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Spatial and temporal variations of *Limnothrissa miodon* stocks and their stability in Lake Kivu

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ABSTRACT: *Limnothrissa miodon* is a small pelagic clupeid that was introduced into Lake Kivu in the late 1950s to fill an empty niche. Since then, it has become the main fishery in the lake. The fish stocks were estimated by hydroacoustics between 2012 and 2018 to provide information on the fishery in the current context of changing environmental factors. The main objectives were to determine the most appropriate season for assessing stock dynamics, to characterize temporal and spatial distribution in *L.miodon* populations and to compare with previous surveys to help predict status of its stocks. The fish size distribution showed that the long dry season was the most appropriate season for assessing the stocks, as it provides information of recruitment for the year. The south and west basins always had higher densities (1.23 m²/ha) and biomass (21-22.7 kg/ha) than the north basins (0.62-0.77 m²/ha; 15.3-16.5 kg/ha). The stock showed declining trend from 7,000 t in 1985 to 1,000 t in 2012 and thereafter consistently increased to 4,000 t in 2018. This last value is similar to previous estimates of 1990s and 2008, showing that the stocks of *L. miodon* are stable. The low 2012 values could be due to particular environmental conditions in 2012-2014, when there was a shift from diatoms and cyanobacteria to green algae. There is therefore a need to combine high-quality environmental data with fishery surveys to better understand the dynamic of fish and fishery especially under the increasing influence of climate change on lake productivity processes.

Keywords: hydroacoustics, large African lake, clupeid, biomass, nutrient, phytoplankton

Introduction

Inland fisheries are a main livelihood resource for the human population in the African Great Lakes. They are currently dominated by small pelagic fish species, which are endemic or introduced (Kolding et al., 2019). Over the last three decades, stocks of small pelagic clupeids fisheries have increased rapidly in many African lakes resulting in a shift of fisheries from large species to smaller ones (Kolding et al., 2019). The contribution of small pelagic fishes to commercial catches in many African lakes increased since the 1970s to 45% in Victoria, 35 % in Malawi, 65 % in Tanganyika, 60 % in Kivu, 80 % in Lake Albert, and 17 % in Kyoga (Ogutuhwayo et al., 2013; Ogutuhwayo et al., 2000) due to a shift, for example, to *Rastrineobola argentea* from *Lates niloticus* in Lake Victoria (CIFA 1984), and in Lake Malawi from *Oreochromis lidole* to *Engraulicypris sardella* (Kolding et al., 2019). Several factors are possibly contributing to this shift, such as overexploitation of large species or increased eutrophication of the ecosystem (Kolding et al., 2008). Ogutuhwayo et al. (2016) mentioned that FAO (2010) has predicted that fisheries will shift to small pelagic opportunistic species and the increases in many African lakes may be associated with the increasing variability and change in climate of these lakes and its effects on lake productivity processes.

Small pelagic clupeids represent a more sustainable resource than large species because of their better resilience to natural and anthropic disturbances (Jul-Larsen et al., 2003; Kolding et al., 2019). Clupeid stocks are known to fluctuate strongly according to environmental conditions due to their low trophic level in the food web and rapid maturity (Karengere and Kolding, 1995; Marshall, 1982; Trochta et al., 2020). As clupeids are mainly zooplanktivorous, their stock level is mainly driven by nutrient inputs and primary production, so it can vary greatly within and between years (Kolding et al., 2019). Clupeid stocks are resilient to high fishing intensity because they mature much faster than large fish species (Mangeni-Sande et al., 2019) and have multiple spawnings per year in tropical areas like Lake Kivu (Marshall, 1990).

In the African Great Lakes regions, small pelagic clupeid fisheries make important contributions to reducing poverty and improving food security and nutrition. For example, in 2005, 30 to 45 million people in Africa depended on fish for their livelihoods (Béné and Heck, 2005). These small fishes also contribute to gender equality with women and youth dominating in the processing and marketing (Funge-Smith and Bennett, 2019). *Limnothrissa miodion* is one of the three predominant fish species of Lake Tanganyika (Kimirei and Mgaya, 2007; Plisnier et al., 2009), where it is endemic. It also dominates the fisheries of

lakes and reservoirs where it has been introduced, like the Itezhi-tezhi reservoir (where it was introduced in the beginning of the 1990s) (Kolding et al., 2019), Lake Kariba and Cahora Bassa (at the beginning of the 1960s) (Balon and Coche, 1974), and Lake Kivu (at the end of the 1950s) (Kaningini et al., 1999).

Located between the Democratic Republic of the Congo (DRC) and Rwanda, Lake Kivu is in a region where the annual climate consists of two dry and two rainy seasons (Thiery et al., 2014). It is a meromictic lake with mixolimnion (oxygenated layer) mixing until a maximum depth of around 60 m during the dry season (Reusens, 1987; Schmid and Wüest, 2012). The environmental conditions of Lake Kivu can respond quickly to atmospheric conditions linked to climate change (Schmid and Wüest, 2012). In 2012-2014, the mixing of the mixolimnion was modified by changes in wind patterns, which led to a significant change in the composition of the phytoplankton communities, with green algae supplanting diatoms and cyanobacteria (Rugema et al., 2019).

L. miodon was introduced to establish a pelagic fishery in what was originally an impoverished fishery by colonizing the pelagic zone, which was a vacant ecological niche (Collart, 1960). The introduction has been considered a successful one (Gozlan, 2008; Marshall, 1995). The catches of *L. miodon* may represent up to 75% of total catches (Kolding et al., 2019). This fishery supports more than 6,500 fishermen (Guillard and Richard, 2017) and provides nutrition for the 2 million people around Lake Kivu (Wüest et al., 2012).

The pelagic stock of *L. miodon* in Lake Kivu was assessed by FAO using hydroacoustic methodology during the daytime over different seasons each year from the early 1980s to the beginning of the 1990s (Lamboeuf, 1991; Reusens, 1987). The stock of *L. miodon* was estimated at 7,000 t (35 kg/ha) before 1989 and 4,000 t (18 kg/ha) in the 1990s, with high seasonal fluctuations. Fish were mainly scattered between depths of 15 and 45 m without a clear spatial pattern (Lamboeuf, 1991). Around 80% of the detected fish sizes were estimated between 4 and 10 cm.

