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Is the fishery of the introduced Tanganyika sardine (*Limnothrissa miodon*) in Lake Kivu (East Africa) sustainable?

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A R T I C L E   I N F O

A B S T R A C T

Limnothrissa miodon, a small pelagic clupeid fish introduced at the end of the 1950s into Lake Kivu, became an important resource for the human populations of this area. The total stock of pelagic fish populations of this lake was estimated in 2008 by two hydroacoustic surveys, using an EK60 split-beam sounder (frequency 70 kHz). The total fish stocks were estimated to be approximately 5000 t in the rainy season and 6000 tons in the dry season. These values are similar to previous estimations performed in the 1980s. During 2008, the stock did not fluctuate throughout the seasons; however, the spatial distributions were different in the two hydrological seasons. Interestingly, the *L. miodon* stock has appeared to remain stable over the last two decades, which suggests that the pelagic fishery in Lake Kivu has not been overexploited and that it is sustainable.

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Introduction

Introductions of species are widely regarded as detrimental (Gozlan, 2008; Leprieur et al., 2009; Vitule et al., 2009) and are considered as a major threat to biodiversity (Sala et al., 2000; Vitousek et al., 1997). Worldwide, but particularly in the African continent, introductions have been aimed to develop fisheries (Moreau et al., 1988). Often, the consequences have been reported as catastrophic for the native fauna, for the ecosystems, and for the well-being of the human populations, such as in the African Great Lakes (Ogutu-Ohwayo et al., 1997). However, some cases have been reported as successful, as far as the fishery is concerned (Gozlan, 2008). For instance, the introduction of Tanganyika sardines, *Limnothrissa miodon* (Boulenger, 1906), in Lake Kivu (Spliethoff et al., 1983) seems to be productive even though the effects on the ecosystem and on the geochemistry of the whole lake are still matter of debate (Dumont, 1986; Isumbisho et al., 2006; Pasche et al., 2010).

Lake Kivu has a species-poor fish fauna compared to other large lakes of the East-African Rift valley (Beadle, 1981). While Lake Tanganyika and Lake Malawi harbour hundreds of endemic species, mostly Cichlidae, only 29 species have been described from Lake Kivu. Four of these species have been accidentally or deliberately introduced (Collart, 1960; Marshall, 1993; Snoeks et al., in press): three cichlids [*Oreochromis macrochir* (Boulenger, 1912), *Oreochromis leucostictus* (Trewavas, 1933) and *Tilapia rendalli* (Boulenger, 1897)], and one clupeid *L. miodon* (Boulenger, 1906). Recently, a fifth species, *Lamprichthys tanganicanus* (Boulenger, 1898), endemic to Lake Tanganyika (Coulter, 1991) has appeared in the commercial catches from several sites in Lake Kivu (Muderhwa and Matabaro, 2010), but with low occurrence in the pelagic area (Masilya, 2011). The species-poor fish fauna of Lake Kivu is due to profound geologic disturbances that occurred approximately 11,000 years BP (Haberyan and Hecky, 1987). Snoeks et al. (1997) gave a detailed account of the history and status of the ichtyofauna of Lake Kivu, providing evidence for the existence of 15 endemic haplochromines.

Among the introduced species, the most famous is the Tanganyika sardine, locally known as "Isambaza", *L. miodon*, which was deliberately introduced in 1959 (Collart, 1960) from Lake Tanganyika to occupy the pelagic area of Lake Kivu, which previously lacked pelagic fish species. *L miodon* was introduced in an attempt to establish a pelagic fishery in Lake Kivu based on the pelagic planktonic food web. Despite the fact that this introduction might be considered as a disturbance of the pelagic ecosystem (Darchambeau et al., in press; Dumont, 1986; Isumbisho et al., 2004; Kaningini et al., 2003), it permitted the development of an important pelagic fishery with an

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annual exploitable stock that was estimated at approximately 7000 t (FAO, 1992; Roest, 1999). However, rather pessimistic predictions on the sustainability of the *L. miodon* fishery were made by Dumont (1986), based on observed changes in the composition and biomass decline of mesozooplankton in the lake.

Major projects were enacted to manage the pelagic fishery of Lake Kivu, including the "*Isambaza*" project conducted by PNUD-FAO in Rwanda in the 1980s and the "Pêche du Sambaza au filet maillant dans le lac Kivu" conducted in Congo (Kaningini et al., 1999). Despite the systematic collection of data on total fishery yield by the Rwandan administration, the fishery pressure on different species is poorly known. Furthermore, no fishery independent survey has been conducted since the study of Lamboeuf (1991). Thus, a pelagic fishery management plan based on reliable data cannot proposed.Therefore, the only way to assess the sustainability of the pelagic fishery was to conduct a comprehensive stock assessment of the *L. miodon* with hydroacoustic methods, and compare our results with estimates reported by Lamboeuf (1991) 20 years earlier.

The use of hydroacoustic methods to estimate fish abundance in aquatic ecosystems is well accepted (Simmonds and MacLennan, 2005), particularly for the pelagic zones of lakes (Dunlop et al., 2010; Guillard et al., 2006; Johnson et al., 2004). By contrast, the use of gillnets for assessing fish stocks is likely to provide a biased picture of species composition and size-structure because of known issues with capturing small (<10 cm) fishes using this equipment (Kurkilahti et al., 2002; Prachalováa et al., 2009).

We conducted two hydroacoustic stock estimation surveys, during both rainy (February 2008) and dry (July 2008) seasons using a sampling design similar to that of Lamboeuf (1991), in order to determine whether or not the pelagic fish population has declined as predicted by Dumont (1986). In addition to the comparison with historical data, fish distributions across seasons were also studied.

