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Spatial and temporal differences in life history parameters of *Rastrineobola argentea* (Pellegrin, 1904) in the Lake Victoria basin in relation to fishing intensity

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Abstract

The small pelagic cyprinid, *Rastrineobola argentea* (Pellegrin), commonly known as dagaa, accounted for 60% of the total fish biomass and 40% of the commercial catches in Lake Victoria in 2015. However, some aspects of the biology of species (from which management interventions are based) have changed since 1970s; and yet harvest regulations have remained the same. In this study, spatial and temporal variations in life history traits of dagaa in the northern portion of Lake Victoria were examined in relation to fishing intensity to offer guidance on possible adjustments in managing the fishery. The mean standard length halved, whilst the length at 50% maturity (Lm_{50}) reduced by 27%, between the 1970s and 2015; however, the decline in Lm_{50} was more pronounced in males than females. Data collected between 2014 and 2015 showed that immature individuals are largely harvested from inshore and mid-island areas, whilst most of the fishes caught in open water areas are largely mature irrespective of the size of the gear used. The causes of the changes in these biological aspects, and the need for policy adjustment, are discussed in the context of changes in fishing pressure.

KEYWORDS
biomass, dagaa, fishing gear, fishing ground, length at 50% maturity, overfishing

1 | INTRODUCTION

Lake Victoria, which is the largest tropical lake in the world (Fryer & Iles, 1972), with a surface area of 68,800 km^2, has historically supported one of the most diverse fish communities among the African Great Lakes. During the early 20th Century, the lake hosted a multi-species fishery dominated in biomass by >500 species of haplochromine cichlids (Kaufman, Chapman & Chapman, 1997; Witte & van Oijen, 1990; Witte et al., 1992) and large table fish (>20 cm total length), such as the endemic tilapiines (*Oreochromis variabilis* Boulenger and *O. esculentus* Graham), catfishes (*Clarias gariepinus* Burchell and *Bagrus docmak* Forsskål), marbled lungfish, *Protopterus aethiopicus* Heckel and Mormyrid species (Witte & van Densen, 1995). The large table fishes, especially the native tilapines, had shown signs of overfishing before 1950s, and non-native species, including the voracious predator, Nile perch, *Lates niloticus* (L.), were introduced in 1950s and 1960s to boost the commercial fishery (Ogutu-Ohwayo & Hecky, 1991). Dramatic changes were observed at the beginning of the 1980s, when the Nile perch population expanded, haplochromines in sub-littoral and offshore areas vanished, the remaining large native fishes declined, the lake became eutrophic and the fishery became dominated by three species; the two non-native species, Nile perch and Nile tilapia, *O. niloticus* (L.), and the pelagic cyprinid, *Rastrineobola argentea* (Pellegrin), commonly known as dagaa (Hecky, 1993; Ogutu-Ohwayo, 1990; Verschuren et al., 2002; Witte et al., 1992). These changes were largely attributed to

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predation by Nile perch (Ogutu-Ohwayo, 1990; Ogutu-Ohwayo & Hecky, 1991; Taabu-Munyaho, Marshall, Tomasson & Marteinsdottir, 2016; Witte et al., 1992), although other researchers suggest that climate variability and change played a more significant role in alteration of ecosystem factors that culminated into the changes (Hecky, Mugidde, Ramlal, Talbot & Kling, 2010; van Zwieten, Plank, Kolding, Seehausen & Law, 2016).

Despite the decline in overall biodiversity of the lake, the commercial fishery expanded in terms of total biomass, total landed catches and fishing effort. The fish biomass increased from about 700,000 t in 1970s (Kudhongania & Cordone, 1974) to about 2.6 million tonnes in 2011 (Taabu-Munyaho et al., 2016). Total landed catches increased tenfold from 100,000 t in 1980 to one million tonnes in 2010, whilst the number of fishers increased fivefold from about 40,000 to 200,000 over the same period (Kolding, Modesta & Mkumbo, 2014). Before 1993, Nile perch and Nile tilapia accounted for most of the landings. However, the stocks of these fishes were reduced due to intensive fishing (Balirwa et al., 2003; Mkumbo & Marshall, 2015; Taabu-Munyaho et al., 2016) and the catches were later dominated by dagaa.