In 2008, two hydroacoustic surveys led to similar conclusions on the vertical distribution of fish in the water column, the size distribution, and the absence of a clear geographical pattern (Guillard et al., 2012). The stock levels were estimated at 4,400 t to 5,000 t, and it was concluded the fisheries had been sustainable over the intervening two decades (Guillard et al., 2012). This conclusion is contrary to the possible collapse proposed by Dumont (1986) based on changes in the assemblages and decline in biomass of mesozooplankton. The mixolimnion zone of Lake Kivu is not entirely mixed every year, which is probably due to climate change, and the phytoplankton show modification of the

assemblage (Richard et al., 2020; Rugema et al., 2019). These modifications of the environmental conditions and functioning can affect the stock of *L. miodon*.

Stock estimates were carried out from 2012 to 2018, and in 2013 and 2014 using hydroacoustic methods. The surveys were carried out during the daytime in the pelagic zone using the same sampling method (vertical echo-sounding) and the same water layers as previous surveys (2-15 m, 15-30 m, 30-45 m and 45-60 m). The population size, structure, and fish density were analyzed with special emphasis on spatial variations (between basins) and temporal variations (seasonal and inter-annual). From these analyses, the most appropriate season to evaluate the stocks of *L. miodon* in Lake Kivu was established in relation to the reproductive behavior pattern of the species (Kaningini, 1995). Because environmental conditions had changed between the 2000s and 2010s (Richard et al., 2020; Rugema et al., 2019), the fish densities and size structures were compared with previous assessments, and spatial geographical patterns were analyzed. Finally, the evolution of the fish stock at the scale of the whole lake was analyzed relative to the historical time series.

Material and methods

Study area

Lake Kivu (1°34'30''- 2°30'S; 28° 50'-29°23' E, Fig. 1) has a surface area of 2370 km² and is located in a geographical region with four seasons: a short dry season (January to February), a long rainy season (March to May), a long dry season (June to September), and a short rainy season (October to December) (Thiery et al., 2014). The lake can be divided into five basins (Fig. 1), each with different wind patterns of, precipitation, fishing effort, and governance (Kwetuenda et al., 1989). Due to its high altitude (1463 m above sea level), the water's surface temperature is lower than in other African great lakes and usually ranges from 23.5 to 25°C (Katsev et al., 2014).

Below around 60 m, the deep monimolimnion is anoxic with high concentrations of dissolved methane in the deeper layers (Tassi et al., 2009). The maximum depth is 485 m in the northern part (Data Environnement, 2011; Descy et al., 2012). Lake Kivu is oligotrophic (Isumbisho et al., 2006), and it has only 29 fish species (of which 5 were introduced). This is due to profound geologic disturbances that occurred around 11,000 years BP and because it is at the upper part the basin of species-rich Lake Tanganyika (Haberyan and Hecky, 1987). Presently, the pelagic zone of the mixolimnion is dominated by *L. miodon* (Collart, 1960) and fish are not present at depths below 60 m (Guillard et al., 2012; Lamboeuf, 1989b).

Acoustic sampling

Hydroacoustic surveys were performed on a small craft using the same equipment and protocol as the previous surveys performed by Guillard et al. (2012). They were performed using a SIMRAD (Kongsberg Maritime AS, Horten, Norway) EK60 scientific echosounder equipped with a 70-kHz split-beam transducer (SIMRAD ES70-11) with a half-power beam angle of 11° (at - 3dB) beaming vertically. The transducer was regularly calibrated *in situ* using a copper sphere with 23-mm diameter according to procedures recommended by Foote et al. (1987) and the manufacturer. The transducer was attached to a pole along the boat and positioned at 0.7 m below the water surface to sample the water column in the range of 2 m below the surface to 65 m.

The echosounder's ping rate was set to 5 pings per second, and the pulse duration was fixed at 0.256 ms (Godlewska et al., 2011). A Global Positioning System (GPS) was coupled to the echosounder, and the boat speed was around 8 km/h. To identify whether results from hydroacoustic surveys were representative of the pelagic stock of the lake, the degree of coverage was computed according to Aglen (1989). The degree of coverage was obtained by dividing the total length of the path (km) by the square root of the studied surface (km²). The result should be at least 3.0 and preferably above 6.0 to obtain a reliable assessment (Emmrich et al., 2012).

The hydroacoustic surveys were carried out in the pelagic areas (areas with bottom depth deeper than 50 m) for each of the five basins (North Rwanda, North DRC, East, West, and South) using zigzag tracks (Fig. 1) (Guillard and Vergès, 2007). Seasonal surveys were performed in 2013 and 2014 to identify the best season to perform stock estimation (Rudstam et al., 2012).

The annual surveys from the best season regarding stock estimation were then analyzed from 2012 to 2018 to provide inter-annual and spatial variations of fish density, size, structure, and total biomass. Finally, annual stock estimates were compared with historical data using the same season (Guillard et al., 2012; Lamboeuf, 1989a, 1991). Hydroacoustic surveys were not carried out for some basins or periods due to staff availability, failure to obtain legal authorizations, boat issues, or bad weather (Table 1).

Hydroacoustic sampling is usually carried out at night due to fish behavior because fish are scattered and individual size estimations are possible, in contrast to the daytime, when fish are mainly in schools or close to the bottom (Coll et al., 2007; Girard et al., 2020; Prchalová et al., 2003). However, as the historical surveys were performed during the daytime (Guillard et al., 2012; Lamboeuf, 1991), the hydroacoustic surveys in the present study were

performed during this photoperiod between 05:00 and 16:00. Moreover, both safety and legal reasons necessitated that the hydroacoustic surveys be performed during the daytime.

Data analyses

The software Sonar5-Pro (Balk and Lindem, 2014) was used to process the data. The processing thresholds were set at -60 dB for single targets detection and -66 dB for echo integration. A difference of 6 dB between the threshold intensity and the detection thresholds is recommended (Parker-Stetter et al., 2009). The data were cleared of different types of noise (e.g., bottom structure, false bottom, bubbles, debris) at the appropriate thresholds by using manual deletions to conserve only fish echoes for analyses (Draštik et al., 2017; Emmrich et al., 2012). The analyses were stopped at 60 m because fish are not present below this depth (Guillard et al., 2012). However, echograms were checked to verify that this was always true. The elementary sampling distance unit (ESDU) was fixed *a priori* at 1000 m according to Muzana and Guillard (2014) and served as replicates (Yule et al., 2013).

