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Estimates of life-history and growth parameters of exploited fish species in Lakes Edward and George: Implications on exploitation status, population dynamics, management, and conservation of native species

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Abstract
Adequate knowledge is an essential requirement for responsible inland fisheries. However, many inland fisheries lack monitoring, and hence, decision-making for fisheries management is not reliable. In this paper, we used data from surveys and literature to estimate the life-history and growth parameters of 16 exploited fish stocks in the Ugandan part of Lake Edward and Lake George (East Africa). The estimated parameters are pivotal indicators of fish stock status, particularly in data-poor fisheries. The estimated parameters included maximum length (L_{max}) and mean length (L_{mean}) as indicators of size structure in experimental and commercial catches, coefficients of length-weight relationships, length at 50% maturity (L_{m50}), fecundity, von Bertalanffy parameters, total mortality (Z), and natural mortality (M). These parameters were estimated using empirical formulae, statistical methods, and analyses of length frequencies. Only two stocks of semutundu *Bagrus docmak* exhibited significant and increasing trends in L_{max} (Lake Edward) and

L_{mean} (Lake George). The estimates for the remaining parameters were consistent with those in FishBase and other literature resources, either for the same species or related species. This consistency indicates their reliability for application in decision-making and further assessments. Some paramters showed evidence of unsustainable fishing. For example, estimates of L_{m50} for four of the assessed stocks belonging to two species (Nile tilapia *Oreochromis niloticus* and marbled lungfish *Protopterus aethiopicus*) were lower than baseline estimates in the studied waterbodies. Furthermore, the L_{mean} in catches for all the stocks were less than the optimum lengths (L_{opt}), which maximize catches with minimal impact on biomass and size structure. No significant changes in L_{mean}, length-frequency distributions, and size at maturity could be attributed to the management changes implemented in 2018 probably because it is too early to observe changes in these parameters. However, there are positive signs attributable to the changes in management as shown by a high proportion of mature individuals in commercial catches for most of the stocks for which the proportion was calculated, and an increase in L_{mean} and L_{max} for some stocks such as *B. docmak* in commercial or experimental catches. New estimates from this study will enhance decision-making and further assessments of fisheries. Routine monitoring is recommended to update and improve the estimates.

Keywords: Fisheries management, Inland fisheries, Overfishing, Small-scale fisheries

1 Introduction

Stakeholders in fisheries research, policy, management, advocacy, and industry agreed to the 10 steps for responsible inland fisheries (FAO & MSU, 2016). The steps aim at addressing the challenges that inland fisheries face to sustain their contribution to biodiversity, food security and livelihoods (FAO and MSU, 2016; Lynch et al., 2017). Challenges faced by inland fisheries include high fishing pressure, pollution, and invasive species (Welcomme et al., 2010; FAO & MSU, 2016). Improving the assessment of inland fisheries is the first of the 10 steps.

Challenges to inland fisheries particularly in developing countries are persistent because policymakers overlook these fisheries (Cooke et al., 2016; Lynch et al., 2017). This emanates from limited access to information because most inland fisheries are not subjected to adequate monitoring and assessments (Cooke et al., 2016; Elliott et al., 2019). As a result, these fisheries are notably absent in global governance processes such as the Sustainable Development Goals (Cooke et al., 2016; Lynch et al., 2017; Elliot et al., 2022). Improving assessments, therefore, is envisaged to alleviate the information limitations and mainstream inland fisheries into governance processes at all levels. However, this (improved assessment) is not adequate in isolation because well-assessed fish stocks may also not be effectively managed due to, for example, limited political will (Froese & Quaas, 2012).

Life-history parameters of fish such as size at which 50 % of individuals in a fish population attain maturity (L_{m50}), maximum length (L_{max}), fecundity, mortality rates, coefficients of length-weight relationships, and parameters of the von Bertalanffy growth function (VBGF) including length at infinity (L_{∞}) are derived from stock assessments. The VBGF is the most popular model of fish growth in terms of increase in length or weight (von Bertalanffy, 1938). In data-poor fisheries, these parameters could be the only tools available to tell the status of the exploited species (King & McFarlane, 2003). These parameters also serve as inputs to stock assessment and ecosystem models, both of which generate more robust information and tools for decision-making (Froese et al., 2018). Therefore, more reliable and updated fish life-history parameters and growth parameters could tell the status of exploited stocks and support decisions to improve the management of fisheries and conservation of species.

This study estimated life-history and growth parameters for the exploited fish stocks in the Ugandan part of Lake Edward and Lake George. With a combined annual catch of approximately 48,000 t, supporting about 23,000 fishers in Uganda and the Democratic Republic of Congo (DRC) ((NBI, 2019, 2021)), these lakes do not only support fisheries that are of economic importance to local communities, but also habour fish species of conservation importance especially the haplochromine cichlids (Vranken et al., 2019; Decru et al., 2020). However, the populations of the exploited fish stocks in these lakes lack updated life-history and growth parameters. Indeed, a recent assessment of the fish stocks using an approach that requires some of these parameters (L_{m50} and L_{∞}) as inputs relied on old inputs from FishBase or estimates from empirical formulae (Musinguzi et al., 2021).