Material and methods

Lake Kivu is a large (surface area 2370 km^2), deep (maximum depth 489 m), oligotrophic lake that belongs to the African Eastern Rift. The lake is meromictic, with oxygenated waters limited to the upper 60 m and permanently separated from deep waters by several steep salinity gradients (Degens et al., 1973). Given the location of Lake Kivu, just 2° south of the Equator, but at relatively high elevation (1463 m), the average surface temperature ranges from 23 to 24 °C and the temperature gradient is only 1 to 2 °C between the surface and the bottom of the mixolimnion. Therefore, surface cooling occurring in the dry season reduces the temperature gradient and promotes mixing of the first 60 m, which increases the nutrient availability in the euphotic zone (ca. 18 m on average) and promotes phytoplankton development (Sarmento et al., 2006). The dry season mixing also oxygenates the water over the whole mixolimnion. Thus, mixing events extend the oxic layer, and provide the pelagic fish with access to increased planktonic resources, whereas the rainy season conditions reduce both the depth of the oxic layer and food resources for planktivores (Isumbisho et al., 2006; Sarmento et al., 2006).

The lake can be divided into four large basins (Fig. 1, Table 1) and two bays, the Bukavu Bay in the south and Kabuno Bay in the north. Kabuno Bay was not included in our surveys. The basins have different patterns of wind and precipitation resulting shift of several weeks of the dry season between the North and the South basins (Kwetuenda et al., 1989). The inshore area represents less than 10% of the area of Lake Kivu and was considered separately in our analyses. The two 2008 surveys were performed in two contrasted seasons: from February 15–22 (rainy season), and from July 05–11 (dry season), before the occurrence of the two seasonal peaks in fish reproduction (August to October and March to May, Kaningini et al., 1999). Surveys were performed during the daytime for both safety reasons and to be consistent with historical surveys (Lamboeuf, 1991). The routes (Fig. 1) covering 252 km in February and 345 km in July, were designed to cover all areas of the lake and have a cover ratio as defined by Aglen (1989) of approximately 6 (5.37 in February and 7.35 in July). Some transects were shortened due to periods of strong winds and for logistic reasons (mainly safe places to rest for the night). In the analyses, samples recorded in areas with bottom depths of <50 m were considered as inshore areas. In addition, a night survey was repeated on a single daytime transect to highlight the variation between night and day. Temperature and oxygen vertical profiles (Fig. 1) were obtained using an YSI 6600 multiparameter probe.
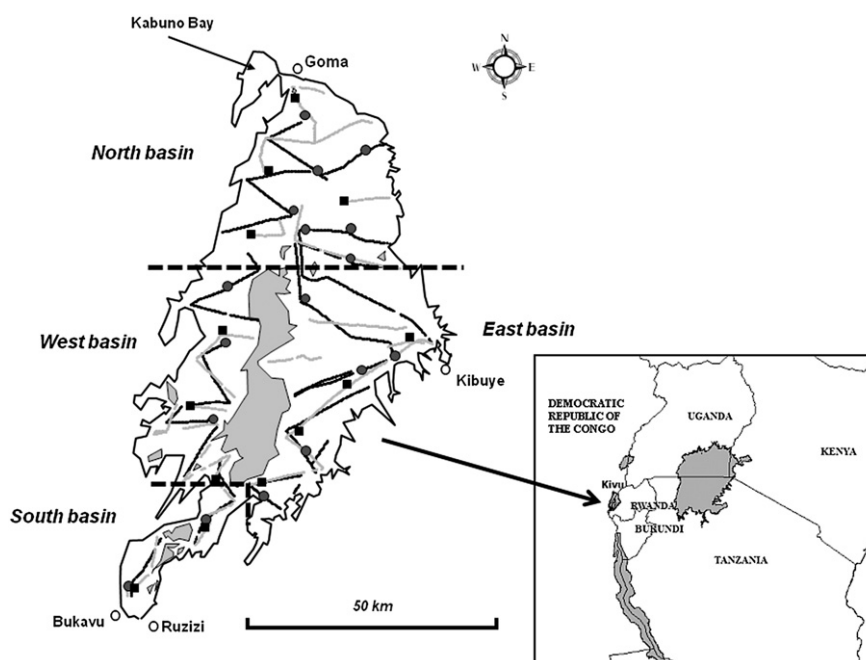

Fig. 1. Map of Lake Kivu showing the February 2008 (grey line) and July 2008 (black line) tracks and localization of the YSI profiles (February, black squares, July black circles). The dotted black lines showed the limit of the basins.

Table 1
Morphometry of the pelagic area of the four main basins, and of the inshore area of Lake Kivu (from Kaningini et al., 1999).

Basin	North	East	West	South	Inshore area
Surface (km²)	900[a]	900[a]	320	97	50[a]
Depth max (m)	489	400	225	105	50

[a] Estimated.

The echosounder used was a Simrad EK60 equipped with a 70 kHz split-beam transducer with a half-power beam angle of 11°. A GPS system was used to record boat positions. The collection parameters were a pulse-length of 0.256 ms (Godlewska et al., 2011) and 5 pulses per second. Sounder calibrations were performed annually in a large basin (IFREMER, Brest) according to the standard protocol of Foote et al. (1987), and the system was stable (gain variation < 0.4 dB). The sound speed parameter and the attenuation coefficient α were adjusted for temperature based on collected profiles. Surveys were performed from a wooden boat, at a mean speed of 8 km h^{-1}; the transducer was vertically attached to a pole along the boat at a depth of 0.5 m. The acoustic data were analyzed using the Sonar5-Pro software (Balk and Lindem, 2006) to calculate the total acoustic fish biomass in each depth layer and the acoustic size distributions. The processing thresholds were set at −60 dB for single targets and −55 dB for echointegration data, for consistency with those of Lamboeuf (1991). The Elementary Sampling Distance Unit (ESDU) was *a priori* fixed to 250 m, according to previous analyses in other lake ecosystems (Guillard and Marchal, 2001). Previous studies on Lake Kivu (Lamboeuf, 1989) have demonstrated that fishes are not present at depths > 60 m due to the permanent lack of oxygen: therefore, data were recorded below this lower limit with *in situ* checking. Data were analyzed by vertical layers of 15 m, like in the surveys carried out by Lamboeuf (1991): surface to 15 m, 15 to 30 m, 30 to 45 m, and 45 to 60 m. Fish area being proportional to acoustics backscattering (Simmonds and MacLennan, 2005), values were initially expressed in acoustic energy (s$_a$ expressed m² ha^{-1}) (MacLennan et al., 2002) reflected per layer and per unit of area, hereafter called acoustic biomass. Layered acoustic energy values were summed up by ESDU and the arithmetic mean acoustic biomass was computed for each basin. The arithmetic mean can be regarded as an unbiased estimate of the average in the area, if the effort is distributed in a homogeneous way, without initial statistical assumption (Smith, 1990). This estimator is similar to estimators obtained by other methods of calculation if the sampling effort is close to that recommended by Aglen (1989) (Guillard and Vergés, 2007). The whole lake acoustic biomass was given by the sum of each basin-specific mean acoustic biomass multiplied by the respective area of each basin. To estimate lake biomass, individual fish length and biomass were computed from single-echo observations. Single-echo detections criteria included echoes having 0.8–1.6 relative pulse widths, one-way beam compensation < 3 dB, and a maximum phase deviation of 0.3. To be classified as a tracked fish, traces had to include at least three echoes of the same target, separated by a maximum of one missing ping within a 0.3 m gating range (Balk and Lindem, 2006). From each tracked fish (see Fig. 4D), the average target strength (TS, dB) (MacLennan et al., 2002) was calculated in the linear domain. Frequency distribution of TS values was computed for each basin *i*. Each TS distribution was then split into 10 even-spaced frequency classes *c* (i.e., decile classes). Due to the non normality of the distributions, median TS values by frequency class, TS$_{c,i}$, were calculated for each basin and individual scattering cross-section (σ, m²) was calculated following MacLennan et al. (2002):