For each ESDU, we used the hectare acoustic scattering strength (sA , with units m^2/ha) as a proxy for fish density (Boswell et al., 2010):

$$sA = 10^{(Sv/10)} \times T \times 4 \pi \times 10000$$

Sv is the volume backscattering strength in decibels (dB) (MacLennan et al., 2002), T is the mean thickness of the domain being integrated, 4π is the steradians in a sphere that converts a “backscattering” cross section to “scattering” cross section, and 10,000 is a conversion factor (m^2/ha) (Yule et al., 2013). sA can be considered as a proxy of the density in this study because pelagic areas of Lake Kivu are dominated by a single species with homogeneous sizes. Seasonal variations of sA were analyzed using the Sheirer Ray-Hare (SRH) test on the mean values for 2013 and 2014 and for each basin while considering the seasons and the water layers as factors. These years were chosen because at least 3 or 4 seasons were sampled in these years, unlike other years (Table 1).

The water column was split into four layers (2-15 m, 15-30 m, 30-45 m, and 45-60 m), as performed by Guillard et al. (2012). The SRH test was followed by the Conover-Iman test with Bonferroni correction to identify the modalities of the factors that induce a difference and how the mean sA varies. The inter-annual and spatial variations of sA were examined by applying a two-way ANOVA test to the mean values with the basins and the years considered as factors. Afterwards, a post-hoc Tukey’s honestly significant difference (HSD) test was performed to identify the modalities of the factors that induce a difference and how the mean sA varied.

For each tracked fish and each transect, the mean individual target strength (TS) was calculated in the linear domain in dB (MacLennan et al., 2002) as a proxy for total individual length (Simmonds and MacLennan, 2005). The parameters used in software Sonar5-Pro the same mention by Guillard et al. (2012). To estimate fish size in cm (TL = Total Length), Love's equation (Love 1971) was used (Emmrich et al., 2012; Love, 1971):

$$TL = 10^{\frac{TS - 0.9 \times \log_{10} 70 + 62}{19.1}}$$

The equation for TS is still relevant and is usually used in freshwater studies (MacNamara et al., 2016; Morrissey-McCaffrey et al., 2018; Ye et al., 2013).

To consider *L. miodon* exclusively, which presents a maximal standard length of 17.5 cm in Lake Kivu (De Iongh et al., 1995; Kolding et al., 2019) only individual fish with TS less than -39 dB according to Love (1971) were considered. The proportion of individuals in three size classes (small, medium, and large) were determined. The small fish correspond to individuals smaller than 5 cm. The upper boundary for the medium size was set to 12 cm, which is two-thirds of the maximum total length (Harmelin-Vivien et al., 1985).

Seasonal variations were addressed using the frequency distribution of fish sizes, which were computed for each season and basin for 2013 and 2014. The fraction of small fish (< -50 dB, around 5 cm according to Love) was then compared between seasons and basins as independent variables using logistic models with logit transformation (Peng et al., 2002), which was performed separately for each year (2013 and 2014). The significance of the variables was tested using likelihood-ratio (LR) tests compared to a χ^2 distribution, followed by Wald tests to compare coefficients between seasons. The inter-annual and spatial variations of the mean total size were analyzed using a two-way ANOVA test while considering the basins and years as factors. Post-hoc Tukey's HSD tests were then performed to identify the differences of mean sizes and how they varied in space and time.

From *sA* values and TS, the fish biomass (ρ_a ; kg/ha) per basin was estimated using Forbes and Nakken's (1972) equation:

$$\rho_a = \frac{sA}{4\pi * 10^{TS/10}}$$

Furthermore, the average individual fish weight \bar{w} (kg) was calculated from individual sizes based on Minns (1995) equation:

$$W = 0.01 (TL)^3$$

W is the weight of a fish in grams and TL in cm. The total biomass for each basin and for the whole lake was calculated by multiplying the biomass per kg/ha by the surface of the pelagic zone of the basin or the total area of 2217 km² of Lake Kivu (2217 km², Kaningini et al.,

1999). The surface of the pelagic zone for the five basins was estimated using the software ArcGIS 10.3 (ESRI, Redlands, CA). For the estimated biomass, confidence intervals were generated by a bootstrap procedure with 100 iterations.

In 2012, the total biomass for the whole lake was estimated from only three sampled basins (North Rwanda, East, and South) instead of five. To determine whether this value was comparable with other data, a Wilcoxon signed-rank test was performed to check whether the biomass extrapolations from all 5 basins differed from those obtained using only three basins (North Rwanda, East, and South). The statistical analyses were conducted using the software R 3.5.1 (R Development Core Team, 2009). All tests were considered significant for p-values less than 0.05.

Results

Degree of coverage

The degrees of coverage by basins mostly ranged between 3 and 6 (Table 1). About 15% of the ratios were less than 3, which were concentrated among the surveys performed in 2013 and 2014. Only two basins showed values less than 2 (4%). For 2012, 2015, 2016, and 2018 (Table 1), all coverage ratios were greater than 3. When Lake Kivu was considered as a whole, the result was always greater than 6. Thus, the present results can be considered as representative of the pelagic zone when considering Lake Kivu as a whole or by basin.

*sA values as a proxy of density of *L. miodon* stock*

In the study of seasonal variations in 2013 and 2014, the SRH tests showed a significant interaction between the season factor and the water-layer factor (Table 2) regarding the mean *sA* values. The Conover-Iman tests indicated that the mean *sA* was always lower at 45-60 m than in the other layers (Fig. 2). These tests also showed that the mean *sA* was usually higher at 15-30 m than in the other layers. During the long dry season, the mean *sA* was higher at 15-30 m and 30-45 m than at 2-15 m (Fig. 2).

Concerning the inter-annual *sA* variation, the two-way ANOVA showed no significant interaction between the year and basin ($F = 1.397$; $p = 0.128$), but there was a significant difference between years ($F = 22.288$; $p < 0.001$) and between basins ($F = 28.922$; $p < 0.001$). The post-hoc Tukey's HSD test indicated that the mean *sA* was lower in 2012 and higher in 2018 than in other years (Table 3). Furthermore, the mean *sA* was lower in 2014 than in 2015 and lower in 2016 than in 2015 (Table 3). The post-hoc Tukey's HSD tests indicated that the

mean *sA* of North Rwanda, North-DRC, and East basins were lower than those of the West and South basins (Table 3).

