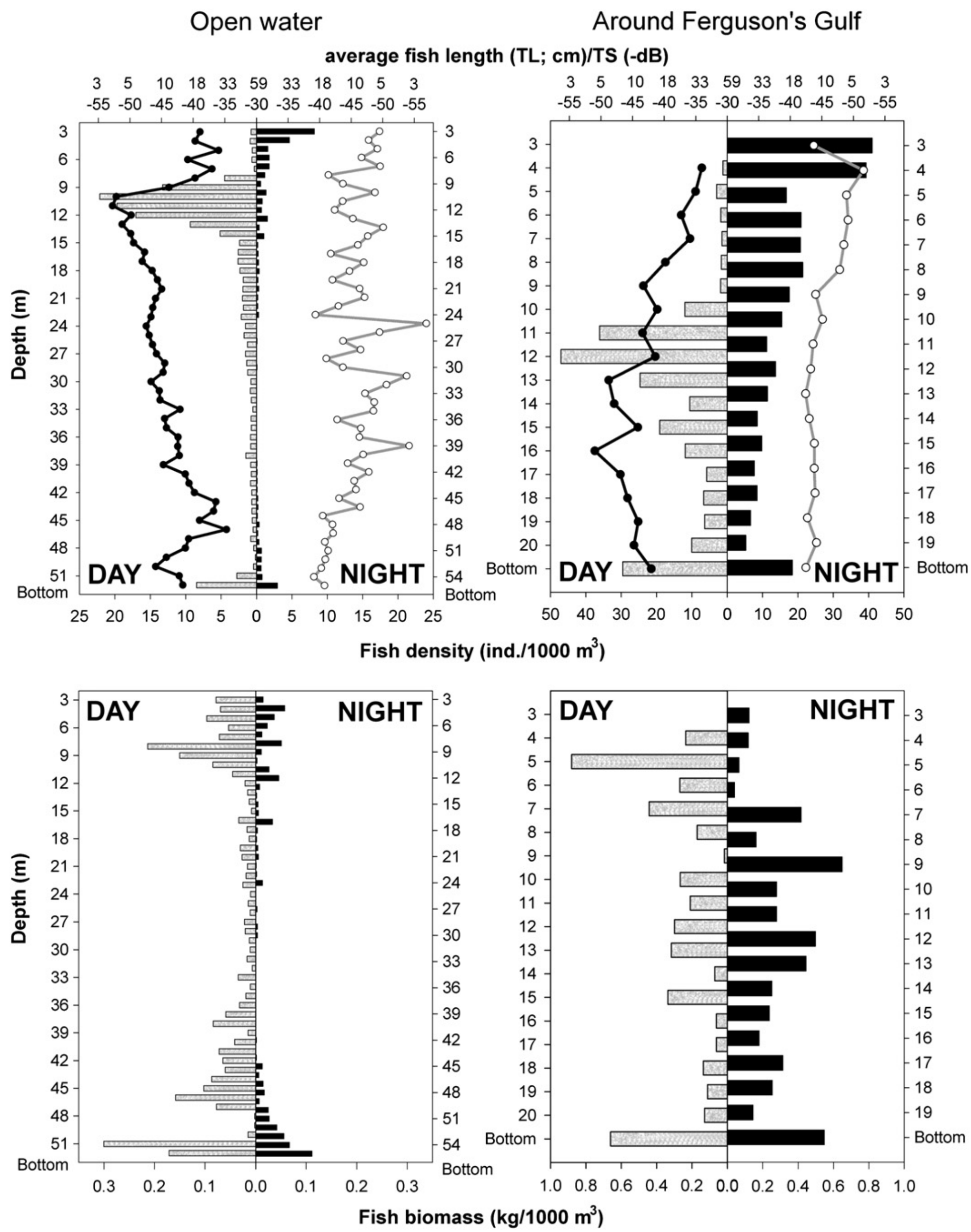

Fig. 5. Day and night vertical distribution of acoustic fish density (ind./1000 m^3) and biomass (kg/1000 m^3) in the open water region (left column) and shallow areas around Ferguson's Gulf (right column). The bars denote fish density/biomass at each depth. The lines in upper graphs denote average fish length [TL (cm); TS (dB)] at each depth.