$$\sigma_{c,i} = 10^{\left(\frac{TS_{c,i}}{10}\right)} * 4\pi$$

Median individual fish lengths were calculated by basin for each TS frequency class using the TS-length relationship given by Lamboeuf (1991) for *L. miodon* in Lake Kivu:

$$TS_{c,i} = 20\log_{10}L_{c,i} - 67.6$$

where L = total fish length (cm). Median individual fish weights (W, g) were calculated by basin for each TS frequency class using the length-weight relationship given by Lamboeuf (1989) for *L. miodon* in Lake Kivu:

$$W_{c,i} = 0.055\, L_{c,i}^{2.27}$$

The whole biomass per basin was calculated using the following equation:

$$W_i = \sum_{c=1}^{10} \frac{p_{c,i} sa_i}{\sigma_{c,i}} W_{c,i}$$

where s$_{ai}$ is the mean acoustic biomass of basin *i* and p$_{c,i}$ is the proportion of the acoustic biomass for the TS frequency class *c* in basin *i* and is given by:

$$p_{c,i} = \frac{\sigma_{c,i}}{\sum_{c=1}^{10} \sigma_{c,i}}.$$

To generate confidence intervals for the fish biomass per basin and for the whole lake, we used a bootstrap approach that incorporated uncertainty in each of the following two estimates used to calculate the fish biomass: the mean s$_a$ per basin, the fish size structure. First, we randomly selected s$_a$ per basin with replacement and calculated a mean acoustic biomass, s$_{ai}$. Next, we randomly selected target strengths with replacement and calculated median TS values by frequency class, TS$_{c,i}$. We then applied above-mentioned equations for calculating the whole biomass per basin, W$_i$. This process was repeated 2500 times to generate a distribution of biomass estimates and calculate 95% confidence interval. The whole lake biomass was obtained by summing the four basin biomass plus the biomass observed in littoral areas.

The parametric one-way analysis of variance and post-hoc Tukey's HSD tests were used to compare acoustic biomass between basins and seasons. The heterogeneity of spatial distribution was given by the coefficient of variation (CV = SD/mean) of acoustic biomass. Multiple CV were compared using the Bennett's test as modified by Shafer and Sullivan (1986). The Kruskal-Wallis one-way analysis of variance was used to compare the estimated fish length distributions between seasons and areas. Bootstrap confidence intervals of biomass estimates were compared using Student's *t* test.

Results

Temperature and oxygen

The water temperatures in the surface layer varied between 23.5 and 24.0 °C regardless of the season (Fig. 2). In February, a thermocline around 30–40 m was recorded, while temperatures were almost constant in the mixolimnion during July (Fig. 2). During each survey, no difference in temperature and oxygen profiles was observed between basins: only the two profiles in the Bukavu Bay had a significantly lower surface temperature (23.0 °C). In February, the oxygen concentration rapidly decreased below 30 m, with an oxycline ending at 35 to 50 m depending on the location (Fig. 3). In July, the oxycline was located at greater depths, ending between 50 and 60 m. Waters below the oxycline were always anoxic.
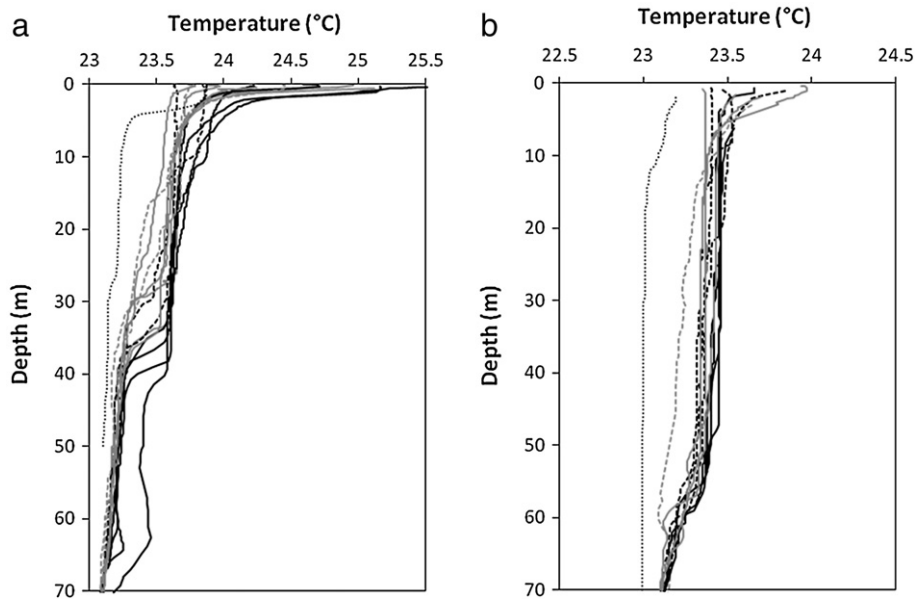
Fig. 2. Vertical temperature profiles in February (a) and July (b) 2008 in Lake Kivu. The continuous black lines represent the vertical profiles of the North basin, the continuous grey lines of the East basin, the dashed black lines of the West basin, the dashed grey lines of the South basin and the dotted black line of Bukavu Bay.