Size distribution of L. miodon

The frequency distribution of predictive fish sizes showed that the medium class size represented 50 to 68% of the total sample, irrespective of basin, season, and year (Fig. 3). Generally, the fish size distribution was unimodal with a mode at ≈ 6 cm during the short dry, long rainy, and short rainy seasons. However, during the long dry season, the fish size distribution was bimodal with modes at 3 cm in 2013 and 2 cm in 2014, and a second mode at 6 cm in 2013 and one at 5 cm in 2014 (Fig. 3). For both years, the proportion of small fish (< 5 cm) differed between seasons and basins, and there was significant interaction between the two factors (LR tests, $p < 0.001$). Higher contributions of small fish were observed during the long dry season (between 36% and 46% depending on the basin in 2013 and between 27% and 48% in 2014) compared to the other seasons (Wald z tests, $p < 0.001$).

Considering only the long dry seasons from 2012 to 2018, the two-way ANOVA showed significant interaction between the year factor and the basin factor on fish size ($F = 92.61$; $p < 0.001$). The post-hoc Tukey's HSD test indicated that in 2012, the mean sizes were similar between basins (5.5 or 5.6 cm). In this year, the basins presented the same percentages regarding each size category (Table 4). In 2013 and 2014, the mean sizes were lowest in North DRC (5.8 and 5.4 cm, respectively; $p < 0.001$), followed by North Rwanda (6.1 and 6.3 cm, respectively; $0.03 > p < 0.001$). In other basins, they were between 6.2 and 6.4 cm in 2013 and between 5.8 and 6.2 cm in 2014.

In 2013 and 2014, the percentages of large fish were lower in the two North basins (2.0 to 4.5% vs. 4.3 to 5.5% for other basins), and the percentages of small fish were higher for these two basins (41.7 to 47.3% vs. 35.2 to 44.5% for other basins; Table 3). Since 2014, the mean sizes were always higher in the West basin than in the other basins (between 6.2 and 7.5 cm; $p < 0.001$). This basin always presented lower percentages of the small category (Table 4). The post-hoc Tukey's HSD test indicated that for all the basins, the mean sizes were always higher in 2018 than other years ($p < 0.001$), except for the East basin, where it was highest in 2015, followed by 2018 ($p < 0.001$). Furthermore, for each basin in 2018, the percentages of small fish were always lower than in other years.

Biomass of L. miodon stock

Regarding seasonal variation, the estimated fish biomass was higher during the long rainy season than the long dry and short rainy seasons in 2013 for each basin (Table 5). In 2014, the fish biomass was generally higher during the short dry season, while similar fish biomass was estimated for the long rainy and long dry surveys of all basins. Regarding interannual variations, the fish biomass increased over time, although the biomass showed a slight drop in 2014 and 2016 in almost all basins (Table 5). In 2012, the biomass ranged between 3.8 and 10.3 kg/ha, whereas in 2018, it ranged between 11.9 and 22.7 kg/ha (Table 5).

The South and West basins usually had biomass greater than 11 kg/ha, while the other basins had biomass less than 10 kg/ha. The total biomass estimated by basin ranged between 100 and 389 t in 2012 and between 204 and 1,069 t in 2018. The total biomass estimated by basin ranged between 100 and 389 t in 2012 and between 204 and 1,069 t in 2018. The total biomass of pelagic fish in all of Lake Kivu was estimated at 1,056 t in 2012 and reached 4,067 t in 2018 (Fig. 4). The estimates of total biomass based on either all sampled basins or only three basins (North Rwanda, East, and South) for the years 2013 to 2018 indicated no significant difference (Wilcoxon signed-rank test; $v = 12$; $p = 0.3125$). This result confirms that the lack of one or two sampled basins during the survey (in 2012 and 2015) is not likely to change the estimates of total fish biomass.

Discussion

In this study, a seasonal pattern was observed for the frequency distribution of predictive fish sizes. Most distributions were unimodal, except during the long dry season, when they were bimodal, corresponding to two cohorts. During the first two months of life, the mean growth rate of *L. miodon* is 1.23 cm per month (Kaningini, 1995), while between 3 and 6 months, they grow at 1 cm per month, reaching around 10 cm after 1 year (Snoeks et al., 2012). It follows that individuals belonging to the size class of 2-3 cm should be 2-3 months old, and those in the class of 6-7 cm should be 6-7 months old in Lake Kivu (Mannini, 1990; Spliethoff et al., 1983).

L. miodon showed two reproduction peaks in Lake Kivu (Kaningini, 1995) although its reproduction is continuous over time (Richard et al., 2020). The first peak occurred from March to May (long rainy season), and the second was from September to October (short rainy season) (Kaningini, 1995). Thus, the smallest mode observed during the long dry season should represent the cohort arising from March-May spawning, whereas the second mode represents the cohort resulting from the short rainy-season spawning.

Mature males and females of *L. miodon* are around 6.0 cm in Lake Kivu (Marshall, 1993; Richard et al., 2020). Reproduction takes place in shallow waters of littoral areas (Kaningini, 1995; Marshall, 1993; Snoeks et al., 2012), and the juveniles remain in these areas before moving to the pelagic areas when their sizes is close to 4 cm (Marshall, 1993). The present study indicates that in Lake Kivu, this migration could start earlier when juveniles reach 2-3 cm. Thus, the present study highlights that the long dry season seems to be the most appropriate season to carry out hydroacoustic surveys for *L. miodon* in the pelagic zone of Lake Kivu, because it gives access to both adults and recruitment at the beginning of the year.

The density and biomass of *L. miodon* showed seasonal fluctuations without any clear seasonal pattern. This was also observed by Marshall (1990), who considered catches and fishing effort. These results were not surprising because clupeid recruitment can fluctuate according to seasonal environmental conditions (e.g., nutrient inputs, light), which drives phytoplankton availability which in turn affects the availability of zooplankton that are the main prey of *L. miodon* (Karengé and Kolding, 1995; Marshall, 1982; Trochta et al., 2020). Furthermore, the environmental conditions for a season can be highly variable (Kolding et al., 2019).