The two lakes have been subject to high levels of fishing effort and a high prevalence of illegal fishing practices and fishing gear (Bassa et al., 2014; Lubala et al., 2018). However, since 2018, major changes occurred in the management of both lakes in Uganda. To strengthen the enforcement of fishing regulations, a Fish Protection Unit (FPU), drawn from the Uganda Peoples Defense Forces (UPDF) was deployed on the waterbodies to improve adherence to fishing regulations by banning illegal fishing gear, crafts, and practices such as fishing in near-shore areas designated as fish breeding areas (NPA, 2019). Therefore, in addition to estimating the life-history and growth parameters, the changes in the life-history parameters that could be attributed to the changes in management were examined where applicable. We hypothesized that the values of the parameters before and after 2018 differed, with those before 2018 signaling unsustainable fishing. The estimated parameters enhance our understanding of the exploited fish stocks, ultimately contributing to more effective management measures.

2 Materials and methods

2.1 Lakes Edward and George

Lake George is located entirely in Uganda, while Lake Edward is shared between Uganda (29 %) and the DRC (71 %). The two lakes are connected by the 40 km long Kazinga Channel (Figure 1). Fish species of economic importance in the waterbodies are marbled lungfish *Protopterus aethiopicus* Heckel *1851,* North African catfish *Clarias gariepinus* (Burchell 1822), semutundu *Bagrus docmak* (Fabricius 1775), Ripon barbel *Labeobarbus altianalis (Boulenger* 1900)*,* Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758), blue-spotted tilapia *Oreochromis leucostictus* (Trewavas 1933), and to a lesser extent, elephant-snout fish *Mormyrus kannume* Forsskål 1775, and omuruma *Labeo forskalii* Rüppell 1835 (Lubala et al., 2018; NaFIRRI, 2019). Based on the contribution to the annual catches of 2020 (NBI, 2021), *O. niloticus* is the most important in the Ugandan section of Lake Edward with 38.2 % of the catches, followed by *P. aethiopicus* (21.2 %), *B. docmak* (20.0 %), *C. gariepinus* (8.8 %), *M. kannume* (7.0 %), and *L. altianalis* (4.8 %). In Lake George, *P. aethiopicus* is the most important with 35.8 % of the catches, followed by *B. docmak*

(26.4 %), *O. niloticus* (18.1 %), *C. gariepinus* (17.0 %), *M. kannume* (2.4 %), and *L. altianalis* (0.2%). In both lakes, the contribution of the haplochromines to the catches of 2020 was negligible. Lakes Edward and George are mostly surrounded by protected areas. The entire Congolese part of Lake Edward is located within the Virunga National Park. In Uganda, the whole of the Kazinga Channel lies within the Queen Elizabeth National Park (QENP), while most of Lake George and the entirety of Lake Edward (Uganda) are surrounded by the QENP (Figure 1). The presence of these protected areas limits farming (Uganda Wildlife Authority, 2012), making fishing a vital source of sustenance for riparian communities. Therefore, efforts to sustain fishing activities are crucial.

2.2 Data used and its sources

We analyzed secondary data from catch assessments (fishery-dependent) and experimental gillnet surveys (fishery-independent) conducted on the Ugandan part of Lake Edward and George by the National Fisheries Resources Research Institute (NaFIRRI), a public research institute with a mandate to conduct fisheries research in Uganda (Table S1). From the catch assessment surveys (CAS), we obtained length measurements of fish samples from commercial catches. Measurements were available from 2006 to 2017 for Lake Edward and from 2000 to 2017 for Lake George, but with temporal gaps. We obtained data on length, weight, sex, and gonadal development stage from experimental gillnet surveys conducted in 1995, 2006, 2007, 2011, 2012, 2013, 2016, and 2019 for Lake Edward and 1994, 1995, 2011, 2012, and in 2016 for Lake George.

We conducted supplementary data collection in the two waterbodies. The data collection on Lake Edward only covered the Ugandan section of the lake (Figure 1). Supplementary experimental gillnet surveys were conducted in 2021 (Lakes Edward and George) and 2022 (Lake Edward only), following standard operating procedures for studies in fish biology and ecology in the region (LVFO, 2007). In 2021, we conducted four surveys, two in each lake between January and August. In 2022, we conducted six consecutive monthly surveys from June to November 2022 on Lake Edward. Alongside the experimental surveys in 2022, we collected length measurements of fish specimens in commercial catches on the lake. However, no surveys were conducted on Lake George.