Detected biomass

Echograms

Observations performed during the daytime showed no target in layers close to the surface and in layers below 60 m. Several kinds of structures were identified (Fig. 4) including individual fish, aggregations and more or less dense schools. High-density schools (Fig. 4A) were mainly observed in the inshore area or in pelagic areas close to shallows. Large differences in the nature of aggregations were observed in different areas and in various vertical strata. During the night survey, fishes were scattered and no aggregations structures were observed (Fig. 4C).

Acoustic biomass

The acoustic biomass detected per sampling unit showed spatial and seasonal heterogeneities (Figs. 5 and 6). Regarding the vertical distribution, fishes were mainly observed in the intermediate layers (15–30 and 30–45 m) in February (layer effect $F_{3,4016} = 85.81$, $p < 0.001$); however, fishes were more abundant in the upper layers (3–15 and 15–30 m) in July (layer effect $F_{3,5504} = 352.5$, $p < 0.001$). Furthermore the acoustic biomass was always low in the deepest layer (45–60 m) with 84% and 61% of ESDUs without fish in February and July 2008, respectively (Fig. 6). However, when considering all of the layers, the percentage of units without fish detection became negligible, <1% during both seasons. The highest acoustic biomass were observed in February in the southern and western basins (one-way ANOVA and post-hoc Tukey test, basin-effect $F_{3,1001} = 45.66$, $p < 0.001$) while in July only the South basin showed higher values than the others (basin effect $F_{3,1373} = 6.739$, $p < 0.001$).

The acoustic biomass detected in inshore areas were 3 to 8 times greater than in pelagic areas during both seasons ($F_{1,2611} = 565.4$, $p < 0.001$; Table 2). The coefficients of variation (CV) of acoustic
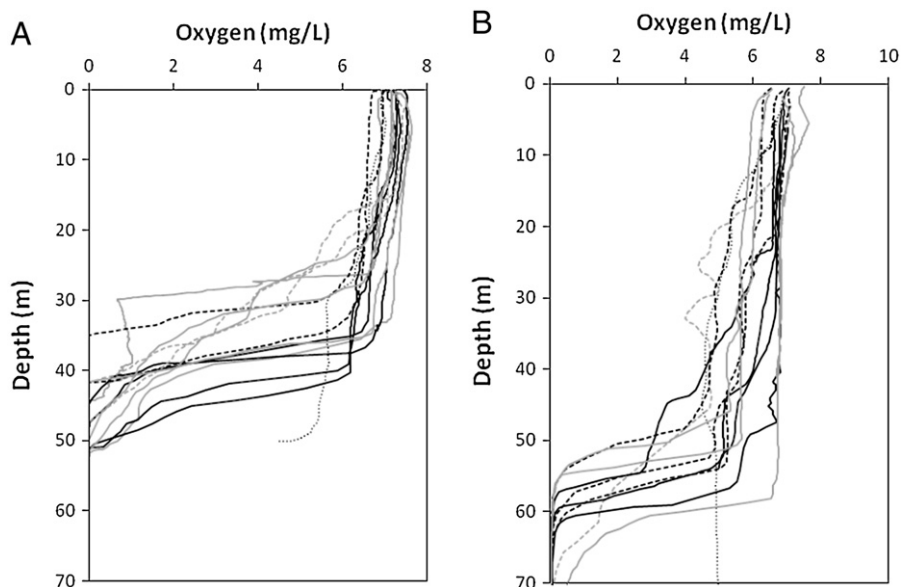

Fig. 3. Vertical profiles of dissolved oxygen in February (A) and July (B) 2008 in Lake Kivu. The continuous black lines represent vertical profiles of the North basin, the continuous grey lines of the East basin, the dashed black lines of the West basin, the dashed grey lines of the South basin and the dotted black line of Bukavu Bay.
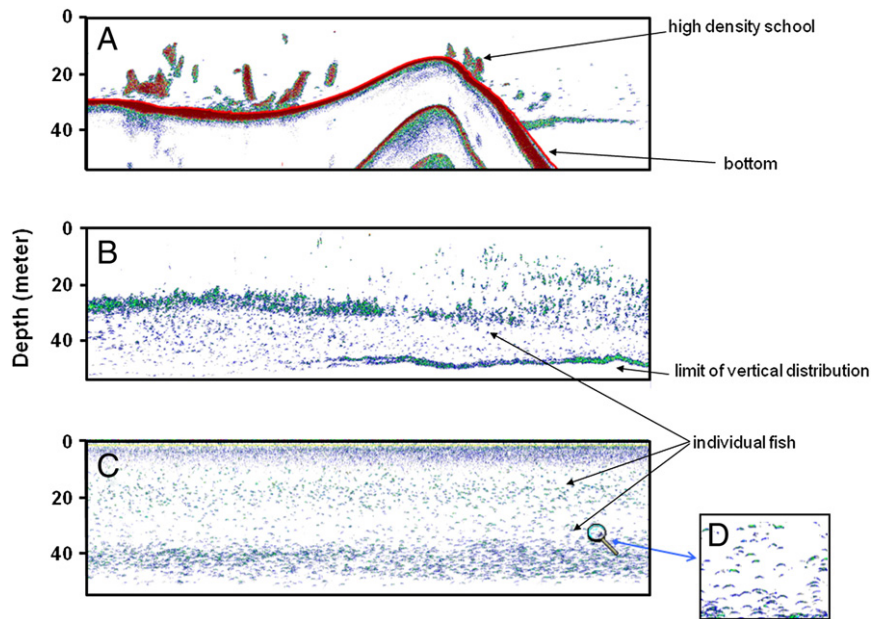
Fig. 4. Examples of echograms captured in the inshore area (A) and in the pelagic area (B) of Lake Kivu during daylight, in the pelagic area at night (C), and a zoom on individual fishes (D).

