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Aspects of the biology and population structure of *Oreochromis niloticus*, *Coptodon zillii* and *Oreochromis leucostictus* tilapia in Lake Naivasha, Kenya

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Abstract

The Nile tilapia (*Oreochromis niloticus*), Redbelly tilapia (*Coptodon zillii*) and Blue spotted tilapia (*Oreochromis leucostictus*) were introduced into Lake Naivasha in the 1950s to diversify and boost the lake fisheries. These species have since been exploited in the commercial gillnet fishery. The fish stocks, however, are currently facing problems of pollution, wetland degradation and intense fishing pressures. Accordingly, the present study investigated some aspects of the biology and population structure of the three tilapiine species in light of changing lake conditions. Fish samples were collected from January to December 2019 using multifilament gillnets of 2.0-to-6.0-inch mesh sizes. Immediately after their capture, the fish specimens were transported to the lab for morphometric measurements and analysis of maturity. The highest and lowest mean (±SD) total length (TL) were exhibited by *O. niloticus* (22.9 ± 5.2 cm) and *C. zillii* (14.5 ± 2.1 cm), respectively. Similarly, *O. niloticus* exhibited a higher mean weight (268.4 ± 18.0 g) and body depth (7.6 ± 2.5 cm), compared to the other species. *O. niloticus* exhibited an isometric growth pattern, while *C. zillii* and *O. leucostictus* exhibited negative allometric growth. The fish species were in good condition, with mean condition factors of 1.59 ± 0.07, 1.51 ± 0.06 and 1.23 ± 0.03 for *C. zillii*, *O. leucostictus* and *O. niloticus*, respectively. Furthermore, the condition factors for *O. leucostictus* and *O. niloticus* varied by size class, exhibiting a decreasing trend with increased fish size. The male:female sex ratio revealed significantly more males than females for *O. niloticus* (2.30:1.0) and *O. leucostictus* (2.36:1.0), although not for *C. zillii* (1.15:1.0). *O. niloticus* (28.0–29.0 cm TL) matured at a larger size, followed by *O. leucostictus* (21.0–26.0 cm TL), and *C. zillii* (15.0–17.0 cm TL). In comparison, values of length-weight parameters, condition factor, sex ratio and size at first maturity of the studied fishes varied in Lake Naivasha, Victoria, Albert and George. The gillnet mesh ≤3.0″ mainly targeted small-sized immature fish, while mesh ≥4″ targeted mature fish, particularly *O. niloticus*. It was concluded that gillnets with ≥4.0″ mesh could safely be applied for this fishery in Lake Naivasha, whereas the use of smaller mesh should be controlled to protect the juveniles as a means of maintaining sustainable fisheries. Furthermore, the present study also provided useful information, including size at maturity that is vital for setting mesh size for managing the lake fishery.

KEYWORDS
fisheries management, gillnets, length-weight, maturity, overfishing, tilapiines

1 | INTRODUCTION

Lake Naivasha is a freshwater body in Kenya, providing a source of food, income and water to the communities (Hickley et al., 2002). The lake originally contained only one native fish species; namely, black lampeye (*Micropanchax antinorii*)(Seegers et al., 2003). The lake fishery was enhanced by the introduction of non-native fish species, including Common carp (*Cyprinus carpio*), Nile tilapia (*Oreochromis niloticus*), Blue spotted tilapia (*Oreochromis leucostictus*), Redbelly tilapia (*Coptodon zillii*), Largemouth bass (*Micropterus salmoides*) and African sharptooth catfish (*Clarias gariepinus*) (Mutethya et al., 2020; Njiru et al., 2017). *Oreochromis leucostictus* was introduced into Lake Naivasha in 1956 from ponds near Lake Victoria (Hickley & Harper, 2002). Although a serial breeder, it has been reported to have only one spawning peak in April in Lake Naivasha (Hickley et al., 2002). This fish can tolerate harsh environmental conditions, including high temperature and salinity levels (Jembe et al., 2006). *Oreochromis leucostictus* naturally co-exists with *O. niloticus*, which prefers rather deeper waters, so the two species appear to have complementary niches (Froese & Pauly, 2019).

Coptodon zillii was also introduced into Lake Naivasha in 1956 from the Lake Victoria basin, having been exploited within a commercial gillnet fishery since its introduction into the lake (Hickley & Harper, 2002). It grazes mainly on aquatic plants and can breed throughout the year (Siddiqui, 1977). Unlike *O. leucostictus*, *C. zillii* exhibits less niche overlap with *O. niloticus* (Gu et al., 2016). *Oreochromis niloticus* was first introduced into Lake Naivasha in 1967 in order to diversify and boost the lake fisheries (Kundu et al., 2010; Waithaka et al., 2020). It is primarily herbivorous, with aquatic macrophytes, algae and diatoms comprising more than 90% of its diet, while also ingesting other food items such as aquatic insects, crustaceans and fish eggs (Njiru et al., 2004; Outa et al., 2014). Its stocks declined from Lake Naivasha in 1971, probably attributable to predation by *M. salmoides* (Gozlan et al., 2010; Njiru et al., 2017) and was later re-introduced into the lake during 2011. Cichlids, particularly tilapiines, are known to have the potential to alter the aquatic communities into which they have been introduced (Canonico et al., 2005; Peterson et al., 2004). They colonize new habitats due to their adaptability to varying environmental conditions, prolific breeding habits, short generation time, extended breeding season, territoriality and the ability to feed at a range of trophic levels (Canonico et al., 2005; Yongo et al., 2021).

The fish stocks are facing pollution problems, wetland degradation, exotic species introductions and intense fishing pressure in Lake Naivasha (Njiru et al., 2017). The rapid human population growth around Lake Naivasha has increased domestic wastes discharges into the lake, causing pollution (Waithaka et al., 2020). Wetland degradation reduces suitable habitats for fish breeding and nursery grounds to replenish the declining stocks. The increased population of the introduced *C. carpio* could also have several detrimental effects on the Lake Naivasha ecosystem (Petr, 2000). *C. carpio* feeds by uprooting aquatic plants, thereby increasing water turbidity and reducing light availability for the productivity of phytoplankton and submergent macrophytes (Ojuok et al., 2008). Reduced algae and macrophytes biomass can, in turn, threaten the food base for phytoplanktivorous *O. leucostictus* and herbivorous *C. zillii*. Disturbance of the lake bottom by *C. carpio* would seriously affect *C. zillii*, which lays adhesive eggs on the lake bottoms with pebbles or sand and with abundant vegetation (Coward & Little, 2001). The *C. carpio* and *C. zillii* both lay sticky eggs, thereby competing for substratum to attach their eggs (Petr, 2000).