During the experimental gillnet surveys, three sets of gillnets were placed in predetermined locations. The selected locations cover diverse habitats in the lakes, including near-shore, river mouths, rocky, and offshore (Figure 1). The sets comprised multifilament gillnets (different from monofilament gillnets of one twine by having multiple twines) of mesh sizes ranging from 25.4 mm (1 inch) to 203.2 mm (8 inches), 90 m long and 26 meshes deep. Mesh sizes ranging from 25.4 mm to 139.7 mm (5.5 inches) were in increments of 12.7 mm (0.5 inches) while mesh sizes 152.4 - 203.2 mm (6 to 8 inches) were in increments of 25.4 mm. The gillnets were set in the evening and retrieved in the morning. A wide range of mesh sizes and habitats were used to increase the chances of obtaining representative samples by capturing fish specimens in all habitats and size classes. The mesh sizes also included the legally approved size (4.5 inches or 114.3 mm). After capture, fish were sorted by species based on the knowledge and experience of research technicians and scientists at NaFIRRI. For small catches, all individuals were measured, while a random manageable subsample was taken if catches were deemed (subjectively) to be too large to handle. Data on catch composition by weight was not analyzed as it fell out of the scope of this study. Data was collected on total length or fork length for species with a forked caudal fin, weight, sex, and maturity stage of gonads. The gonads were given maturity stages ranging from 1 to 6, with stages 1 to 3 considered to be immature and stages 4 to 6 considered to be mature. The assignment of the maturity stages was based on standard procedures (LVFO, 2007). Ovaries of stages 4, 5 and 6 were retained to estimate fecundity.

2.3 Data processing and analysis

2.3.1 Size structure

We determined the size structure of the fish stocks in commercial and experimental catches separately for each waterbody. Size structure was determined in terms of L_{max} and mean length (L_{mean}) in the catches, indicators used for evaluating the exploitation status of stocks (Shin et al., 2005). The estimates for these indicators were determined for each year with data to allow comparisons across years. The presence of trends in the indicators of size structure and their significance was examined using Mann-Kendall tests where four or more samples (years) were available (Hassig et al., 2010). These tests were performed in R using the *Kendall* package (McLeod, 2011).

The length measurements used to determine size structure were distributed into appropriate length intervals to create histograms for each year to visualize the size structure in both experimental and commercial catches by species. Only years with 30 or more length measurements for a stock were included in the histograms. Length-frequency distributions are multi-model, a principle that reflects the presence of individuals of multiple age or size classes in fish populations (Gulland & Rosenberg, 1992). Therefore, the status of stocks could be deduced from length-frequency distribution patterns, with a steady decline from larger to smaller individuals showing a good status and vice versa (Neumann & Allen, 2007). Based on this principle, the patterns of the length-frequency histograms for the stocks were visually examined for insights into the status of the stocks.

The presence of significant differences in size structure was examined by: (i) comparing the L_{mean} in catches over years using the Kruskal-Wallis test; and (ii) comparing length-frequency distributions using the Kolmogorov–Smirnov two-sample test with a Holm–Bonferroni correction (Neumann & Allen, 2007). Dunn's test for pairwise multiple comparisons using the Benjamini-Hochberg method was applied when the Kruskal–Wallis test was significant. The Kruskal-Wallis and Dunn's tests were implemented in R using the *stats* package (R Core Team and contributors worldwide, 2023). The Kolmogorov–Smirnov two-sample test was implemented in python using the *scipy.stats* module (Seabold et al., 2010).

2.3.2 Length-weight relationships and Fulton's condition factor (K_c)

Linear models were fitted to $\log_{10}$-transformed total length or fork length and weight data from experimental catches to generate *a* and *b* coefficients of length-weight regressions for each stock. The length-weight regressions were conducted for each lake separately. Data for all years were aggregated for each stock to increase the sample size. The aggregated years were 2011, 2012 and 2021 for Lake George. In the Ugandan part of Lake Edward, the years aggregated were 2006-07, 2011-13, 2016, 2019, and 2021-22. However, most (86.6%) measurements were from 2019, 2021 and 2022. The length and weight data were cleaned to remove outliers and improve the models. The validity of the values of *a* and *b* was evaluated by comparisons with the values for each species available in literature or FishBase (Froese & Pauly, 2023).

We determined the Fulton's condition (K_c) of the fish stocks as W/L^3*100 (Fulton, 1904). The W and L are the observed weight and length, respectively. The K_c is useful for indicating the growth condition of fish. A fish stock is in good condition when K_c is greater than 1 and vice versa (Ravikumar et al., 2023).

2.3.3 Sex ratios and size at first maturity

Sex ratios were determined as the ratio of the number of females to the number of males captured in experimental catches. We used the chi-square test (X^2) to determine whether the observed sex ratio for each stock was significantly different from 1:1, the general sex ratio in natural populations (Fisher, 1930).