biomass by basin, which is a measure of spatial heterogeneity, ranged between 0.80 and 1.38, depending on basin and survey (Table 2). The fish population showed a greater heterogeneous dispersion (higher CV) at both basin and whole-lake scales in February than in July 2008. Indeed, at whole-lake scale, the CV of acoustic biomass was higher in February than in July 2008 (modified Bennett's statistic = 29.452, $p<0.001$), and at basin scale there was a significant difference between basin-specific CVs during the February survey (modified

Bennett's statistic = 4.218, $p = 0.040$) but not during the July survey (statistic = 1.292, $p = 0.256$).

Size assessment

Individual fish lengths, converted from TS data, ranged from 2 to 20 cm (Fig. 7). Some differences in fish length distributions were observed between basins or seasons (Kruskal-Wallis one-way analysis of variance, statistic = 1609.7, p<0.001; Fig. 7). Particularly, fishes
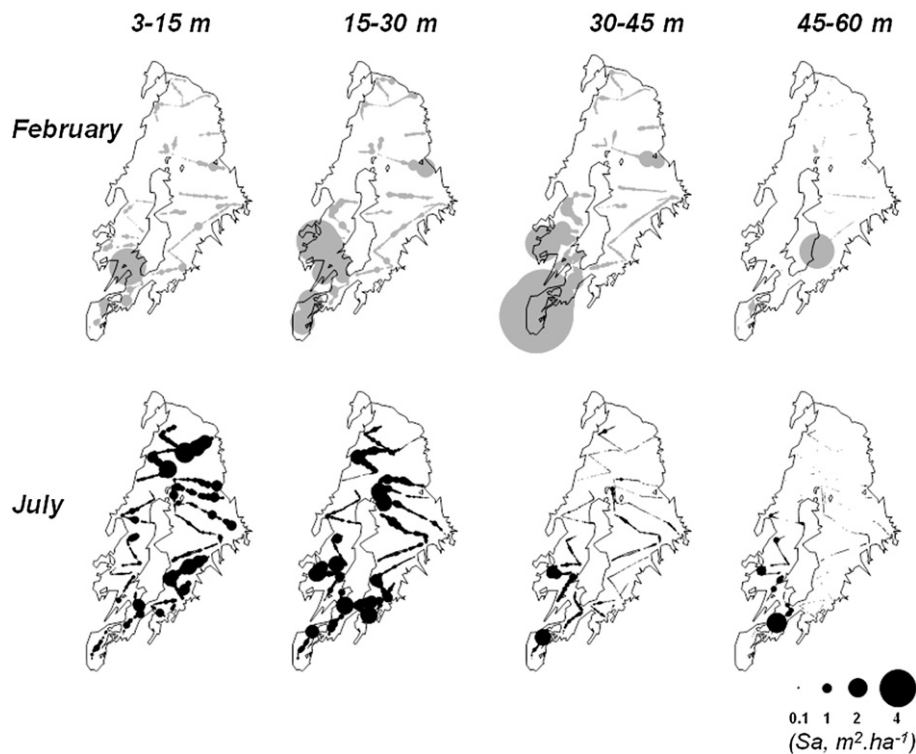

Fig. 5. Fish acoustic biomass detected by ESDU in the four vertical layers (3–15, 15–30, 30–45, 45–60 m) in February (grey) and July (black) 2008. The values are in m² ha^{-1}.
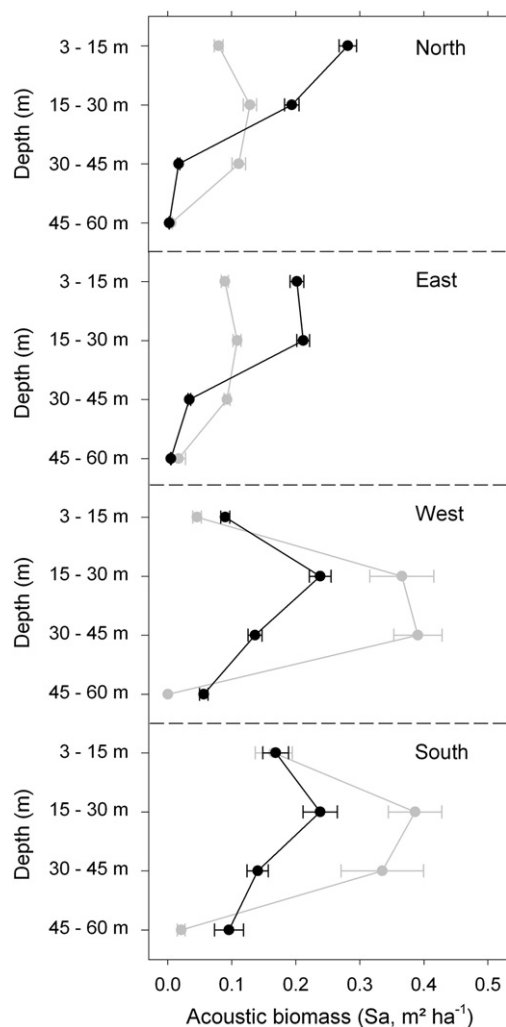
Fig. 6. Mean acoustic biomass (±standard deviation) of the four vertical layers per basin in February (grey line) and July (black line) 2008.

longer than 10 cm were relatively more abundant in July than in February (p<0.001): they represented 25% (acoustic biomass-weighted mean) of total numbers of fishes in February for 34% in July.