The fisheries management practices in Lake Naivasha include licensing, closed fishing seasons and areas, mesh size regulations based on biological limits (>4.0″ stretched mesh) and prohibition of illegal gears, such as monofilament gillnets, beach seining and cast-nets (Njiru et al., 2017). Enforcement of some of these measures, however, has been limited by socio-economic and political factors, with illegal fishing activities in Lake Naivasha proliferating as a result. The lake is subsequently experiencing over-exploitation because of use of illegal gears (e.g. seine and monofilament nets) leading to reduced fish size and abundance. The fishers regularly use illegal gears to fish in the shallow areas used as breeding and nursery grounds by most fishes in the lake. There is also rampant use of gillnets of 3.5 inches (″) and below that target smaller-sized *O. leucostictus*, *O. niloticus* and *C. zillii*. (Njiru et al., 2017). At the same time, however, there are limited studies on the biology and population structure of these species in the lake (Waithaka et al., 2020). Accordingly, the present study investigated some aspects of the biology and population structure of *O. leucostictus*, *O. niloticus* and *C. zillii* in Lake Naivasha. The focus was on body length, weight, body depth, length-weight relationship, condition factor, sex ratio, size at first maturity and catch composition of the species by different gillnet meshes. The results of the present study will be useful for comprehensive stock assessments and sustainable management of the lake fishery.

2 | MATERIALS AND METHODS

2.1 | Sampling and data collection

Lake Naivasha is a shallow endorheic freshwater lake situated in warm and semi-arid conditions in the eastern Rift Valley of Kenya at 00°46′S, 36°22′E and an altitude of 1890-m (Figure 1). It is relatively small, approximately 145 km^2, surrounded by a swamp that covers an area of about 64 km^2 (Hickley et al., 2008). Its mean depth varies

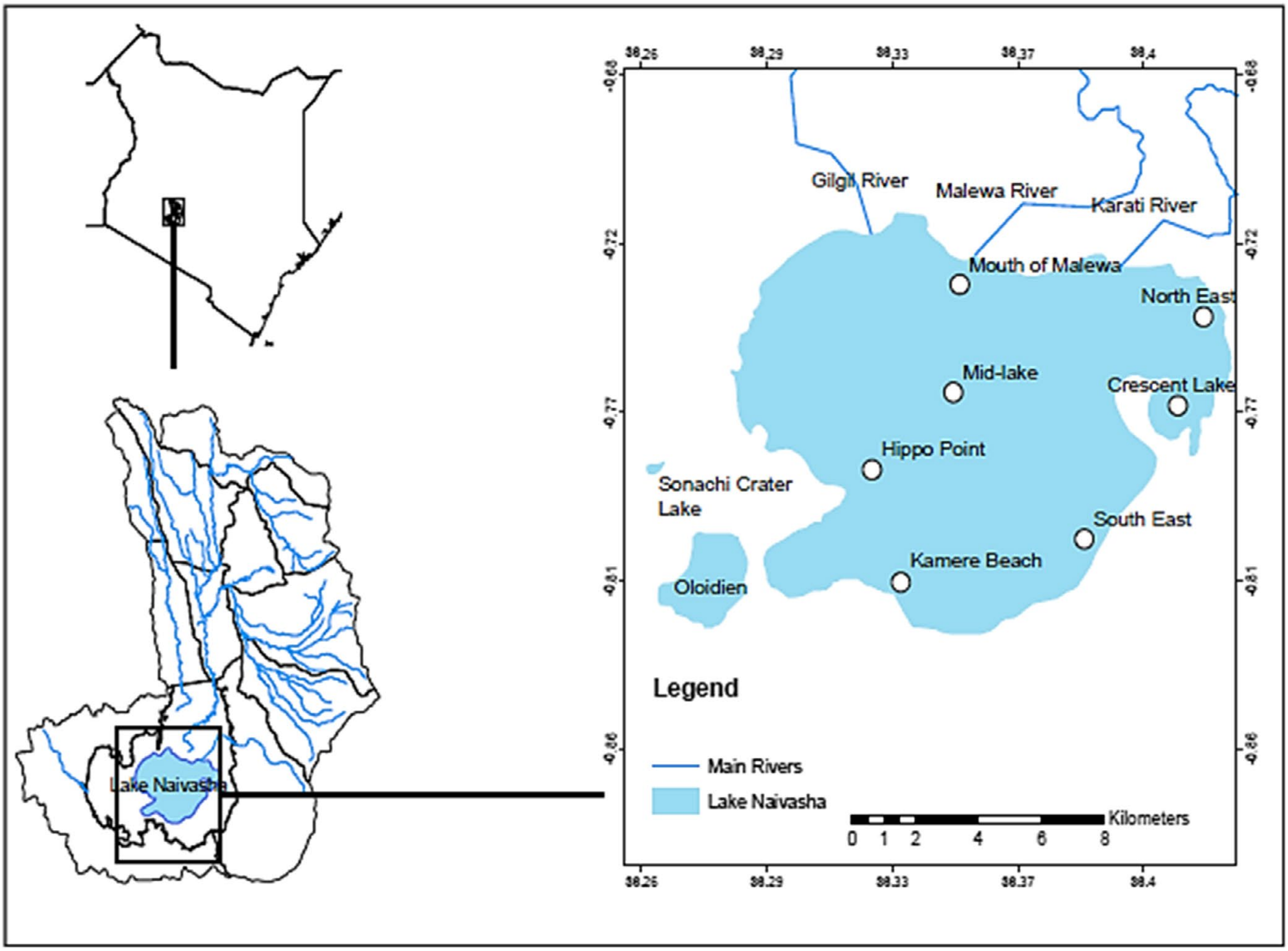

FIGURE 1 Map of Kenya and geographical location of Lake Naivasha (circles indicate sampling areas)