Size at first maturity was calculated as L_{m50}. This was determined by fitting numbers in length-frequency bins to a logistic regression curve, using the least squares method (Sparre and Venema, 1998). The estimates of L_{m50} were based on maturity data collected in this study in 2019, 2021, and 2022 in Lake Edward and 2021 in Lake George. Size at maturity is highly variable (Hutchings, 2002) and for this reason, we avoided aggregating data over a long period (beyond five years). The values of L_{m50} were estimated for both sexes combined and for males and females separately whenever the sample size was adequate. The L_{m50} was determined using the R package, *sizeMat* (Torrejon-Magallanes, 2020). Using the estimates of L_{m50} for both sexes combined, we calculated the percentage of mature individuals in the catch, an indicator of overfishing (Froese, 2004). This was done for the stocks with adequate length measurements in commercial catches sampled in 2020 and 2022.

For some stocks in the Ugandan part of Lake Edward (*O. niloticus*, *O. leucostictus*, *B. docmak*, and *L. altianalis*), adequate maturity data was available for periods before (from secondary data) and after the change in management in 2018 (from this study). The maturity data before the change in management was aggregated for the period from 2006 to 2016. For these stocks, we determined whether the logistic regression models of maturity between the two time periods were significantly different to examine the effect of the change in management. To implement this, we made a factor variable representing each of the two time periods. The effect of change in management was examined by fitting logistic regression models that cater for the effect of the derived factor variable using the *glm* function in the MQMF (Modelling and Quantitative Methods in Fisheries) package in R (Haddon, 2020).

2.3.4 Fecundity

Standard procedures were used to process preserved ovaries and to count oocytes (LVFO, 2007). Ovaries were collected in 2021 and 2022. All oocytes in small ovaries were counted to obtain the total number of eggs (absolute fecundity). For big ovaries, where enumeration of all oocytes was impractical, the total weight of the ovary was measured, followed by counting oocytes in two sub-samples of known weight. The total number of oocytes was then determined by extrapolating the average number from the sub-samples to the whole ovary using its total weight. Linear regressions on $\log_{10}$-transformed data were performed on total or fork length (cm) and absolute fecundity to generate regression equations for each stock, useful for predicting fecundity for a fish of known length and vice versa. The sample size for fecundity was small for most stocks, ranging from 2-162 (average 34). As a result, samples for both the Uganda part of Lake Edward and George were combined for the linear regression analyses.

2.3.5 *Growth parameters and mortality rates*

The growth parameters were based on inputs from literature and new observations from secondary and primary data aggregated in this study. Focus was on the length at infinity (L_∞), weight at infinity (W_∞), the rate at which L_∞ and W_∞ are attained (K), optimum length of capture to maximize yield (L_{opt}), natural mortality (M), total mortality (Z), fishing mortality (F), and exploitation rate (E) using empirical equations (e.g., Froese & Binohlan, 2000) and the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938).

The values for L_∞ were estimated from its relationship with maximum length (L_{max}) (Equation 1). In each lake, L_{max} was the observed length of the largest individual in the experimental and commercial catches. The W_∞ was estimated from L_∞ using the a and b values from the length-weight relationships determined in this study. The L_{opt} was estimated from Equation 2.

$$log(L_\infty) = 0.044 + 0.9841 * log(L_{max}) \quad (1)$$

$$log(L_{opt}) = 1.042 * log\,(L_\infty) \; - 0.2742 \quad (2)$$

Estimates of K were derived from Equation 3, where t_{max} is the maximum life span of the species listed in FishBase (Froese & Pauly, 2023).

$$K = \frac{3}{t_{max}} \quad (3)$$

Equations 1 to 3 were adopted from Froese & Binohlan (2000). Total mortality (Z) was estimated from two approaches i.e., the Beverton & Holt (1957) estimator (Equation 4) and the length–converted catch curve (see below, Z^*). The value of L_c in Equation 4 is the minimum fully selected size (the size at which all fish are caught by a particular fishing gear) in the fishery assumed to be minimum length in commercial catches while L_{mean} is the mean length of fish specimens larger than L_c. This approach was implemented in R using the function *bheq* in the package *fishmethods* (Nelson, 2014). This method was not implemented for fish stocks lacking adequate samples from commercial catches: *L. forskalii*, *M. kannume*, and *O. leucostictus* (Lake George).

$$Z = \frac{K(L_\infty - L_{mean})}{L_{mean} - L_c} \quad (4)$$

Natural mortality (M) was estimated from Equation 5 (Pauly, 1980). Temperature (T) in the equation refers to the mean temperature for the habitat, i.e., each of the waterbodies, and was obtained from Stoyneva-Gärtner et al. (2020).

$$log_{10}(M) = -0.0066 - 0.279log_{10}(L_{\infty}) + 0.6543log_{10}(K) + 0.463log_{10}(T) \quad (5)$$

For the Ugandan part of Lake Edward, we also estimated total mortality (Z^*) based on the VBGF using the length measurements from the six consecutive experimental gillnet surveys performed in 2022 combined with the corresponding measurements from commercial catches. We used the Electronic Length-Frequency Analysis function (ELEFAN 1) implemented in the software FISAT for this approach (Pauly, 1987). The L_{∞} and K are priors to estimate Z^* in ELEFAN 1. The value of K (K^*) used was estimated using the K-Scan routine in ELEFAN I by fixing the L_{∞} values to those derived from the empirical formulae in this study. The routine returns a value of K^* with the best fit for the fixed L_{∞}. Using the values of L_{∞} and derived K^* values, Z was estimated as the slope of the length–converted catch curve (Ricker, 1975).