At the OW locality (35 m deep), *Schilbe uranoscopus*, *Synodontis* spp. and *Haplochromis macconneli* numerically dominated the catch of the bottom gillnets (Fig. 6b). In terms of biomass, *Bagrus bayad*, *Synodontis* spp. and *Lates* spp. contributed most significantly to the total catch of bottom gillnets. The catch of mid-water gillnets was numerically dominated by *S. uranoscopus* and *B. ferox*, while *Synodontis* spp., *S. uranoscopus*, *Lates* spp. and *H. forskalii* represented major component in terms of biomass (Fig. 6b).

Discussion

Pelagic fish density at Lake Turkana has been assessed only four times in the past, during a trawling survey in 1975 (Hopson et al., 1982) and during hydroacoustic surveys in the 1980s conducted by Lindem (1984, 1985, 1986). Although we used different equipment and analysis methods compared to Lindem, our results are likely comparable. Rudstam et al. (1999) found that fish density obtained with the single-beam method used by Lindem was within 85% of density obtained by split-beam unit in Lake Erie. The results of previous studies are summarized in Table 1. The average fish density detected in the central sector of Lake Turkana during the current hydroacoustic survey (1381 ind./ha) is the lowest ever recorded. The average fish density in the mid 1980s ranged from 2467 to 5432 ind./ha (mean 4397 ind./ha; Lindem, 1986). However, the density of 1763 ind./ha estimated by a trawl survey in September 1975 (Hopson et al., 1982) is quite similar to our results.

The horizontal pattern of pelagic fish distribution revealed in the present study confirms the results of previous studies, which found a decreasing gradient in fish density from the western to the eastern shore of the central sector of Lake Turkana (Hopson et al., 1982; Lindem, 1986). Lindem (1986) consistently found the highest densities in areas near FG. We recorded the highest fish abundance west