between 4 and 6 m, and it receives inflow mainly from the Malewa, Gilgil and Karati Rivers (Kitaka et al., 2002). The lake water temperature ranges between 20° and 23°C (Oyugi et al., 2011). It was once one of the most treasured tourist sites in the world because of its biodiversity richness that led to its subsequent designation as a Ramsar site. Lake Naivasha provides a source of fish, drinking and irrigation water and non-fish benefits that include food security, employment, community development, education, recreation, conservation and tourism (Hickley et al., 2015). Experimental fishing for the present study was conducted in Lake Naivasha (Figure 1) from January to December 2019, using multifilament gillnets made of 210 D/3 twine, with mesh sizes of 2.0, 2.5, 3.0, 3.5, 4.0, 5.0 and 6.0 inches stretched. Each gillnet had a dimension of 50 × 9 3 m, and a hanging ratio of 0.5. The choice of these mesh sizes was based on knowledge of the existing fishery operations in Lake Naivasha, noting the Lake Naivasha fishers often use the recommended gillnets of 4″ mesh and above. Most fishers, however, tend to reduce the mesh size in order to increase their catches. During the fishing experiment, gillnets were set at around 17.00 h and retrieved at around 08.00 h the following day. The total catch by each mesh for each species was recorded to determine the composition of the catch. Immediately after their capture, *C. zillii*, *O. leucostictus* and *O. niloticus* specimens were transported to the Kenya Marine and Fisheries Research Institute (KMFRI) Naivasha station laboratory for morphometric measurements and analysis of maturity stages. The total length (TL), standard length (SL), body depth (BD) and total weight (W) of each specimen were measured in the laboratory using a measuring board and a balance to the nearest 0.1 cm and 0.1 g, respectively. The fish were then dissected for determination of sex and maturity stages, based on the scheme of Witte and van Densen (1995). Depending on their degree of maturity, gonads were rated as stage I and II (immature), III (active), IV (ripe), V (mature) or VI (spent) under this scheme.

2.2 | Data analysis

2.2.1 | Length-weight relationships

The formula of Le Cren (1951), $W = a \times TL^b$, was used to estimate the relationship between weight and total length of the fish. The linear regression of the log transformed equation used in this analysis was as follows:

$$\text{Log}\,W = \text{Log}\,a + b\,\text{Log}\,\text{TL} \quad (1)$$

where a = intercept and b = slope of the length-weight relationship.

2.2.2 | Relative condition factor

The relative condition factor (*Kn*) was calculated according to LeCren (1951) as follows:

$$\text{Kn} = \frac{W}{(a \times \text{TL}^b)} \quad (2)$$

where Kn = relative condition factor; W = weight of fish (g); TL = total length of fish (cm), with a (intercept) and b (slope) being constraints of the regression equation.

2.2.3 | Sex ratio, length frequency and size at first maturity

The male:female sex ratio was calculated as a ratio of number of males and females for each fish species. To determine the length frequency, the TL data for each species were classified into size classes (10–15; 16–20; 21–25; 26–30; 31–35; 36–40 cm) to compare the number of males and females in each size class. The length at first maturity (Lm_{50}) was estimated by classifying the gonads as immature (stage I and II) and mature (from stage III to V) fish. The mean Lm_{50} was determined using the method described by Gunderson et al. (1980). The method fits the percentages of mature fish that were grouped in 1-cm length classes to the logistic equation:

$$P_L = \frac{1}{(1 + \exp^{(bL+a)})} \quad (3)$$

where P_L = proportion of mature fish at length L, with a and b being the intercept and slope, respectively of the logistic regression. The Lm_{50} was then estimated from the relationship:

$$Lm_{50} = -a/b \quad (4)$$

2.3 | Statistical analysis

All data were analysed using IBM SPSS statistics 21. The level of significance used for all analyses was $\alpha = 0.05$. Descriptive statistics were used to determine the mean and standard deviation of the weight, length and body depth of the fish species. Chi-square (χ^2) was used to compare sex ratio data to 1:1 for each fish population. Additionally, χ^2 was used to test the association between gillnet mesh size and fish species type/sex. Kruskal–Wallis was used to test for the differences in condition factors in relation to sex and size class of the fish species. For length-weight relationship predictions, the data of log TL were linearly regressed against log WT, while data of TL were regressed against SL for length-length predictions. The coefficient of determination (R^2) was used, to measure the quality of the linear regression predictions, with a value close to 1 implying a better model.

3 | RESULTS

3.1 | Catch composition and morphometric parameters

A total of 1332 fish specimens comprising *C. zillii* (113), *O. leucostictus* (293) and *O. niloticus* (926) were caught, contributing 8.5%, 22.0% and 69.5%, respectively, of the catch. There was a statistically significant association between gillnet mesh size and fish species caught ($\chi^2 = 274.48$, $p < .05$). Higher proportions of the fish species were caught by meshes 2.0, 3.0 and 4.0″, respectively (Figure 2), whereas meshes of 2.5 and 3.5″ size yielded the lowest catches. The 5.0 and 6.0″ mesh mainly targeted *O. niloticus* (Figure 2). There was also a statistically significant association between gillnet mesh size and sex of fish caught ($\chi^2 = 28.40$, $p < .05$). Meshes 2.0, 3.0 and 4.0″ caught higher proportions of male fish than females for nearly all the species (Figure 2). Gillnets of meshes 3.0″ and below caught immature fish, while mature fish were caught mainly by 4″ and above mesh sizes (Figure 3). Regarding the morphometric parameters, the highest and lowest mean (±SD) TL was observed for *O. niloticus* (22.9 ± 5.2 cm) and *C. zillii* (14.5 ± 2.1 cm), respectively. Similarly, *O. niloticus* exhibited a higher mean weight (268.4 ± 18.0 g) and body depth (7.6 ± 2.5 cm), compared to the other species. The mean TL, SL, BD and WT of *O. niloticus* and *O. leucostictus* increased significantly with increasing mesh sizes, although there were no distinct trends for *C. zillii* regarding these parameters in relation to mesh sizes (Figure 4). There was a statistically significant difference in mean BD and WT of *O. niloticus* and *O. leucostictus* caught by the different meshes ($p < .05$), whereas the mean weight did not differ significantly between the mesh sizes ($p > .05$) for *C. zillii*.