Although density did not present a seasonal pattern, it varied by depth. *L. miodon* was scarce below 45 m and was not present below 60 m. This result is supported by those of previous studies, which observed the same vertical distribution (Lamboeuf, 1989a; Lamboeuf, 1991; Guillard et al., 2012). The layer at 45-60 m is less favorable to *L. miodon* because dissolved oxygen is often limited in this deeper layer (Schmid and Wüest, 2012). Indeed, the mixolimnion is only mixed to ~60 m during the dry season (Reusens, 1987; Schmid and Wüest, 2012). Increases in temperature due to climate warming is reported to have been accompanied by decreased wind speed, relative humidity and water levels of Lake Kivu over the last part of the 20th century may have led to reductions in nutrient recycling and lake productivity and contributed to decline in stocks especially of the introduced clupeid (*L. miodon*) (Akonkwa et al., 2015). Similarly, gas exploitation could lead to changes in the lake's parameters that might change lake productivity processes and vertical distribution of *L. miodon*. Hydroacoustic surveys would be useful in monitoring vertical distributions of fish and relating it to environmental factors in future.

The present results showed an inter-annual spatial pattern in the distributions of *L. miodon*. The South and West basins had higher densities, mean sizes, and biomass than the North-Rwanda and North-DRC basins. These results are consistent with those of Guillard et

al. (2012), who also found higher concentrations and biomass in these basins, but not those of Lamboeuf (1991), who found no spatial pattern. The conclusions of Lamboeuf (1991) are linked to the fact that spatiality was coupled with seasonality, meaning that the seasonal variation could have hidden the spatial variation.

It seems that environmental conditions are more favorable for *L. miodon* in the southern basin. For example, Sarmiento et al. (2006) showed that phytoplankton concentrations were higher in these regions. Thus, the main food resource of *L. miodon*, zooplankton, could be more available in these basins because zooplankton dynamics has been shown to be mostly bottom-up controlled (i.e., mostly driven by the primary production), at least during the period of 2002-2004 (Isumbisho et al., 2006). This spatial pattern could also be due to lower fishing effort in these basins, thus explaining the larger mean size as well. Indeed, fishing pressure can decrease the mean length of individuals (Ruth, 2002), but this was not demonstrated for *L. miodon*. Testing these hypotheses will require additional studies on the spatial distributions of the zooplankton communities and fishing effort as this information is currently incomplete (Descy et al., 2015; Richard et al., 2020).

The density, mean size, and biomass of *L. miodon* were all higher in 2018 than 2012. The lower values in 2012 could come from underestimation due to a partial survey design because sampling was only carried out in three out of five basins. However, this hypothesis is unlikely because for the other surveys, the total biomass estimated from these three basins gave comparable values to those estimated from all five basins. The low 2012 values could be due to particular environmental conditions that occurred at this time.

Rugema et al. (2019) identified a considerable change in the phytoplankton community of Lake Kivu between 2012 and 2014 with a shift of diatoms and cyanobacteria to green algae. They also reported a difference in nutrients between 2002-2008 and 2012-2014 (an increase of nitrogen and phosphorus) due to a modification of the mixing of the mixolimnion linked to climate variability. Recent analyses of the phytoplankton community revealed a stable concentration of chlorophyll *a* in 2017-2018 compared to 2012-2014, but there were some changes in phytoplankton composition, with a decrease of green algae and an increase of cyanobacteria in recent years (Richard et al., 2020). These changes in the phytoplankton community induced shifts in the zooplankton community, leading to a return to conditions that are closer to the community of 2002-2008.

Zooplankton constitute the only food of juvenile *L. miodon* (de Iongh et al., 1983). Thus, a modification of the zooplankton community could have affected the population, particularly the juveniles. However, it was not possible to test this hypothesis because information

regarding variation of the zooplankton community in the pelagic areas was not available for the period of the present study and some years before. It is possible that a change of abiotic factors that occurred between 2011 and 2012 could have led to the decline of *L. miodon* stock by negatively impacting their recruitment, reproductive cycle, or natural mortality rate. Marshall (1990) highlighted that abiotic factors (e.g., wind, rainfall) impact the density of *L. miodon* in Lake Kivu. High rainfall resulting in high water levels positively influenced the catch per unit effort, while high surface water temperature had a negative influence (Akonkwa et al., 2015; Marshall, 1990). This was also observed in Lake Kariba (Chifamba, 2000). However, Kaningini (1992) pointed out a lack of knowledge concerning the influence of abiotic factors on the physiology of *L. miodon*, which is still true today. Even if it is not possible to identify the mechanisms leading to an increase of the *L. miodon* stock, the increase was highlighted.

In the beginning of the 1980s, the biomass of *L. miodon* were estimated at around 6,000 and 7,000 t (Fig. 4), and in the late 1990s and 2000s, they were around 3,500 and 5,500 (Fig. 4). In 2018, the stock estimate was similar to the 1990s. This long time series of biomass clearly shows that a change occurred in the beginning of the 2010s, which is concurrent with the change in the phytoplankton community detected by Rugema et al. (2019) but has since then showed an upward trend. This is possible because clupeids have a huge annual regenerative capacity (Marshall, 1990). Overall, the *L. miodon* stocks have been stable over time. There is need to monitors the stocks of *L. miodon* and explore the factors that determine stability in the stocks this species.

Conclusions

The present study indicated that the long dry season was the most appropriate season to assess the *L. miodon* stock in the pelagic zone of Lake Kivu. The stock was concentrated above depths of 45 m and was more abundant it the South and West basins, at least during the long dry season. Even though the *L. miodon* stock showed downward trends between 1985 up to 2012, the stocks have shown an upward trend since then up to the current estimate of 2018 and have over this whole period been stable at around 4000 tons.

This evaluation showed that the *L. miodon* stocks of Lake Kivu have been stable over a long period. It has not experienced a decline predicted by Dumont (1986) or more recently Akonkwa et al. (2015), which were respectively based on a depletion of prey and climate change (increased water surface temperature and decreased water level due to lower rainfall). The introduction of *L. miodon* can still be considered successful as qualified by Gozlan

(2008). The low stock recorded in 2012 on the basis of which Akonkwa et al. (2015) predicted a decline has been reversed.