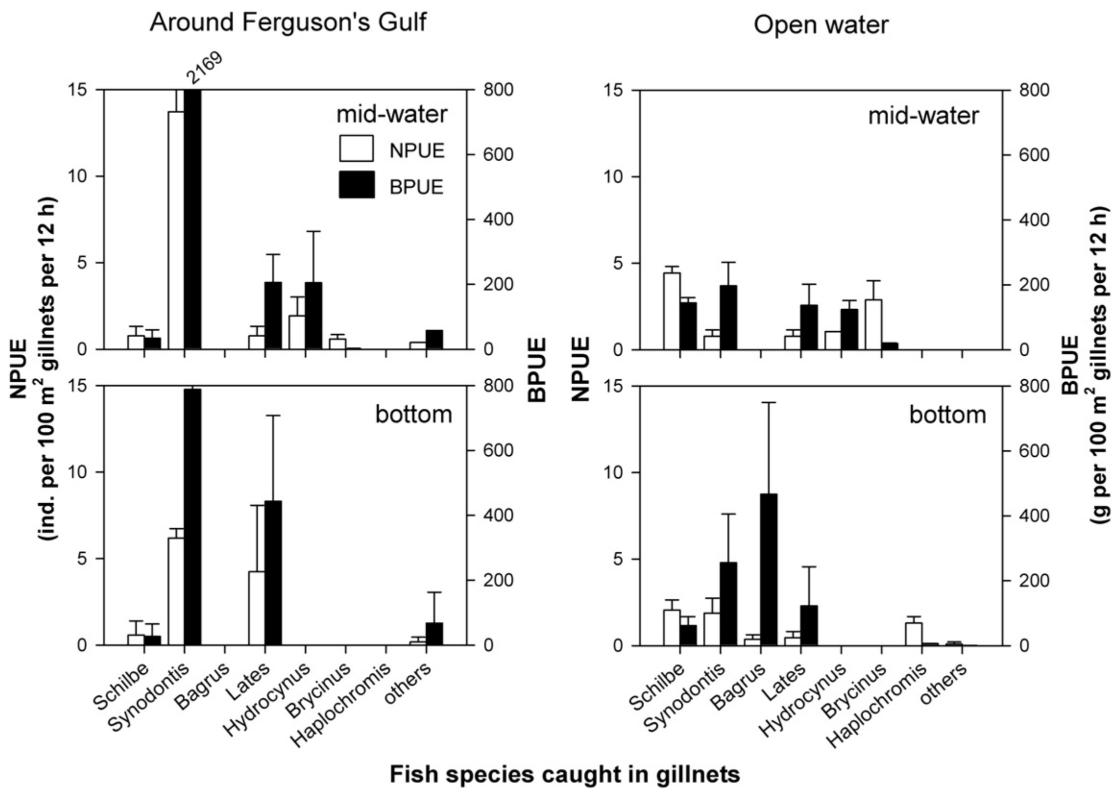

Fig. 6. Mean (+SD) catch per unit effort of mid-water and bottom gillnets at around Ferguson's Gulf (left column; 25 m deep) and open water (right column; 35 m deep) localities, both expressed in terms of fish numbers (NPUE) and biomass (BPUE).

of CI and around FG and the lowest abundance east of CI, which is in good accordance with Lindem's results. Hopson (1982) suggests that this east–west gradient in pelagic fish abundance is produced by surface currents generated by the strong south-east winds that prevail at Lake Turkana. These currents transport the surface water mass (an upper layer up to 6 m thick) with a maximum speed of 7–9 cm/s from the eastern to western shore (Ferguson and Harbott, 1982). In this way, zooplankton is carried towards the western shore where it serves as food for the abundant pelagic fish (Ferguson, 1982).

Our hydroacoustic biomass estimate from the central sector is similar to estimates based on trawls from Hopson et al.'s (1982) whole lake survey in the open water of Lake Turkana. Lindem (1984, 1985, 1986) did not assess the fish biomass, but we calculated the fish biomass from his fish densities and size distribution estimates. The hydroacoustic biomass varied between 8.6 up to 40.4 kg/ha, with an average of 25.1 kg/ha. Surprisingly, both extremes were achieved in the subsequent years 1984 and 1985. Such marked difference in total fish biomass and abundance from year to year could be produced by a real increase of fish assemblage and/or the estimate in year 1984 was biased by the limited extent of the survey.

In comparison with other African Great Lakes, the average total biomass of pelagic fish at Lake Turkana (30.1 kg/ha) is relatively low. Menz et al. (1995) estimated the average hydroacoustic fish biomass in open water of Lake Malawi at 70 kg/ha. The whole-lake hydroacoustic surveys of Lake Tanganyika in 1995–98 revealed a mean pelagic fish biomass of 58 kg/ha (Szczucka, 1998). In the shallowest and most productive (eutrophicated) lake among the African Great Lakes, Lake Victoria, Getabu et al. (2003) in addition to Everson (2006) found a pelagic fish biomass of 310 and 157 kg/ha in the years 1999–2001 and 2005, respectively. On the contrary, the primary production in Lake Turkana is the second highest among African Great Lakes (Table 3). However, phytoplankton in Lake Turkana is dominated by *Microcystis aeruginosa*, a species that is rarely consumed by zooplankton and fish (Hopson and Ferguson, 1982; Ferguson, 1982). Therefore, it has been suggested that a high proportion of the primary production in Lake Turkana passes through bacterial decomposition and therefore is utilized before it can contribute to fish production (Kolding, 1993a).