3.2 | Length-weight relationship and condition factor

Linear regression analysis of length-weight relationships for individual species indicated *O. niloticus* exhibited isometric growth pattern ($b = 3.02$, Figure 5a), while both *C. zillii* ($b = 2.81$) and *O. leucostictus* ($b = 2.80$) exhibited negative allometric growth (Figure 5b,c). The high coefficients of determination ($R^2 = .794$–$.959$) indicated a good quality of weight predictions for all the analysed fish species. Linear regression analysis of TL and SL indicated a good model fit for each species (*O. niloticus* (Figure 5d; $R^2 = .98$); *O. leucostictus* (Figure 5e; $R^2 = .97$) and *C. zillii* (Figure 5f; $R^2 = .93$)). All the fish species were in good condition, with mean relative condition factors of 1.593 ± 0.073, 1.512 ± 0.064 and 1.225 ± 0.033 for *C. zillii*, *O. leucostictus* and *O. niloticus*, respectively. A Kruskal–Wallis test

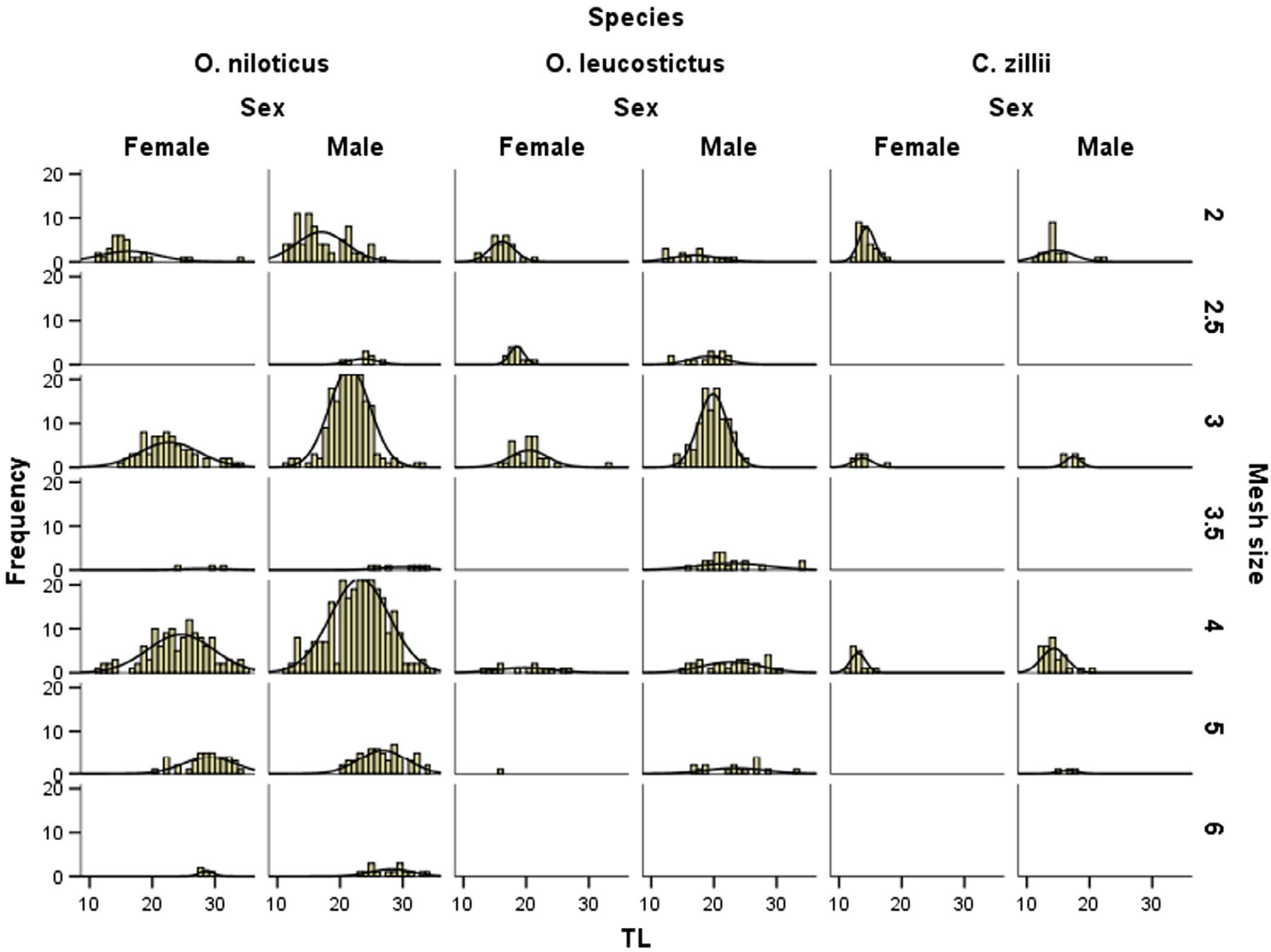

FIGURE 2 Catch composition of male and female *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* by different mesh sizes from Lake Naivasha, Kenya (TL indicates total length)

indicated no significant difference in the condition factor between males and females for all the examined species (Figure 6a), although the condition factor varied by size class for *O. leucostictus* ($H = 65.18$, $p < .05$) and *O. niloticus* ($H = 422.49$, $p < .05$). The condition factor of the fish species exhibited a decreasing trend with increasing fish size (Figure 6b).

3.3 | Sex ratio, length frequency and size at first maturity

Overall, there was a significant difference in the population male:female sex ratio for the three fish species caught in Lake Naivasha. There were significantly more males than females for *O. niloticus* (sex ratio = 2.30:1.0, $\chi^2 = 143.71$, $p < .05$) and *O. leucostictus* (sex ratio = 2.36:1.0, $\chi^2 = 47.37$, $p < .05$). However, for *C. zillii* (sex ratio = 1.15:1.0, $\chi^2 = 0.58$, $p = .45$) the sex ratio was not significantly different from 1:1. The length frequency distributions for male and female *C. zillii*, *O. leucostictus* and *O. niloticus* are illustrated in Figure 7a–c. The fishes ranged from 11.0–23.0, 12.0–38.0, and 11.0–42.0 cm TL for *C. zillii*, *O. leucostictus* and *O. niloticus*, respectively (Figure 7a–c). Female *O. leucostictus* and *C. zillii* exhibited a smaller size at first maturity (Lm_{50}), compared to their male counterparts (Figure 7d,e). *C. zillii* females exhibited the least Lm_{50} (15.0 cm TL; Figure 7d), while *O. niloticus* females had the highest Lm_{50} (28.0 cm TL; Figure 7f). Similarly for the male populations, *C. zillii* had the least Lm_{50} (17.0 cm TL; Figure 7d), while *O. niloticus* had the highest Lm_{50} (29.0 cm TL; Figure 7f).