Thus, as Lake Kivu Monitoring Program (LKMP) established monitoring programs of the main limnological parameters (Richard et al., 2020), including hydroacoustic surveys, it is recommended that this program continues periodically. These surveys should relate fish stocks to environmental parameters. Protocols have to be conducted with accuracy to preserve the data quality of long temporal series, including calibration of the equipment before each survey (Parker-Stetter et al., 2009). As indicated by Robarts and Zohary (2018) and highlighted by Rugema et al. (2019), the present study demonstrates the need of combining high-quality limnological and meteorological data when evaluating freshwater communities, conservation, and governance of the African Great Lakes. For future assessments, it will be necessary to carry out a transdisciplinary study by integrating additional data on fishing effort, the zooplankton community, and climatic factors into analyses to identify the main parameters regulating the *L. miodon* population in Lake Kivu.

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Tables

Table 1

Degree of coverage by hydroacoustic surveys per basin and for the whole lake during different years and seasons. The degree of coverage was obtained by dividing the total length of the path (km) by the square root of the studied surface (km²). The result should be at least 3.0 and preferably above 6.0 to obtain a reliable assessment (Emmrich et al., 2012).

	North Rwanda	North DRC	East	West	South	Lake Kivu
2012 Long dry	5.6	No data	6.2	No data	3.3	7.0
2013 Short dry	6.1	No data	6.1	No data	1.6	6.8
2013 Long rainy	5.5	No data	6.0	No data	3.1	6.8
2013 Long dry	5.1	2.0	1.8	4.8	2.3	6.6
2013 Short rainy	4.3	2.9	3.8	4.3	3.9	8.1
2014 Short dry	3.8	4.2	4.8	4.4	5.1	9.4
2014 Long rainy	3.6	4.9	7.0	4.8	2.6	9.7
2014 Long dry	4.0	5.1	6.7	5.3	2.2	9.9
2015 Long dry	4.8	No data	5.6	5.9	4.7	8.9
2016 Long dry	3.1	7.3	4.0	7.7	6.4	11.6
2018 Long dry	7.2	3.8	3.8	3.3	17.5	12.2

Table 2

Results of the Scheirer-Ray-Hare test for the mean acoustics biomass (sA in m^2/ha ; a proxy for fish density) by basin of Lake Kivu and by year. Significant results are in bold.

Basin	Factor	F-value	P-value
A - 2013			
North Rwanda	Season	36.19	< 0.001
	Water-layer	36.19	< 0.001
	Season x Water-layer	36.19	< 0.001
North DRC	Season	0.15	0.703
	Water-layer	106.64	< 0.001
	Season x Water-layer	36.24	< 0.001
East	Season	36.99	< 0.001
	Water-layer	750.01	< 0.001
	Season x Water-layer	39.87	< 0.001
West	Season	6.82	< 0.005
	Water-layer	47.39	< 0.001
	Season x Water-layer	22.96	< 0.001
South	Season	6.94	< 0.001
	Water-layer	137.70	< 0.001
	Season x Water-layer	9.81	< 0.001
B - 2014			
North Rwanda	Season	40.20	< 0.001
	Water-layer	397.68	< 0.001
	Season x Water-layer	31.78	< 0.001
North DRC	Season	4.46	< 0.05
	Water-layer	131.92	< 0.001
	Season x Water-layer	9.25	< 0.001
East	Season	116.46	< 0.001
	Water-layer	452.09	< 0.001
	Season x Water-layer	32.73	< 0.001
West	Season	42.638	< 2,2 e-16
	Water-layer	231.196	< 2,2 e-16
	Season x Water-layer	60.921	< 2,2 e-16
South	Season	4.4586	0.01197
	Water-layer	131.9234	< 2,2 e-16
	Season x Water-layer	9.2576	1.037 e-09

Table 3

Acoustic biomass (sA in m^2/ha ; proxy for density) of *Limnothrissa miodon* of Lake Kivu by year and basin. IC is the 95% confidence intervals, * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$ were issued from the post-hoc Tukey's HSD test performed on the year and basin factors

	Mean	IC	Tukey's HSD test results
A - Year			
2012	0.40	0.05	2012/2013 *, 2012/2014 *, 2012/2015 ***, 2012/2016 **, 2012/2018 ***
2013	0.79	0.11	2013/2018 ***
2014	0.68	0.06	2014/2015 **, 2014/2018 ***
2015	0.98	0.09	2015/2016 *, 2015/2018 ***
2016	0.72	0.09	2016/2018 ***
2018	1.33	0.17	
B - Basin			
North-Rwanda	0.77	0.10	North-Rwanda/West ***, North-Rwanda/South ***
North-DRC	0.62	0.10	North-DRC/West ***, North-DRC/South ***
East	0.65	0.05	East/West ***, East/South ***
West	1.23	0.15	
South	1.23	0.14	

Table 4

Percentage of *Limnothrissa miodon* per size class in the different basins of Lake Kivu according to year. Small < 5 cm, 5 cm ≤ medium > 12 cm and large ≥ 12 cm.

Year	Size category	North-Rwanda	North-DRC	East	West	South	Lake Kivu
2012	Large	3.0	No data	3.1	No data	3.0	3.0
	Medium	51.8		50.3		52.5	51.4
	Small	45.2		46.6		44.5	45.6
2013	Large	4.5	2.8	5.5	4.3	5.9	4.5
	Medium	53.8	52.1	54.7	60.5	53.3	57.3
	Small	41.7	45.1	39.8	35.2	40.8	38.2
2014	Large	3.4	2.0	4.4	4.4	4.4	4.0
	Medium	49.3	52.5	51.1	59.7	51.1	54.1
	Small	47.3	45.5	44.5	35.9	44.5	41.9
2015	Large	5.0	No data	6.3	8.4	8.8	7.5
	Medium	58.5		58.6	69.1	54.7	62.5
	Small	36.5		35.1	22.5	36.5	30.0
2016	Large	3.3	2.9	2.6	2.3	1.8	2.4
	Medium	46.0	58.4	57.6	62.8	50.3	57.1
	Small	50.7	38.7	39.8	34.9	47.9	40.6
2018	Large	10.7	6.5	7.3	8.1	8.3	8.0
	Medium	55.2	65.0	63.6	68.1	62.1	64.9
	Small	34.1	28.5	29.1	23.8	29.6	27.1

Table 5

Mean fish biomass of *Limnothrissa miodon* (kg/ha) in different basins of Lake Kivu and for the whole lake according to year and season. Values in parentheses are 95% confidence intervals estimated by a bootstrap procedure.