Calculation of biomass

The fish biomass per basin was determined using the mean acoustic biomass, s_{ai}, and TS frequency distribution of the considered basin. Results are given in Table 3. Due to their greater areas, the fish biomass was highest in the northern and eastern basins whatever the season. The western basin showed also a high biomass in February. The littoral areas counted for 12–13% of the total fish biomass while they represent only 2% of the total surface area. There was no difference of total fish biomass between both seasons, with a mean

Table 2
Mean and coefficient of variation (CV) of acoustic energy (s_a m^2 ha^{-1}) in the different lake areas and seasons.

	North	East	West	South	Whole pelagic area	Inshore area
February						
Mean sa (m2.ha−1)	0.324	0.306	0.802	0.908	0.497	2.336
CV	1.13	0.90	1.18	1.38	1.49	1.74
July						
Mean sa (m2.ha−1)	0.495	0.452	0.520	0.642	0.497	2.989
CV	0.85	0.80	0.92	0.84	0.86	1.04

estimation of 5004 tons and 6036 tons, respectively in February and July (Table 3).

Diel vertical migration

In February, a survey was performed before and after dusk on a similar track (Fig. 8) to observe and quantify vertical distributions and changes in aggregation structures. On the echograms (Fig. 8), fish dispersion and migration at dusk to the 10–15 m layer were observed. Before dusk, the percentage of single echoes in each ESDU was near 22%, whereas it was more than 40% during the night, showing a change from aggregations to scattered fish.

Discussion

Our surveys were performed during the daytime, similar to those conducted in the 1980s (Lamboeuf, 1991), with a sampling effort close to that recommended by Aglen (1989). Schooling of fish during daylight (Fréon and Misund, 1999) was observed, similarly to previous observations (Kaningini et al., 1999). Fish dispersion at dusk (Fréon et al., 1996) was also noted in the lake. This behaviour is often interpreted as an anti-predatory mechanism (Parrish et al., 2002; Pitcher and Parrish, 1993), but Lake Kivu has no predatory fish species in the pelagic zone, except large *L. miodon* for which predation upon its own fry in Lake Kivu has been reported (Kaningini, 1995). Acoustic surveys performed during the night, when distributions are more homogeneous, are typically more reliable than those performed during daylight (Simmonds and MacLennan, 2005). In our study, we assumed that daylight surveys were also reliable due to the relatively homogeneous distribution during daytime and because no fish were detected close to the surface. In Lake Kivu, the inshore area is limited due to its steep banks; therefore hydroacoustic sampling in the pelagic area allows reliable estimation of the vast majority of the stock (Brehmer et al., 2006). Nevertheless, although the inshore area of Lake Kivu represented ~2% of the surface area, 12–13% of total biomass resided in this area. In these inshore zones, contrary to offshore zones where *L. miodon* was the dominant species (Kaningini et al., 1999), other fish species are present, especially *L. tanganicanus* (Masilya et al., 2011), leading to a possible overestimation of the *L. miodon* stock. Therefore additional samplings by complementary fishing methods should be conducted in future surveys to check for the abundances of *L. tanganicanus* in this area. Nevertheless, since the occurrence of *L. tanganicanus* is low in the pelagic zone (Masilya, 2011), their presence likely did not significantly biased our assessment of the *L. miodon* stock.

Notable differences in fish distributions in the pelagic zone were found. The biomass were higher in the western and southern basins in February, while only the South basin had higher biomass in July. However, fish biomass was more homogenous among basins during July than during February. Notably, the biomass of the southern and western basins significantly decreased between February and July, while values in the northern and eastern basins increased. Marshall (1991) noted a similar pattern, i.e. CPUE was higher in the South in February and in the North in July, and concluded that *L. miodon* undertook South to North migrations in Lake Kivu. However, due to a high variation in fishery activities (Kaningini et al., 1999) related to seasonal wind and waves conditions, the differences highlighted by Marshall (1991) might be questionable. High concentrations in the South basin in February were also described by Marshall (1991), who hypothesized that the morphology of this basin, with well-developed coastal zones were favorable to *L. miodon* reproduction. Past and present surveys show that fish were always limited to the upper 60 m of the water column (i.e. to the mixolimnion), but the deepest layer, 45–60 m, was devoid of fish in February. In July, this deepest layer supported low fish biomass, despite the whole mixolimnion was well oxygenated, and fishes were closer to the surface than in February. Fishes were not present in the surface layers,
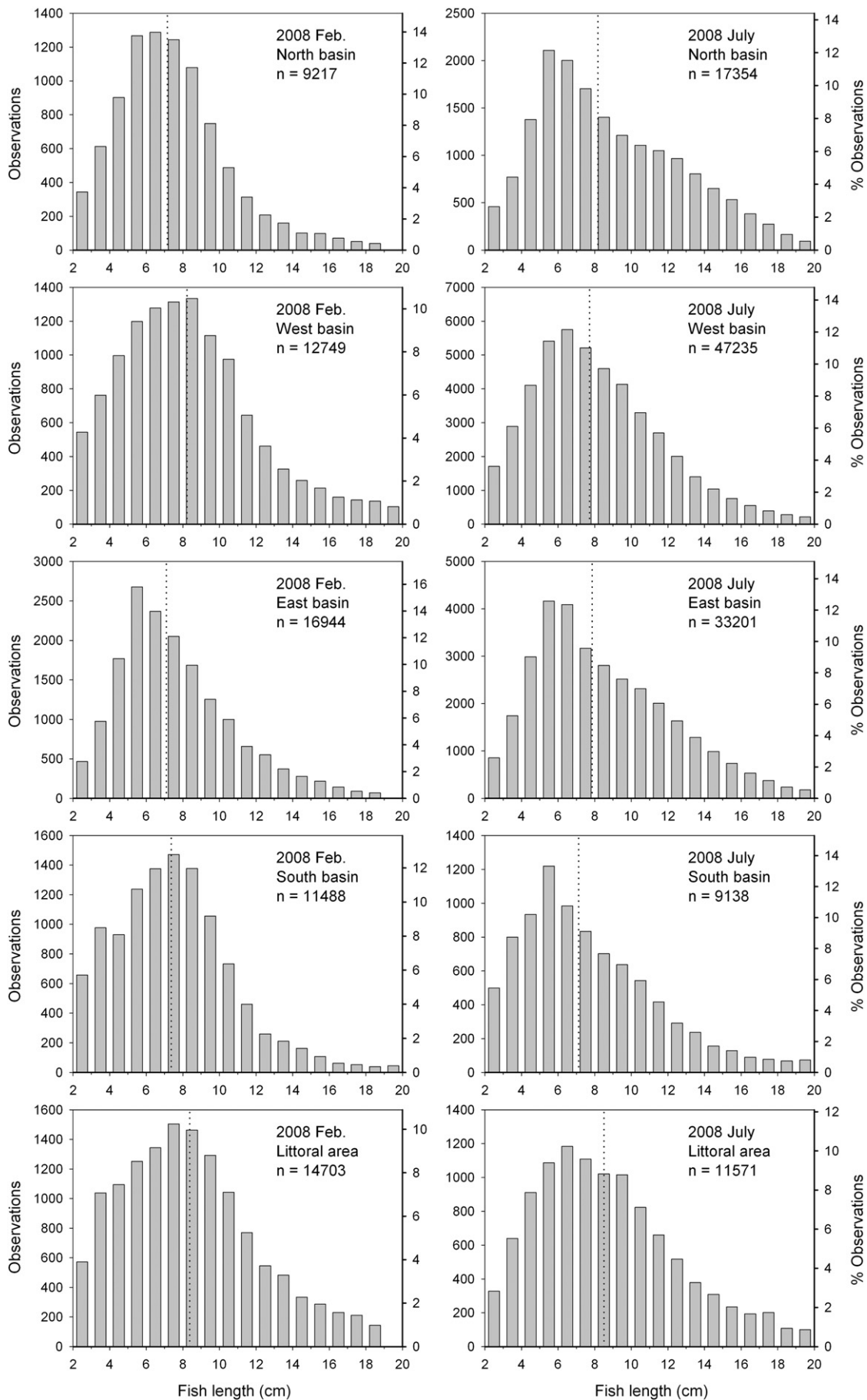
Table 3
Fish biomass in the different lake areas and seasons. 95% confidence intervals (C.I.) were estimated by a bootstrap procedure.