In some instances, single-figure estimates of total mortality (mean) derived from length-based assessments may not be true estimates with the true values lying anywhere in the range of the confidence limits due to data variability (Gulland & Rosenberg, 1992). This was the case with both values of total mortality in this study because relating them with M to estimate F, returned unrealistic, negative estimates of F. As a result, F and E (F/Z) were not determined.

Finally, we estimated growth performance indexes (*Ø*) for the stocks to facilitate the evaluation of the estimates of K and L_{∞} from empirical formula by comparing the indexes derived to those of the species or related species (Froese and Pauly, 2023; Munro and Pauly 1983). The indexes were based on Equation 6 (Munro and Pauly, 1983).

$$\emptyset = log_{10}(K) + 2 \times log_{10}(L_{\infty}) \quad (6)$$

2.4 Ethical statement

In Uganda, this study was conducted by researchers of the National Fisheries Resources Research Institute (NaFIRRI). The institute is one of the seven public National Agricultural Research Institutes (NARIs) in Uganda under the policy guidance and coordination of the National Agricultural Research Organisation (NARO). The Institute is authorized to collect fish for research purposes to fulfil its national mandate to conduct basic and applied fisheries research. The care for the fish collected complied with national guidelines for the use of animals in research and training established by the Uganda National Council for Science and Technology (UNCST).

3 Results

3.1 Size structure

The size structure of the stocks in terms of length (L_{max} and L_{mean}) is illustrated in Figures 2and 3. The Mann-Kendall test revealed only two significant trends in the commercial and experimental catches of the stocks (Table S4). The significant trends, both for commercial catches of *B. docmak*, were an increasing trend in L_{max} (tau=0.65; p=0.021; Figure 2) in the Ugandan part of Lake Edward and L_{mean} (*tau*=0.68; *p*=0.048; Figure 3) in Lake George. Based on estimates of *tau* that are positive and ≥0.5 (Table S4), the Mann-Kendall test also indicated strong but non-significant increasing trends in L_{max} and L_{mean} of commercial catches of *L. altianalis* in the Ugandan part of Lake Edward (Figures 2 and 3). The same trend was observed for *L. altianalis* (L_{max}) and *O. leucostictus* (L_{max} and L_{mean}) in experimental catches of the Uganda part of Lake Edward (Figures 2 and 3; Table S4). Finally, the test also indicated a strong but non-significant decreasing trend in L_{mean} of *B. docmak* in experimental catches of the Uganda part of Lake Edward (Figure 3; Table S4). Unlike the Ugandan part of Lake Edward, only limited experimental fishing was performed in Lake George. Therefore, estimates of size structure for most stocks covered only 1994 and 2021 (Table S5; Table S6). The length-frequency histograms for the stocks in both commercial (Figures S1-13) and experimental (Figures S14-26) catches were mainly interrupted, with an unstable decline from larger to smaller individuals.

The Kruskal-Wallis tests to examine differences in L_{mean} were all significant (p<0.001) apart from that of experimental data of *B. docmak* in Lake George (Kruskal-Wallis test, X^2 =1.14, *df*=1, *p*= 0.285). Subsequent pairwise multiple comparisons showed that the L_{mean} over years within a stock were largely different among years with 80 % of all the possible pairs significantly different. Comparisons of length frequency distributions of the stocks revealed that the distributions were more likely to be significantly different than similar, with 78 % of the comparisons significantly different. In addition, pairs including a year before and a year after the change in management were likely to be as much significantly different or not, as any other pairs. These indicated that no changes in length frequency distributions could be attributed to the changes in management.

3.2 Length-weight relationships and Fulton's condition factor (K_c)

All length-weight relationships had high values of r^2 ranging from 0.88 to 0.99 (Tables 1 & 2), demonstrating that the regression models fitted well with the data from both the Ugandan part of Lake Edward and from Lake George. For all stocks, values of K_c ranged from 0.34 to 1.96 (Tables 1 & 2). Most of the stocks had good growth condition with K_c>1.

3.3 Sex ratios and size at first maturity

For some stocks, the sex ratios were not uniform in the two lakes (Tables 1 & 2). For instance, more females than males were present in the catches of *O. niloticus* in Lake Edward which was not the case for the stock in Lake George. The sex ratios differed from the general sex ratio for natural populations (1:1) in *L. forskalii* (X^2=4.24, *df*=1, *p*=0.04), *L. altianalis* (X^2=12.18, *df*=1, *p*=0.001), *O. niloticus* (X^2=22.64, *df*=1, *p*<0.001), *O. leucostictus* (X^2=40.00, *df*=1, *p*<0.001) in Lake Edward and *O. leucostictus* (X^2=12.11, *df*=1, *p*=0.001) and *P. aethiopicus* (X^2=3.95, *df*=1, *p*=0.05) in Lake George.