	North Rwanda 400 km ²	North DRC 500 km ²	East 900 km ²	West 320 km ²	South 97 km ²	Lake Kivu 2,217 km ²
2012	3.8	No data	4.3	No data	10.3	4.7
Long dry	(2.9-4.7)		(3.7-5.0)		(6.9-13.7)	(4.2-5.4)
2013	8.8	No data	11.5	No data	16.2	10.6
Short dry	(6.6-11.0)		(9.5-13.6)		(5.2-27.2)	(8.9-12.5)
2013	16.0	No data	15.5	No data	29.9	17.1
Long rainy	(11.6-20.4)		(13.1-18.0)		(20.5-39.3)	(14.9-19.3)
2013	8.1	10.2	5.6	14.7	15.6	10.3
Long dry	(6.1-10.1)	(6.5-13.9)	(4.7-6.6)	(11.1-18.3)	(9.9-21.3)	(8.5-11.9)
2013	8.9	8.1	8.7	12.7	15.0	10.0
Short rainy	(6.5-11.4)	(6.3-9.8)	(7.3-10.2)	(9.3-16.1)	(10.8-19.1)	(8.9-11.2)
2014	7.3	7.4	6.1	16.0	18.0	9.8
Short dry	(3.9-10.7)	(5.5-9.3)	(4.4-7.8)	(11.5-20.4)	(12.1-24.0)	(8.4-11.2)
2014	5.6	4.7	10.2	12.3	12.9	9.1
Long rainy	(4.0-7.2)	(4.1-5.4)	(8.4-12.1)	(10.5-14.1)	(10.0-15.7)	(8.3-10.0)
2014	5.3	4.2	8.4	13.7	14.0	8.3
Long dry	(3.6-9.9)	(3.6-4.9)	(7.0-9.8)	(11.1-16.4)	(10.2-17.8)	(7.5-9.2)
2015	11.2	No data	9.7	19.6	15.8	13.5
Long dry	(8.0-14.4)		(8.3-11.2)	(17.1-22.1)	(12.7-18.9)	(12.2-14.7)
2016	4.9	6.3	9.7	11.8	15.0	9.3
Long dry	(3.7-6.2)	(4.5-8.2)	(7.1-12.4)	(9.2-14.4)	(11.2-18.8)	(8.4-10.6)
2018	16.5	15.3	11.9	22.7	21.0	18.3
Long dry	(13.0-19.9)	(11.2-19.4)	(9.3-14.5)	(15.8-29.5)	(15.9-21.0)	(15.9-20.7)

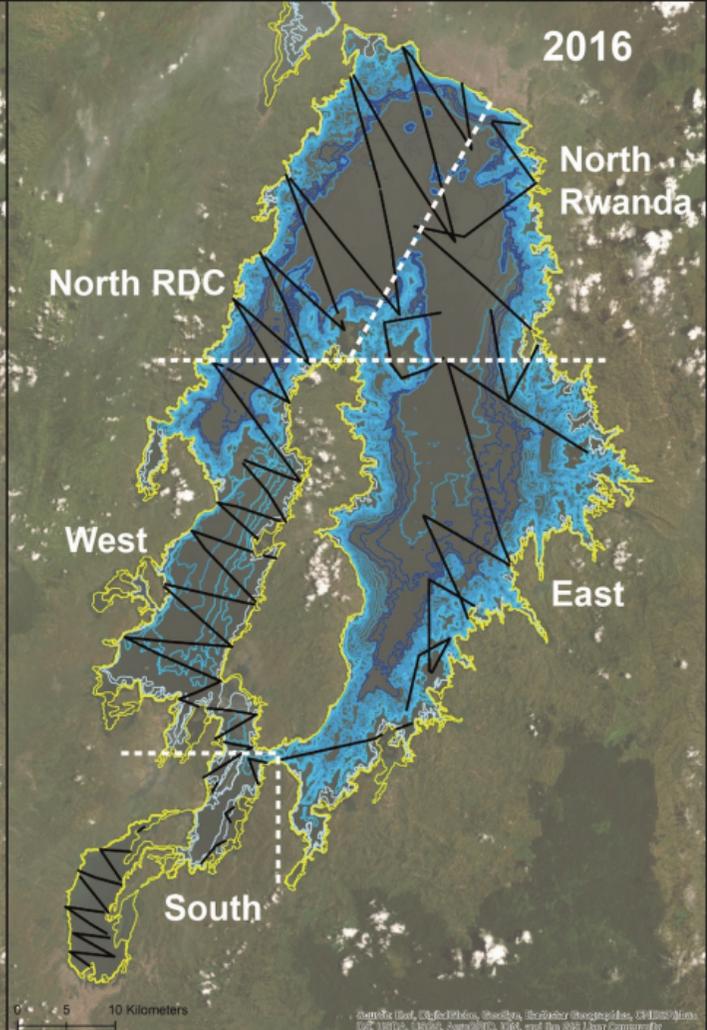
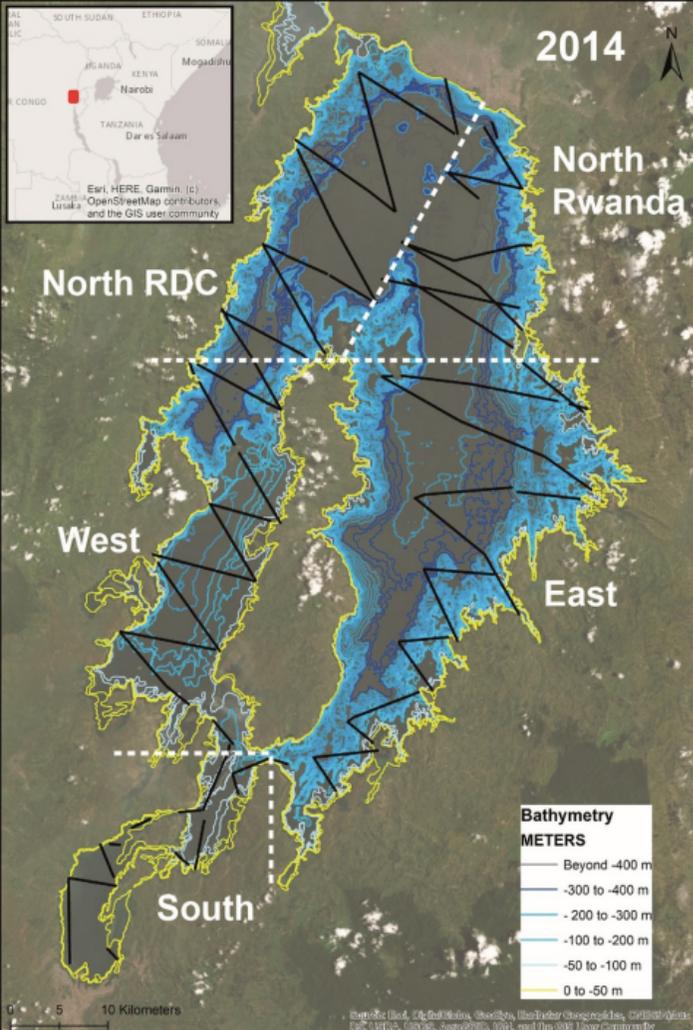
Legends of figures