	North	East	West	South	Whole pelagic area	Inshore area	Whole lake
February							
Biomass (T)	1367	1295	1324	414	4399	605	5004
(95% C.I.)	(1210–1549)	(1184–1426)	(1100–1564)	(338–510)	(3832–5049)	(450–800)	(4283–5848)
July							
Biomass (T)	2183	1969	797	313	5263	773	6036
95% C.I. (T)	(2021–2352)	(1832–2113)	(715–882)	(268–365)	(4836–5712)	(615–945)	(5451–6657)

thus escape behaviours observed elsewhere (Guillard et al., 2010; Knudsen and Saegrov, 2002) should not be an issue. No spatial pattern of fish size distribution was observed in pelagic areas, which is consistent with the previous findings of Lamboeuf (1991). However, the proportion of small fish in the inshore areas was lower than in the pelagic zone whatever the season. Fish sizes were estimated using tracked fish, smoothing the variability due to behaviour and position. The number of detected targets was always considerable and the Sawada indexes were less than 0.1 as recommended by Rudstam et al. (2009). The size distributions were always unimodal (Fig. 7), which is representative of only one fish species, without marked cohorts. As *L. miodon* is by far the major pelagic fish species in Lake Kivu (Masilya, 2011), the transformation of TS to fish length was straightforward. In our study, the percentage of small targets representing juvenile fish (1–6 cm) (Kaningini, 1995), did not vary much in different basins and seasons and was approximately 30% of the total population based on the number of fish detected. Seasonal variation in the abundance of different size classes were noticed by Lamboeuf (1991) who used a single-beam sounder (EY200).

The two fish stock assessments were performed before the two main periods of *L. miodon* reproduction in Lake Kivu, i.e. March to May and August to October (Kaningini et al., 1999). The surveys led to an estimate of total fish stock of 5004 tons in February and of 6036 tons in July. Previous surveys (Kaningini et al., 1999) estimated the total fish biomass to be between 6000 and 10,000 t, while Lamboeuf (1991) estimated the biomass of *L. miodon* at 3445 to 5351 t between April 1989 and June 1991. Also, the mean areal density we observed (23 kg ha^{-1}) was similar to that described by Lamboeuf (1991). Given the similarity of the approaches used and the comparable sampling design, we conclude that there has been no difference in the sardine stock between the end of the 1980s and 2008. It is worth noting that estimates made at the end of the 1980s followed a period of stock decrease from 1981 to 1988, followed by a sharp increase in 1989 and 1990 (Lamboeuf, 1991; Marshall, 1991) and we cannot exclude that fish biomass varied during the two survey periods. While not significant, an approximately 20% increase in fish biomass was noted between February and July 2008. Actually, such a rise in fish biomass is within the range of natural stock fluctuations for this small pelagic fish (Marshall, 1993), and given the estimation errors, it should not be interpreted as a long-term trend. More frequent surveys, complementary with estimates of fisheries catches, should be performed to better understand the natural and human-caused fluctuations, as recently illustrated in Lake Kariba (Magadza, 2011).

A collapse of the *L. miodon* stock in Lake Kivu was predicted by Dumont (1986) due to a drop in the zooplankton size and abundance following the *L. miodon* introduction. Our hydroacoustic surveys demonstrate that the predicted collapse of *L. miodon* did not occur. The capacity of zooplankton communities to recover after a fish introduction has been reported in other lentic systems (see e.g. Harig and Bain, 1998; Knapp et al., 2001). Successful populations of alien species often rapidly increase in abundance, but then decline to what might

be called an "equilibrium level" (Strayer and Malcom, 2007; Williamson, 1996). The *L. miodon* introduction in Lake Kivu might have followed this "boom-and-bust" dynamic, and we can reasonably assume that the zooplankton biomass decrease detected in the 1980s was observed during the boom phase of *L. miodon* invasion. Unfortunately, data on the *L. miodon* dynamics in the years following the introduction are lacking. It is possible that the low zooplankton biomass reported by Dumont (1986) was a short-term effect, and that after some time both zooplankton and fish communities reached a more stable system state in Lake Kivu. This is in accordance to recent observations on the zooplankton community in Lake Kivu (Darchambeau et al., in press; Isumbisho et al., 2006). Re-analysis of past and recent zooplankton records indicates that zooplankton biomass before the sardine introduction may have been as high as 3 g C m^{-2}, whereas the biomass in 2003–2004 was ~1 g C m^{-2}, suggesting a strong decline from the past situation without a planktivore fish. However, the present zooplankton biomass in lake Kivu is comparable to that of other great lakes of the East African rift (Darchambeau et al., in press), and may represent a new equilibrium biomass for zooplankton in the presence of planktivorous fish.