4 | DISCUSSION

4.1 | Length-weight relationship and condition factor

Parameters such as length-weight relationship and condition factor are important for studying the biology of fishes (Lizama & Ambrosia, 2002; Yongo et al., 2017) and can be used to predict fish weight from length measurements obtained from stock assessments (Pauly, 1993). The length-weight relationship and condition factor are also

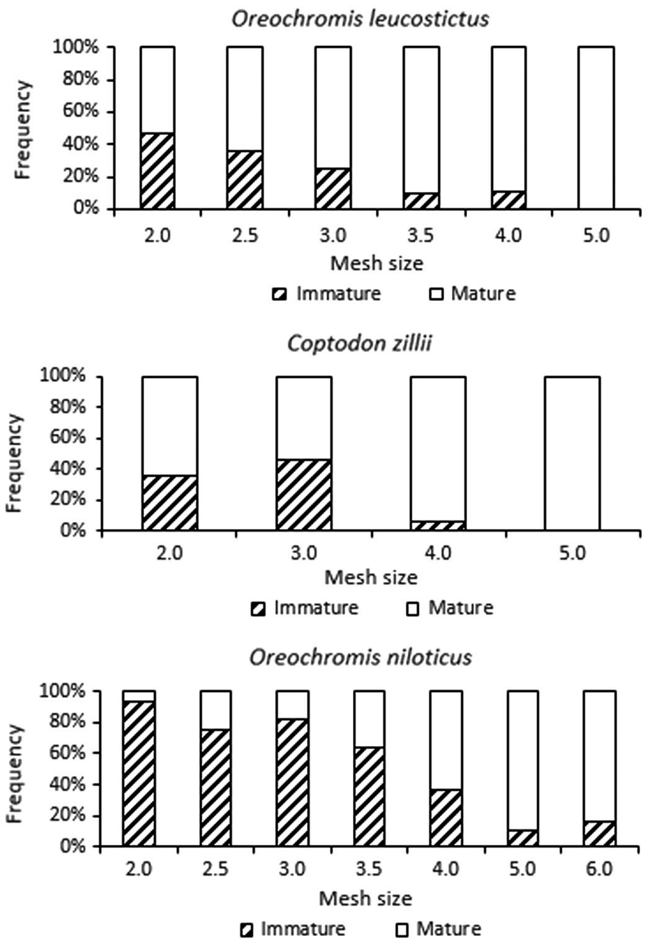

FIGURE 3 Maturity status of *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* collected from Lake Naivasha, Kenya, using different gillnet mesh sizes

important parameters for assessing the health condition of fish (Mortuza & Al-Misned, 2013; Nehemia et al., 2012). Fish can attain either isometric, negative allometric or positive allometric growth patterns. Isometric growth is associated with no change of body shape as the fish grows. Negative allometric growth means the fish becomes more slender as it increases in length, while positive allometric growth implies the fish becomes relatively stouter or deeper-bodied as it grows (Mutethya et al., 2020; Riedel et al., 2007). The negative allometric growth pattern observed in *C. zillii* (b = 2.81) and *O. leucostictus* (b = 2.80) in the present study suggested these species have a relatively slow growth rate and tend to be slender, compared to *O. niloticus* that exhibited isometric growth pattern (b = 3.02). The higher b value of *O. niloticus* in the present study could imply that Lake Naivasha provided a more favourable environment for this species, thereby, facilitating its better growth.

The results of the present study were compared to previous studies on these species from Lake Naivasha and other lakes. Njiru et al. (2006) (b = 3.0) and Yongo et al. (2018) (b = 3.01) reported isometric growth for *O. niloticus* from Lake Victoria, while Outa et al. (2014) (b = 2.31) and Waithaka et al. (2020) (b = 2.86) reported negative allometric growth for the same fish from Lake Naivasha. The b value for *O. leucostictus* from Lake Naivasha reported by Laurent et al. (2020) (b = 2.33) corroborates the negative allometric growth pattern observed in the present study (b = 2.80). Keyombe et al. (2020), however, reported a very low b value for *C. zillii* (b = 1.90) from Lake Naivasha compared to the present findings (b = 2.81). According to Ali et al. (2016) and Yilmaz et al. (2012), fish might exhibit different growth patterns because of factors such as water quality, food availability, habitat conditions, season and life stages. Furthermore, fish growth pattern variations could also be related to the condition of the species itself, its phenotype, specific geographical location and, therefore, its environment (Tsoumani et al., 2006). Thus, the growth process can differ in the same species dwelling diverse locations and influenced by numerous biotic and abiotic factors.

All the fish species observed in the present study were in good condition, with K values >1.0 (LeCren, 1951). The condition factor values for the species in the present study were compared with the finding from previous studies. The K value of *O. niloticus* reported for Lake Naivasha by Outa et al. (2014) (K = 2.46) was higher than those of the present study (K = 1.23). Waithaka et al. (2020), however, reported a low K value for *O. niloticus* (K = 1.01) from the same lake, compared to the present results. Furthermore, the K value observed for *O. niloticus* in the present study (K = 1.23) was higher than the results for the same fish collected from Lake Victoria (Ojuok et al., 2000, K = 0.71; Njiru et al., 2006, K = 0.90; Yongo et al., 2018, K = 1.04). The K value obtained for *C. zillii* (K = 1.59) in the present study was slightly lower than those from the study of Keyombe et al. (2020) (K = 1.59) for the same species from Lake Naivasha. The value observed in the present study for *O. leucostictus* was higher than those of Laurent et al. (2020) from the same lake (K = 1.04). The variations in the condition factor might be partly attributed to the differences in the ecological conditions of the lakes and for different study periods. Additionally, since the condition factor reflects a relation between the length and weight for a particular fish, it can be influenced by the same factors as the length-weight relationship, including species type, season, food availability, sex, reproductive cycles and water quality parameters (Khallaf et al., 2003). The results of the present study also indicated adult fish exhibited lower condition values compared to juvenile, which is attributable to the greater energy that adult fish spend in gonad development and spawning activities.