Fig. 1. Map of Lake Kivu showing the transects sampled. The black lines represent the hydroacoustic survey performed between July 30th and August 14th 2014 and September 7th and 27th 2016 over the five defined regions.

Fig. 2. Mean *sA* values of the four-vertical water layers per basin in Lake Kivu in 2013 and 2014 in short dry season (black solid line), long rainy season (grey solid line), long dry season (black dashed line), and short rainy season (grey dashed line). The horizontal bars are 95% confidence intervals.

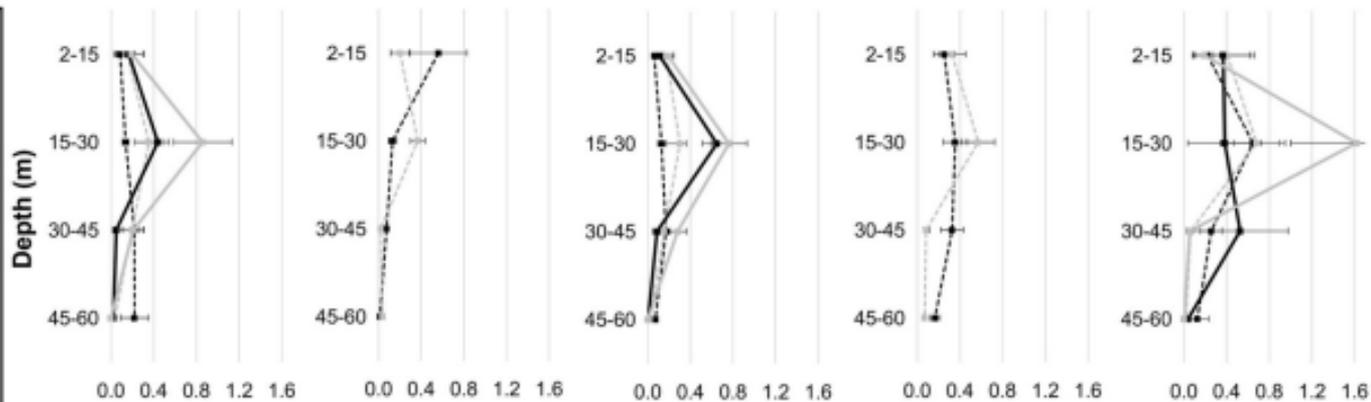
Fig. 3. Length frequency distribution of fish converted from target strength using Love's equation (1971) data in 1-cm classes per basin of Lake Kivu in 2013 in the short dry season (black solid bar), short rainy season (grey solid bar), long dry season (black hatched bar), and long rainy season (grey hatched bar). Arrows indicate peaks.

Fig. 4. Total biomass (tonnes) for all of Lake Kivu by hydroacoustic sampling during different years (present study and historical surveys). The vertical bars are 95% confidence intervals.

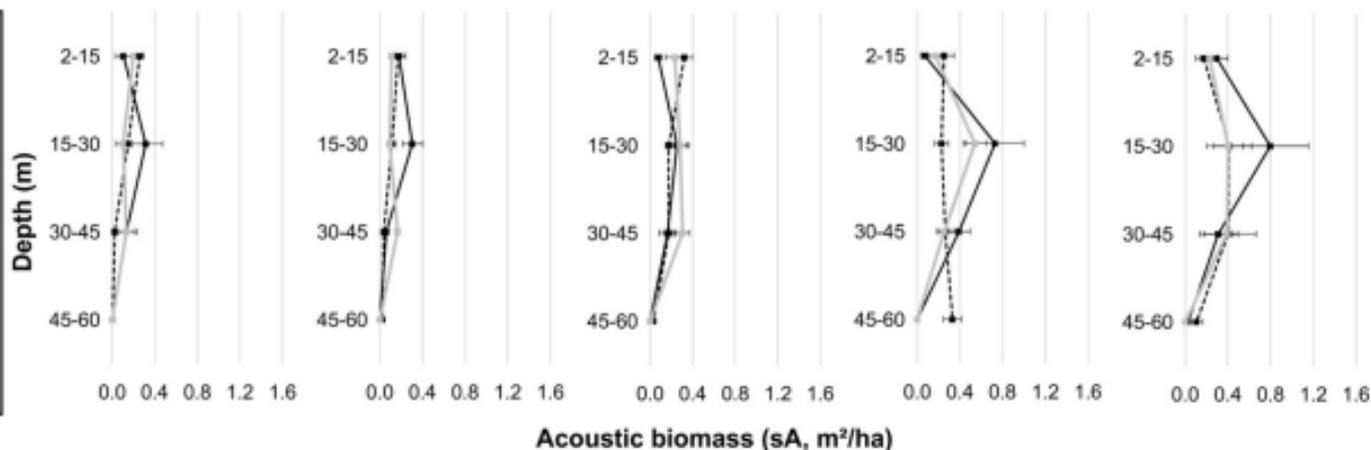


North Rwanda	North RDC	East	West	South
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2013



2014



Acoustic biomass (SA, m²/ha)