As already outlined (Lamboeuf, 1991; Marshall, 1993; Roest, 1999), *L. miodon* densities in Lake Kivu are low in comparison with lakes or reservoirs where the species is naturally present (Lake Tanganyika) or was introduced (Lakes Kariba and Cahora Bassa). The mean *L. miodon* biomass in 2008 in Lake Kivu (23 kg ha^{-1}) is notably lower than the sardine biomass in Lake Tanganyika, where estimates range from 60 kg ha^{-1} (Szczucka, 1998) to 300 kg ha^{-1} (Moreau and Nyakageni, 1988). Worth noticing, however, is that these figures are based on the fishery yield of the two sardine species inhabiting Lake Tanganyika, *Stolothrissa tanganicae* and *L. miodon*. The reasons for the low *L. miodon* density in Lake Kivu are not known (Descy et al., 2012). Indeed, total phytoplankton and zooplankton productions are comparable across East African Great lakes (Darchambeau et al., 2012; Sarmento et al., 2012). Among the possible explanations, large fluctuations in clupeid stocks have been reported from other systems, in which variations of recruitment and larval survival may play a significant role (Kimirei and Mgaya, 2007; Mölsä et al., 2002). In addition local people around Lake Kivu often use illegal fishing techniques for catching young fish in the inshore aeras (Kaningini et al., 1999) where the growth of *L. miodon* larvae and juveniles takes place (Masilya, 2011). This potentially harmful practice, coupled with the incidence of predation by *L. miodon* adults and other fish species in the inshore areas (De Iongh et al., 1983; Masilya, 2011), might significantly reduce larvae survival. Moreover, strong competition for resources may occur in these inshore zones (Masilya, 2011) which harbour almost all the fish diversity in Lake Kivu, with several haplochromine species (Snoeks et al., 1997).

Conclusion

Given that the pelagic area of Lake Kivu is dominated by *L. miodon* (Kaningini et al., 1999; Masilya, 2011) the two hydroacoustic surveys

Fig. 7. Fish length distributions, converted from TS data, from in 1 cm classes by season and for the four basins plus the littoral area. The dotted lines represent the median values.
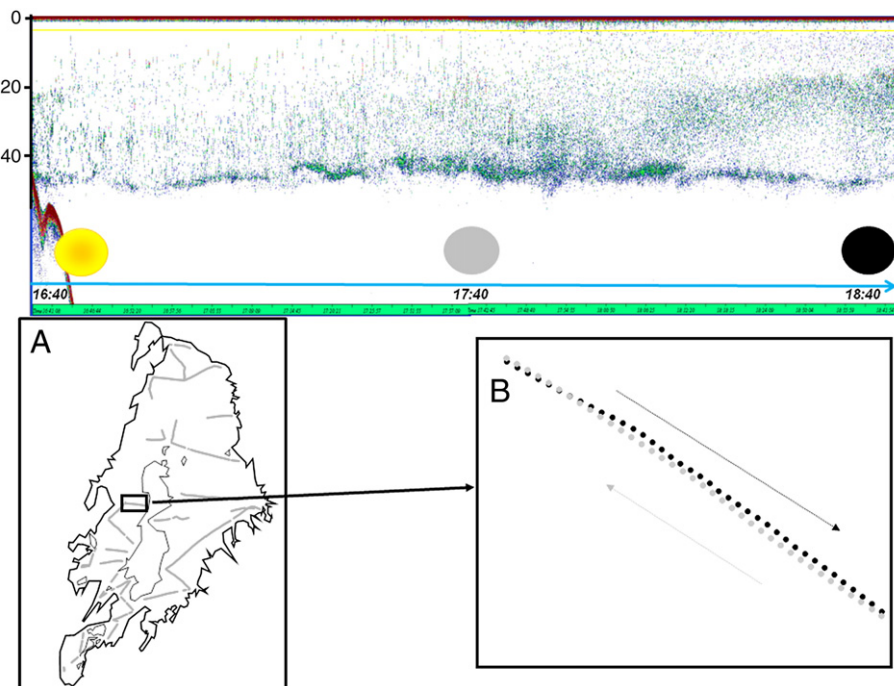
Fig. 8. Echogram recorded continuously from 16:40 to 19:00 GMT (dusk from 17:30 to 17:50 GMT), showing the detected fish (see Fig. 4) with the area (A) where the survey was performed indicated by a black rectangle, and a zoom (B) with the way forward, in grey, and the way back, in black.

performed in 2008 in Lake Kivu provided estimates of *L. miodon* biomass of 5004 tons (February) and 6036 tons (July). These results are similar to those reported at the end of the 1980s. Thus, contrary to predictions based on changes in the zooplankton assemblage, the stock of *L. miodon* did not collapse, but remained stable, despite a likely increase in the fishing effort. Based on the data presented here, the pelagic fishery on *L. miodon* in Lake Kivu appears sustainable. However, further hydroacoustic studies should examine the variations of the fish stocks in the lake. These surveys should be complemented by an assessment of the fishing effort over the whole lake in order to define management strategies for ensuring sustainability in the future. This becomes all the more relevant in the context of the methane exploitation (Nayar, 2009), which may in the long term affect both the environmental conditions and the resources available to the pelagic fish in Lake Kivu (Descy et al., 2012)

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