Kolding (1992) considered the annual river discharge to the lake as the major environmental variable related to Lake Turkana commercial catch rates. Commercial catch rates, represented as annual catch per boat, corresponded to CPUE during experimental gillnetting and both were positively correlated with the annual river discharge, expressed as the annual mean lake level change in the preceding year (Kolding, 1989). Using the dataset of all available (historical and current) hydroacoustic data, we did not find significant relationship between either pelagic fish biomass or density and mean annual lake level change. An increase of water level in Lake Turkana probably has a more pronounced impact on the littoral fish community, which is also primarily exploited by commercial fishermen. It has been documented previously (Kolding, 1993b) that the drying out of FG, the most important and highly productive fishing area within the lake, nearly caused a local fishery collapse.

Only few previous studies examined the vertical distribution of fish in African Great Lakes and its diel changes (Getabu et al., 2003; Goudswaard et al., 2004; Semyalo et al., 2009). Fish in Lake Turkana were unevenly distributed through the water column and even the

Table 3
Phytoplankton primary production and mean pelagic fish biomass in four African Great Lakes. Data from Källqvist et al. (1988) (Lake Turkana, primary production) and present study (Lake Turkana, fish biomass); Pitcher et al. (1996) (Lake Victoria); Sarvala et al. (1999) (Lake Tanganyika); Patterson et al. (2000) (Lake Malawi).

	Primary production ($g\,C\,m^{-2}y^{-1}$)	Fish biomass (average; kg/ha)
Lake Turkana	750	30
Lake Victoria	963	234
Lake Tanganyika	544	58
Lake Malawi	424	70

deep bottom habitats (depth > 50 m) hosted a relatively abundant community due to isothermal conditions and a high oxygen content. The vertical distribution of fish in Lake Turkana agreed with a general distribution pattern defined for the pelagic fish assemblage (Hugie and Dill, 1994), where small zooplanktivorous species avoid the highly illuminated surface water layers and only larger fish are present therein during day. According to Hopson (1982) and Kolding (1989), the daytime surface community at Lake Turkana is mainly represented by piscivorous *H. forskalii* and zooplanktivorous *Alestes baremose*. The hydroacoustic average fish length (25.5 cm TL) estimated in the surface layer during the present study corresponds well to the average length of these species caught during simultaneous mid-water gillnetting (27 cm TL).

A unique feature of Lake Turkana is the daytime occurrence of the MWSL, formed mainly by aggregated small pelagic characids (Kolding, 1992). Nowhere else in African Great Lakes is the pelagic assemblage dominated by characids and small zooplanktivores usually create dense schools (Beadle, 1974) that differ from the thin layer described in this study. An analogous thin condensed layer of *R. argentea* in Lake Victoria has been described in two other studies (Getabu et al., 2003; Tumwebaze et al., 2002), but only during the stratified period when fish were excluded from the anoxic bottom layers and aggregated near the thermocline. The acoustically estimated mean fish size within the MWSL reached 8.6 cm (TL) in OW, which roughly corresponds to a mixture of *B. minutus* (max. 3.7 cm SL) and *B. ferox*. (max. 11 cm SL according to Hopson and Hopson, 1982). The numerical catch of mid-water gillnets in OW was, however, dominated by *S. uranoscopus*, while *B. minutus* and *B. ferox* together represented the second most abundant component. Since our gillnets are not a reliable tool for estimating abundance of small (<50 mm) individuals and species (Prchalová et al., 2009), it is very likely that the actual contribution of *B. minutus* and *B. ferox* to the pelagic Lake Turkana fish community is higher than that reflected in the catch of mid-water gillnets. Hopson et al. (1982) observed that MWSL in Lake Turkana changed its position within the water column in response to the differential light intensity throughout a diel cycle (even clouds crossing the sky affected the vertical position of MWSL) and turbidity. A predation threat is the likely factor leading to the MWSL formation because piscivorous *Lates* spp. inhabit deep offshore areas while *H. forskalii* occupies the surface layer and small characids are their principal prey (Hopson et al., 1982; McLeod, 1982).