The estimates of L_{m50} were calculated for the stocks for which sufficient samples were available (Tables 1 & 2, Table S7). For L_{m50} were segregated by sex, the *estimates* for males were higher than those of females in all the stocks except *P. aethiopicus* and *L. altianalis* (Table S7). The logistic regression models fit to maturity data of the two time periods (before and after the changes in management) were not significantly different, indicating that no effect of the changes in management on the size at first maturity could be detected. The logistic regression models fit maturity data for both sexes combined and the data segregated by sex were weak to strong, with r^2 values ranging from 0.06 to 0.73 (Tables 1 & 2; Table S7).

The percentage of mature individuals in the catches was lowest in stocks of *B. docmak* from both waterbodies (Figure 4). These stocks exhibited the least percentage maturity of 27.9 % in Lake Edward in 2022 (Figure 4). At the end of the spectrum, stocks of *O. niloticus* had the highest percentages with 100 % maturity in Lake Edward and 99.6 % in Lake George.

3.4 Fecundity

The absolute fecundity of the stocks was highly variable (Tables 1 & 2). The absolute fecundity increased with total or fork length although the relationships, based on values of r^2 were weak in *O. niloticus, O. leucostictus*, and *L. altianialis*, and strong in the rest of the stocks (Figure 5).

3.5 Growth parameters and mortality rates

The estimates of growth parameters differed between conspecific populations from the two waterbodies due to different input parameters, especially L_{max} and mean temperature (Table 3). Parameters estimated using two approaches i.e., Z and Z^* from the Beverton and Holt estimator and the length–converted catch curve respectively, and K and K^* from an empirical formula and length frequency analysis respectively, the estimates obtained were different. An exception was *O.*

niloticus in Lake Edward whose estimates of K (K and K^*) were similar and those of Z (Z and Z^*), close (Table 3).

4 Discussion

4.1 Significance of the estimates and their reliability.

The estimates made in this study fill important knowledge gaps for the stocks of lakes Edward and George. Our estimates of L_{m50} for *C. gariepinus*, *L. forskalii* and *O. leucostictus* (Lake Edward) are new for these waterbodies. Apart from an estimate of *O. leucostictus* from Lake George (Ogutu-Ohwayo et al., 1997), all other estimates of fecundity are new. Regarding growth parameters (Table 3), only *O. niloticus* in Lake Edward had estimates of L_∞ and W_∞ in 1989 (Vakily, 1989;). Because life-history and growth parameters support decision-making, especially in data-poor stocks such as the ones assessed (King & McFarlane, 2003), the estimates made in this study are vital for fisheries management.

The reliability of our estimates is based on their consistency with estimates for the same or related species from literature and FishBase (Froese & Pauly, 2023). The consistency is demonstrated for *a* and *b* values from length-weight relationships, fecundity, and *Ø* (Table S8). The length-weight regressions (Tables 1 & 2) also have values of b that lie within the expected range of $2.5<b<3.5$ for fish species as well as high r^2 values (Froese, 2006), and are thus reliable. This means that the estimates in this study are good enough to be applied in further fisheries assessments such as estimating catch from length using *a* and *b* values of length-weight regressions (Garaway and Arthur, 2020).

4.2 Implications on the exploitation status and population dynamics of the stocks

Important inferences can be made on the status and population dynamics of the fish stocks based on the estimates of the life-history and growth parameters. The significant trends observed in L_{max} and L_{mean} in commercial catches of *B. docmak* (Table S4; Figures 2 & 3) suggested an increase of large individuals in its populations and catches. This desirable pattern was also apparent in the commercial catches of most of the other stocks, though not significant (Table S4). These patterns, especially the increase in L_{mean} indicate a decrease in fishing pressure and a recovery of stock size, length, and age structure (Shin et al., 2005). Conversely, a negative trend in L_{max} and L_{mean} in commercial catches may result from the removal of many large individuals or the selection of too many small individuals from fish populations into catches, both of which are not desirable and degrade size structure (Froese, 2004; Shin et al., 2005). Therefore, the negative trends observed for some stocks such as *P. aethiopicus* in both waterbodies, though not significant, are of management concern (Table S4).

The trend in L_{max} in experimental catches could be interpreted in the same way as in commercial catches above. However, the interpretation of L_{mean} in experimental catches could be different if diverse fishing gear to target all size classes are used, as is the case here. Low values of L_{mean} could be because of a high abundance of small individuals. This could explain the strong negative trend in the L_{mean} of experimental catches of *B. docmak* in the Ugandan part of Lake Edward (Figure 3; Table S4), which acts in the opposite direction compared to the trend of the same stock in commercial catches (Figure 3; Table S4).