4.2 | Sex ratio and size at first maturity

The present study findings regarding the sex ratios indicate males were predominant over females for *O. niloticus*, *O. leucostictus* and *C. zillii* caught from Lake Naivasha, which was attributed to the gillnet meshes catching high proportions of male fish because of their aggressiveness than female fish. For comparison purposes, the male:female sex ratios of the species in the present study and from other lakes are summarized in Table 1. They were comparable with previous findings on this factor, which also indicated a predominance of males over females for these species. Njiru et al. (2006) suggested

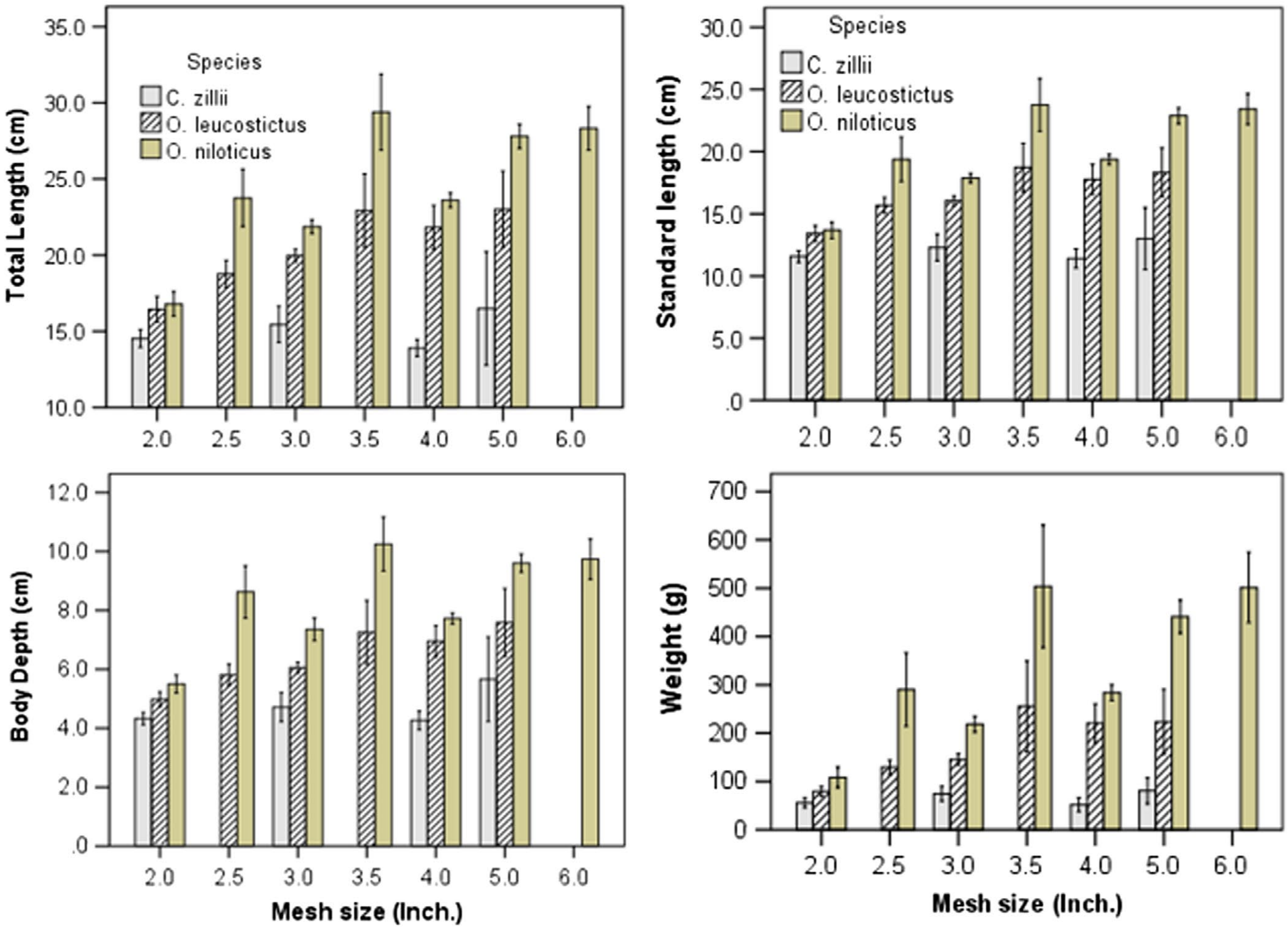

FIGURE 4 Variations in mean total length, standard length body depth and weight by mesh sizes of *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* from Lake Naivasha, Kenya

male tilapiines tend to grow faster and attain bigger sizes than their female counterparts, thereby increasing their probability of capture. To this end, Russell et al. (2012) reported the sex ratio of *O. mossambicus* populations sampled from Northern Australia was biased towards a predominance of females. According to those researchers, the general bias towards females was a potential mechanism to produce more offspring in situations, wherein the populations are under some stress and, as a result, are allocating resources to increase biomass. Moreover, other studies reported that tilapiine sex populations can vary on the basis of location between a predominance of males to females (Arthington & Milton, 1986; Bruton & Boltt, 1975).

The present study results regarding size at first maturity (Lm_{50}) indicated *O. niloticus* had the highest Lm_{50}, compared to *O. leucostictus* and *C. zillii*. For comparison purposes, the Lm_{50} values of male and female *O. niloticus*, *O. leucostictus* and *C. zillii* from different lakes over time are summarized in Table 1. The sizes at maturity of *C. zillii* in the present study were comparable with the values reported by Siddiqui (1977), but were slightly higher than those of Keyombe et al. (2020) for the same fish in Lake Naivasha. The size at maturity of *O. leucostictus* in the present study conformed to the findings of Laurent et al. (2020) from Lake Naivasha and Lowe (1957) from Lake George (Table 1). However, Witte and Winter (1995) and Lowe (1957) reported very low Lm_{50} values for *O. leucostictus* from Lake Victoria and Albert, respectively. The Lm_{50} of *O. niloticus* in the present study agreed with the findings of Waithaka et al. (2020) for the same species from Lake Naivasha. However, Outa et al. (2014) reported very low Lm_{50} values for *O. niloticus* from this same lake. It was noted in the present study that *O. niloticus* from Lake Naivasha matured at slightly smaller sizes compared to their counterparts from Lake Victoria (Njiru et al., 2006; Ojuok et al., 2000; Yongo et al., 2018; Table 1).