The diel vertical migration of small characids between MWSL and surface layer occurring in OW (Hopson et al., 1982) resemble the nocturnal migration of small fish upward to the surface described also in Lakes Victoria and Malawi (Goudswaard et al., 2004; Allison et al., 1996). This migration, together with the reversely oriented habitat shifts of *H. forskalii* (Hopson et al., 1982), was likely responsible for the increase of acoustic fish density in surface waters at night, as well as the simultaneous sharp decline of the average fish length. Unfortunately, this vertical migration shifts part of the pelagic fish assemblage to the acoustic surface “blind-zone”, where they become invisible to the vertically beaming echosounder. The significant diel change in TS distributions, with a higher number of small fish during the day and the increased number of larger fish at night, was apparently the direct consequence of this phenomenon. Similar diel changes of acoustic fish parameters were also observed by Szczucka (1998) in Lake Tanganyika and Djemali et al. (2009) in Tunisian reservoirs. The overall decrease of acoustic fish density in OW during night observed in this study seems to be also affected by the previously mentioned vertical shift to the uppermost water layer. In contrast at the off-FG area, the acoustic fish density and biomass increased during night, which suggests night offshore migration of littoral fish.

The conditions of the fish vertical distribution during day are more favorable for vertically oriented hydroacoustic surveying than those found for the nocturnal distribution. Therefore, the day survey is usually more representative than that from night. A simultaneous survey with a horizontally oriented echosounder can achieve more accurate estimates of fish abundance, especially in lakes where the majority of fish occupy the upper few meters of the water column (Djemali et al., 2009; Knudsen and Sægrov, 2002). Unfortunately, this method is difficult to use under the windy conditions (Mous and Kemper, 1996) that prevail in African Great Lakes; furthermore, it was also not feasible for our survey due to technical and logistical limitations. For these reasons, horizontal hydroacoustic surveying remains a rarely employed method in African waters (Djemali et al., 2009) as compared to the routine vertically-oriented hydroacoustic technique (Getabu et al., 2003; Everson, 2006; Rufli and Vitullo, 1982; Szczucka, 1998).

Overall fish densities found by Hopson et al. (1982) in particular layers of the water column during trawling surveys in 1974–75 are nearly identical to our hydroacoustic results in OW. Such a comparison was not possible for fish biomass however, because the previous study assessed the biomass only for the MWSL and bottom layer (38.8 and 20.7 kg/ha, respectively). Their biomass estimate for the MWSL is much higher than our estimates of 15.6 and 5.4 kg/ha at the off-FG and OW regions, respectively. The decrease of MWSL biomass was previously observed by Kolding (1993a) between 1973 and 1987. This reduction of hydroacoustic density and the slight increase in biomass measured in the 1980s and 2009 suggest that fundamental change from an environment dominated by small characids to one dominated by *Synodontis* spp. and *Lates* spp., still continues. Rapid lake level fluctuations during the last decades have been suggested to be devastating to the endemic characids (Kolding, 1993a) and the generalist *Synodontis* spp. filled the emptied niche. A system dominated by generalist species may have developed in Lake Turkana as a result of unstable and harsh environmental conditions (Kolding, 1993a).

Nevertheless, much larger ecosystem changes may occur with the erection of the Gibe III Dam on the Omo River. The planned reservoir upstream the dam will retain 14 km^3 of water, which is equal to estimated average annual inflow of the River Omo into Lake Turkana (Yuretich and Cerling, 1983). The block of the river's discharge and subsequent seasonal flood cessation will reduce the breeding and nursery areas of littoral species or potamodromous spawners, which dominate the local fishery catches (Kolding, 1989; Ojwang et al., 2010b). The reduction of spate river waters, which bring a huge amount of organic material into the nitrogen limited lake ecosystem, will probably decrease the currently high primary production and therefore affect the whole ecosystem (Källqvist et al., 1988). Despite an international effort to stop the Gibe III project devastating not only Lake Turkana, but also the ecosystems and tribal communities of the lower Omo, dam filling is planned to begin in 2012. Thus, the current study is probably the last report describing the unaffected pelagic fish assemblage of Lake Turkana. However, further monitoring of changes in the lake ecosystem may help us to estimate the time to write the final obituary.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.jglr.2011.11.014.

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