The L_{opt} is recommended as L_{mean} in catches to maximize catches and biomass, and minimize the impact on size structure, thus promoting sustainable fishing (Froese et al., 2016). The estimates of L_{mean} observed in commercial catches in this study for the major commercial fish species (Figure 3) suggested unsustainable fishing that decrease population and stock sizes because they were less than L_{opt} (Table 3; Froese et al., 2016).

The estimates of L_{m50} for *O. niloticus* in this study, 21.2 cm and 17.6 cm (Tables 1 & 2) were lower than the highest ever recorded estimate of 25.2 cm in Lake George (Fry and Kimsey, 1960), and 21.0 cm in Lake Edward (Bassa et al., 2015). This was also the case for *P. aethiopicus* whose current estimates of 47.9 cm and 51.2 cm were lower than the 55-59 cm range reported for samples from lakes Edward, George, and the Kazinga Channel (Kamanyi, 1996). Fish respond to stressors by lowering size at maturity so that their populations can be replenished at a higher rate (Rochet, 2000). Therefore, the lower L_{m50} for these stocks could be in response to high fishing pressure they face in the two lakes (Musinguzi et al., 2021). In addition, values of L_{m50} lower than known estimates in the pastsuggest more selective fishing and vice versa (Law, 2000).

Based on the proportion of mature fish in commercial catches as an indicator of exploitation status with 100 % as the target (Froese, 2004), our observations indicated an improvement for *P. aethiopicus* and *O. niloticus* (Figure 4). For *P. aethiopicus*, Bassa et al. (2014) reported a range of 76- 92 % as a proportion of mature fish in commercial catches of 2011-2013 from both the Ugandan part of Lake Edward and Lake George, compared to a range of 94.3-99.0% observed in this study for both waterbodies. For *O. niloticus,* the proportion ranged from 34-92% in the commercial catches of 2011-2013 for both waterbodies compared to 99.6-100 % currently. For *B. docmak*, the current estimates of 27.9-66.7 %, compared to 63-73 % in the catches of 2011-2013 showed a degradation in the indicator, suggesting the presence of more young individuals in both catches and its population.

4.3 Effect of the new changes in management

The significant differences observed in size structure and length frequencies did not suggest that the change in management was important. Instead, the significant differences could be attributed to high variability common in length measurements of catches (Gulland & Rosenberg, 1992). Likewise, the logistic models of size at maturity before and after the commencement of changes in management were not significantly different. Therefore, it could be contentious to attribute any changes in size structure and size at maturity to the changes in management. However, positive signs of improvements in size structure were evident as some estimates of L_{max} or L_{mean} in commercial and experimental catches increased substantially after 2018 compared to the estimates of the preceding year with data (Figures 2 & 3). This was true for L_{max} and L_{mean} in the commercial catches of *P. aethiopicus* in the Ugandan part of Lake Edward as well as for L_{max} in experimental catches of *B. domak* in the Ugandan part of Lake Edward. In the former, L_{max} and L_{mean} increased from 76.0 cm and 31.4 cm in 2017 to 110.0 cm and 74.2 cm in 2020 respectively (Figures 2 & 3) while in the latter, L_{max} increased from 58.0 cm in 2016 to 84.1 cm in 2021 (Figure 2).

The steady decline from larger to smaller individuals in length-frequency distributions, a pattern that suggests a healthy status of the stocks (Neumann & Allen, 2007), though not widespread, was more prevalent in years after 2018. The pattern was observed for *B. docmak* in commercial catches of 2020 in Lake George (Figure S7) and *C. gariepinus* in commercial catches of 2022 and 2020 in the Ugandan part of Lake Edward (Figure S2) and George (Figure S8) respectively. For *B. docmak*, the steady decline from large to smaller individuals was absent in catches between 2011 and 2017 and only evident again in 2000 and 2001. For *C. gariepinus*, the pattern was also absent in recent years on both lakes, and only evident again in 2001 (Lake George). These observations suggested signs of improvements in size structure after 2018 that could be attained in all the stocks if the management regime is strengthened and maintained. For now, it may be too early for the impact of the changes in management to be clear and widespread. The changes in management strengthened enforcement of fishing regulations by promising to effectively prohibit destructive fishing gear and fishing in nearshore shallow habitats known to be nursery areas for fish. These changes are known to reduce fishing pressure, increase L_{mean}, and build the abundance of young and adult fishes (Shin et al., 2005; Campos-Silva and Peres, 2016; de Moraes et al., 2023).

4.4 Implications on fisheries management and conservation of fish species

Desirable attributes in the fish stocks including an increase in L_{max} or L_{mean} in catches of some stocks, a higher proportion of mature fish in catches, and an improvement in size structure visible in the length-frequency histograms, occur in well-managed fisheries. These attributes are not widespread in the assessed stocks. Moreover, the influence of the present management regime is not significant. This implies that enforcement of fishing regulations must be strengthened to create positive and significant outcomes for all the stocks. Strengthened enforcement will reduce fishing pressure, ensuring a sufficient supply of young fish for recruitment. Consequently life-history parameters such as L_{m50}, which were lower than historical records for *O. niloticus* and *P. aethiopicus*, could improve.