The size at first maturity of all the studied fish species generally varied between lakes, with the highest values recorded for Lake Victoria, followed by Lake Naivasha. The size at first maturity of most tilapiines are known to vary between water bodies in response to environmental conditions (Duponchelle et al., 2000; Tesfaye et al., 2015). In large and stable habitats such as Lake Victoria, for example, tilapiines will tend to exhibit *K*-traits of delayed maturation and extended spawning characteristics (Yongo & Outa, 2016). In unstable environments, however, such as Lake Naivasha and other small lakes where temperatures, dissolved oxygen concentrations, habitat size and water levels can fluctuate considerably, it is advantageous

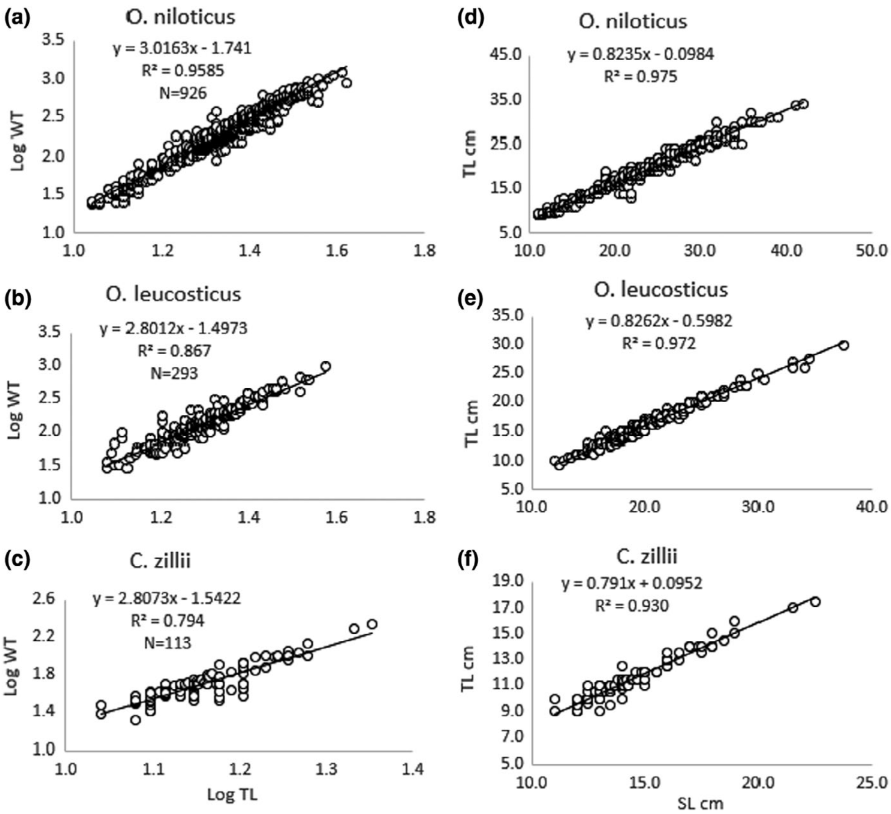

FIGURE 5 Log Weight-Log length and length-length relationships of *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* from Lake Naivasha, Kenya (TL denotes total length)

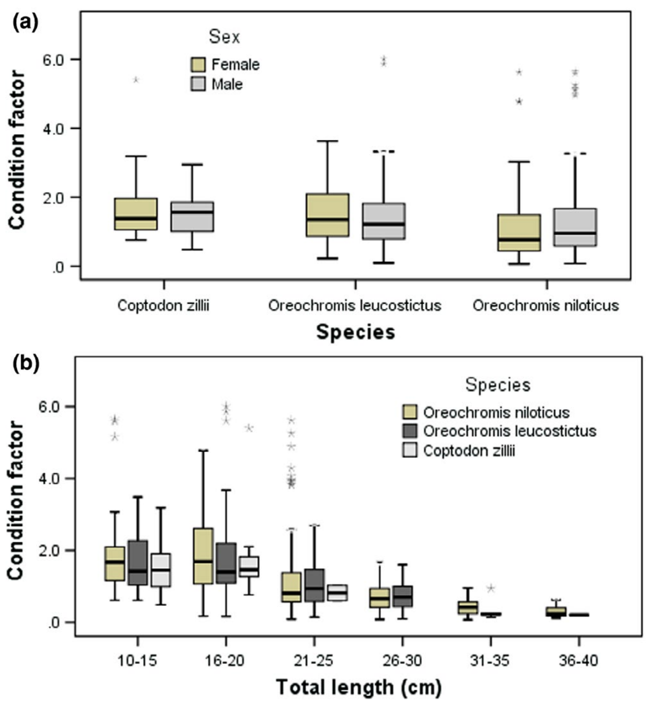

FIGURE 6 Variation in condition factors of *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* collected from Lake Naivasha (Kenya) in relation to (a) sex and (b) size classes

for tilapiines to exhibit *r*- life history traits characterized with early maturation (Russell et al., 2012; Waithaka et al., 2020). The other significant factor affecting tilapiines life history traits is size-selective fishing mortality (Njiru et al., 2008). In Lake Victoria, for example, the length at first maturity of *O. niloticus* have decreased with increasing fishing over the years (Njiru et al., 2008; Yongo et al., 2018). Such a population response to fishing pressure is common in exploited fisheries, with exploitation generally being strongly size-selective on larger individuals (Ojuok et al., 2007; Swain et al., 2007).

4.3 | Catch composition

The small gillnet mesh size of 3.0″ and below mainly targeted small-sized immature fish, while large mesh size of 4″ and above targeted mature fish, particularly *O. niloticus*. These results are comparable to the findings of Njiru et al. (2017) from Lake Naivasha, who reported gears below 4.0″ mesh mainly captured small-sized fish below size at first maturity. Njiru et al. (2017) assessed the catch composition of eight multifilament gillnets ranging from 2.5 to 6.0″mesh size, all being similar with the meshes used in the present study. The present study results, however, differed from those of Tesfaye et al. (2015) for Lake Koka (Ethiopia), which indicated the smallest gillnet mesh 60-mm (2.4″) caught a higher proportion of larger-sized *O. niloticus*, while mesh 80-mm (3.2″) caught few large-sized *O. niloticus*. Tesfaye et al. (2015) used six multifilament gillnets, ranging from 60 (2.4″) to 120 mm (4.7″) mesh size, which are within the range of those of the present study (2.0–6.0″). The difference in gillnet catches might be attributable to gear-related factors (e.g. twine type and size, and mesh sizes), size range and sample size (Tesfaye et al., 2015). Hansen (1974), for example, found a significant increase in the size of fish

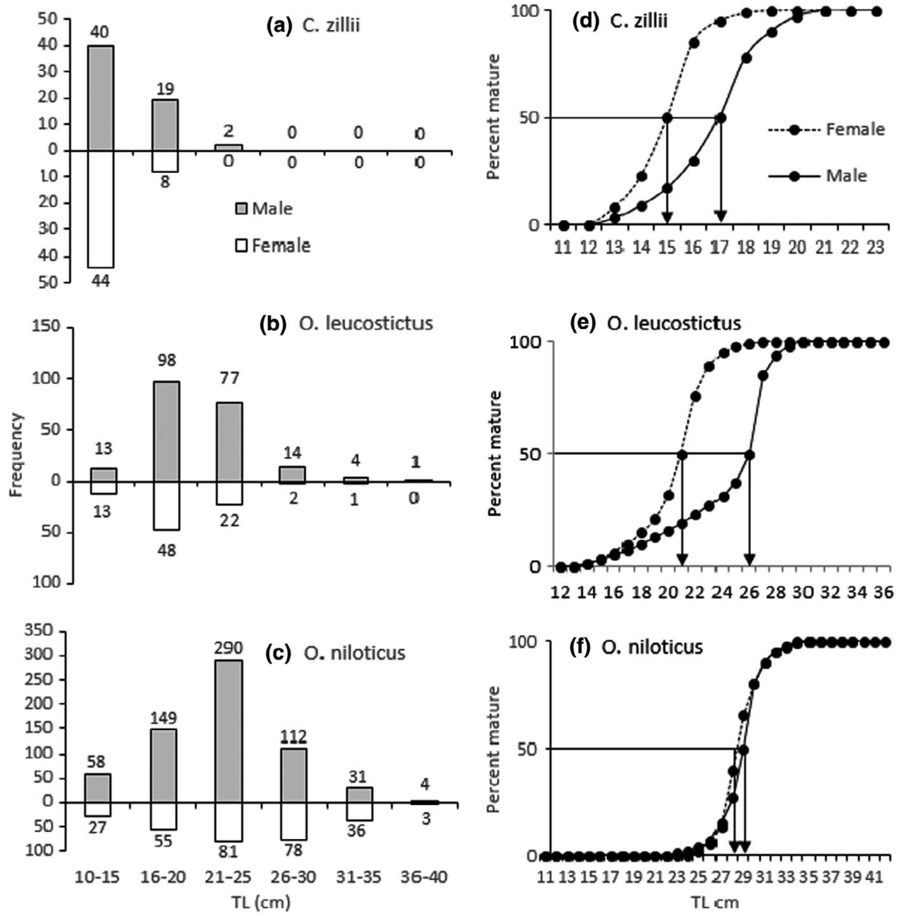

FIGURE 7 Length frequency distribution and size at first maturity of male and female *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* from Lake Naivasha, Kenya (numbers above frequency bars denote sample size; TL denotes total length)

TABLE 1 Sex ratio and length at first maturity (Lm_{50}) of male and female *Oreochromis niloticus*, *Oreochromis leucostictus* and *Coptodon zillii* from different lakes

Lake & period	Species	Male:female sex ratio	Lm_{50} males (TL, cm)	Lm_{50} females (TL, cm)	Source
Naivasha, 2018	*C. zillii*	1.15:1.0	17.0	15.0	Present study
Naivasha, 2016–2018	*C. zillii*	1.10:1.0	13.5	13.5	Keyombe et al. (2020)
Naivasha, 1974–1975	*O. leucostictus*	1.96:1.0	18.0	16.0	Siddiqui (1977)
Victoria	*O. leucostictus*		15.0	12.5	Witte and Winter (1995)
Albert	*O. leucostictus*		14.0	10.0	Lowe (1957)
George	*O. leucostictus*		26.0	26.0	Lowe (1957)
Naivasha, 2017	*O. leucostictus*	2.19:1.0	26.0	21.0	Laurent et al. (2020)
Naivasha, 2018	*O. leucostictus*	2.36:1.0	26.0	21.0	Present study
Victoria, 2014–2015	*O. niloticus*	1.20:1.0	31.0	26.0	Yongo et al. (2018)
Victoria, 2004–2005	*O. niloticus*		31.0	22.0	Njiru et al. (2008)
Victoria, 2000	*O. niloticus*		35.0	25.0	Njiru et al. (2008)
Victoria, 1998–2001	*O. niloticus*		30.0	33.0	Njiru et al. (2007)
Victoria, 1998–2000	*O. niloticus*	1.42:1.0	35.0	31.0	Njiru et al. (2006)
Victoria, 1998–2000	*O. niloticus*	1.49:1.0	34.0	31.0	Ojuok et al. (2000)
Naivasha, 2013–2014	*O. niloticus*	2.24:1.0	17.7	18.0	Outa et al. (2014)
Naivasha, 2017	*O. niloticus*	2.21:1.0	28.0	28.0	Waithaka et al. (2020)
Naivasha, 2018	*O. niloticus*	2.30:1.0	29.0	28.0	Present study

caught with a thinner diameter monofilament twine, compared to the same mesh size with thicker monofilament twine. Monofilament nets have been reported to catch slightly larger fish than multifilament nets (Naesje et al., 2007).

Typically, gillnet meshes that allow for the target species to attain length at first maturity can contribute towards maintaining sustainable fisheries. If the length at first maturity is correctly determined, and size at harvest is larger than the size at maturity, the stock and the fishing yield is more likely to be sustained (de Graaf et al., 2003; Froese, 2004), mainly because it gives individuals an opportunity to breed and add to the stock before being caught. Accordingly, meshes that target intermediate fish sizes, while leaving out juveniles and adults (mega spawners), could be more sustainable (Froese, 2004). Thus, gillnets with 4.0″ mesh and above, could be safely applied to the Lake Naivasha fishery. Nevertheless, in multispecies fisheries, no single mesh size suits all species, and any change could favour one species at the expense of another (Suuronen & Sardà, 2007). Based on the findings of the present study, *C. zillii* contributed only 8.5% to the total catch, meaning giving greater priority to the other two species (*O. niloticus* and *O. leucostictus*) would make sense from a socio-economic perspective. Gillnets of 2.5 and 3.5″ mesh exhibited the least catches for all the sampled species, therefore not being economically suitable for use in the fishery. Meshes 2 and 3″ in the present study resulted in high proportions of small, immature fish. These gears, if used for fishing in the littoral areas where most fish use as breeding and nursery grounds, might negatively impact juveniles and even spawners. To conclude, therefore, gillnets with ≥4.0″ mesh could safely be applied to the Lake Naivasha, whereas the use of smaller mesh should be controlled to protect the juveniles as a means of maintaining sustainable fisheries. Furthermore, the results of the present study provided useful information, including size at maturity data that is vital for determining appropriate mesh sizes to manage the lake fishery. To determine the mesh size that optimizes fish yield while, at the same time, maintaining a large proportion of spawning stock in the fishery, further research on gear selectivity and yield-and biomass-per recruit analysis is required, which should also benefit from the results of the present study.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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