The presence of many immature individuals of *B. docmak* in catches is a concern. Establishing mesh size restrictions for this stock is necessary. The challenge is that the immature individuals of the species are caught in a legal fishing gear of *O. niloticus*.

The recent changes in management might be having positive effects, but more time for implementation is needed to assess their full impact. Management should therefore also prioritize monitoring not only to enable its evaluation but also to facilitate adaptive management measures as needed. In Lake Edward, illegal fishing from the DRC section of the lake, which is rampant (The Independent, 2021; Lutaaya, 2022) could undermine the potential benefits from the improved management in Uganda. Therefore, the cooperation between fishery management authorities in Uganda and DRC is necessary for assured benefit from the current management efforts.

With about 60 endemic haplochromine cichlids and other 15 native non-*Haplochromis* species (Greenwood, 1991; Snoeks, 2000; Vranken et al., 2019; Decru et al., 2020; Musinguzi et al., 2023), lakes Edward and George are important for the conservation of fish species. Generally, our estimatesof the life-history parameters suggest that the management of exploited fish species should be improved by strengthening the enforcement of fishing regulations. This is important for the conservation of both exploited and unexploited species. Improved management could benefit exploited species, especially those present in the catches but perceived to be of low abundance, i.e., *L. forskalii* and *M. kannume* (Poll & Damas, 1935; Worthington, 1932). The haplochromine cichlids in the waterbodies are endemic and, therefore, of immense conservation importance (Vranken et al., 2022). Stronger enforcement of fishing regulations could benefit these species by protecting them from fishing pressure through sustaining populations of exploited fish species. In addition, the haplochromines utilize diverse aquatic habitats. Therefore, stronger enforcement of fishing regulations contributes to conservation of the species by protecting their habitats from degradation by unsustainable fishing practices such as beach seining (Akwetey et al., 2024).

4.5 Limitations of the study and future perspectives

This study encountered limitations related to sample size and availability of data. For some species in Lake George, fecundity and L_{m50} could not be determined (Table 2). Insufficient sample size may have contributed to the high variability observed in estimates of fecundity, low r^2 values for the linear regressions of fecundity and length, and some estimates of L_{m50} (Tables 1 & 2). The low r^2 value for the logistic regression model of *L. altianalis* (Table 1; Table S7) contrasts with previous observations in Lake Edward which reported a strong correlation (Aruho et al., 2018). The reasons for the weak correlation in this study could be high variability in the data possibly due to a misclassification of maturity stages, or taxonomic confusion with a related species, *Labeobarbus somereni* (Boulenger, 1911). *Labeobarbus somereni* occurs in the rivers flowing into the lakes, and hence could venture into Lake Edward.

Regarding growth parameters, F and E could not be estimated because relating M and Z to estimate F resulted in unrealistic values. This could be due to limitations in the available data. In addition, estimates from ELEFAN 1 were based on six sampling events. Whereas this is adequate if sample sizes are large (Gulland & Rosenberg, 1992), which was the case in this study (Table 3), the ideal is to have 12 samples taken consecutively for 12 months (Hoenig, 1987; Pauly, 1984).

These limitations can be addressed by more frequent data collection to increase sample size and make more data available. The data collection efforts should consider both fishery-dependent and independent surveys as complementary methods. Fishery-dependent surveys will enable more frequent acquisition of data because they are cheap. On the other hand, fishery-independent surveys offer opportunities for standardized data collection and collection of data on fish species that do not appear in commercial catches. The availability of more data will improve the understanding of the exploitation status and the population dynamics of the stocks using life-history and growth parameters. This will, in turn, improve decisions for fisheries management and conservation of native species. Only the Ugandan part of Lake Edward was assessed due to the lack of data from the part of the Lake in DRC. Collecting data from this this part of the lake should therefore be prioritized in future data collection efforts.

There are new aspects that could be covered in future research to generate more accurate information useful for research. These include aspects of ageing fish, examination of recruitment patterns of the fish stocks, and changes in all the aspects of fish life-history and growth parameters in relation to productivity of the waterbodies and climate change. These aspects can also change with season and therefore, seasonal patterns in all these aspects (not explored in this study) should also be considered in future research.

No significant changes in life-history parameters could be attributed to the enhanced management that commenced in 2018. However, there is optimism from the enhanced management exhibited by signs of improvement in L_{max}, L_{mean}, and high percentage of maturity in catches of some stocks among others (section 3.5.2). The effect of the changes could become significant with time if the management regime is maintained and strengthened. Therefore, future research should consider re-examining the effects as a way of evaluating the performance of the management regime.

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