In Lake Victoria, dagaa is the only native fish species that persisted and expanded into a dependable and sustainable fishery after the ecological transformation of the lake in 1980s. The dagaa fishery, which had been harvested (at the beginning of the 20th Century) from inshore areas using traditional papyrus seines and long cone-shaped basket traps mainly by women for domestic consumption (Graham, 1929; Okedi, 1981), was later exploited commercially by light fishing using traditional kerosene pressure lamps (Witte & van Densen, 1995), whilst other fishers started using catamaran technology from 1990s. The catches of dagaa expanded in three phases (1980–1990, 1991–2004 and 2006–2015) with the total catches doubling during every transition (Figure 1). Whereas fishing effort both in terms of number of fishers and fishing boats also doubled at every transition (Kolding et al., 2014), these high catches could only have been sustained by a proportional increase in biomass.

The biomass time series data of dagaa in Lake Victoria does not cover as many years as those of the catches; however, available data (1999–2015) show a positive relationship between catches and biomass. The biomass of dagaa doubled, similar to catches, from around 400,000 t during 1999–2004 to about one million tonnes during 2006–2011 (Figure 1). By 2015, the biomass of dagaa had approached 1.4 million tonnes, which suggests that the increase in catches was not a simple response to increased fishing effort, but also high standing stock. The increase in standing stock of dagaa has been attributed to competitive release following the decline in zooplanktivorous haplochromine cichlids in the 1980s (Sharpe, Langerhans, Low-Décaries & Chapman, 2015; Wanink & Witte, 2000), morphological adaptations such as increased number of gill filaments to withstand anoxia from eutrophication and decreased number of gill rakers to improve feeding efficiency on large prey in new habitats, and capacity to undergo vertical migrations to reduce predation risk by Nile perch and competition for food and space (Wanink, 1999; Wanink & Witte, 2000; van Zwieten et al., 2016).

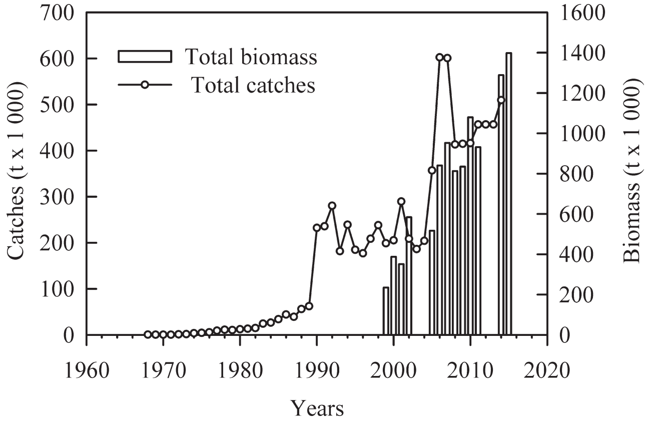

FIGURE 1 Variation of dagaa catches and biomass over time on Lake Victoria (Data adopted from Kolding et al., 2014; LVFO, 2015a)

Despite the growing biomass of dagaa, the life history characteristics of the species that directly affect exploitation and fishing behaviour of fishers, such as size (length) and length at maturity, decreased (Manyala & Ojuok, 2007; Sharpe, Wandera & Chapman, 2012; Wanink, 1998; Wanink & Witte, 2000). This was followed by a shift from large legal mesh sizes of 10 mm to smaller illegal mesh sizes between 3 and 8 mm (LVFO, 2005, 2016), with some fishers going to the extent of switching to domestic mosquito nets as small as 1-mm mesh, operated in the near-shore habitats. Fishing in the littoral habitats is known to be detrimental to fisheries given their importance as critical breeding and nursery grounds for dagaa and other larger commercial species (Balirwa et al., 2003; Manyala & Ojuok, 2007; Wandera, 2005a). These changes in fishing methods, in response to changes in the size of the fishery, have created conflicts between fishers and the resource managers. The legal mesh size of nets for harvesting dagaa on Lake Victoria, of 10 mm (FAO, 1994), was put in place before the changes in size of fish were evident.

To address the existing conflict, there is need for policies that accommodate the current changes in the dagaa fishery. Adjustment of existing policies for sustainable exploitation and management of dagaa fishery, amidst increasing biomass, however, requires an understanding of the biological aspects of the species that are used to set exploitation methods, especially mean length and length at maturity, and how these relate to existing management measures. In this study, data on how mean length, Lm_{50}, condition and fecundity of dagaa have changed are provided, and how these aspects vary in different habitats with varying levels of fishing intensity. Although this study is not meant to be exhaustive, available data are used to recommend policy adjustments that can facilitate sustainable exploitation and management of the dagaa fishery.

2 | METHODS

Fish biometric data (standard length, weight, sex, maturity status, fecundity) of dagaa were collected monthly using standard methods

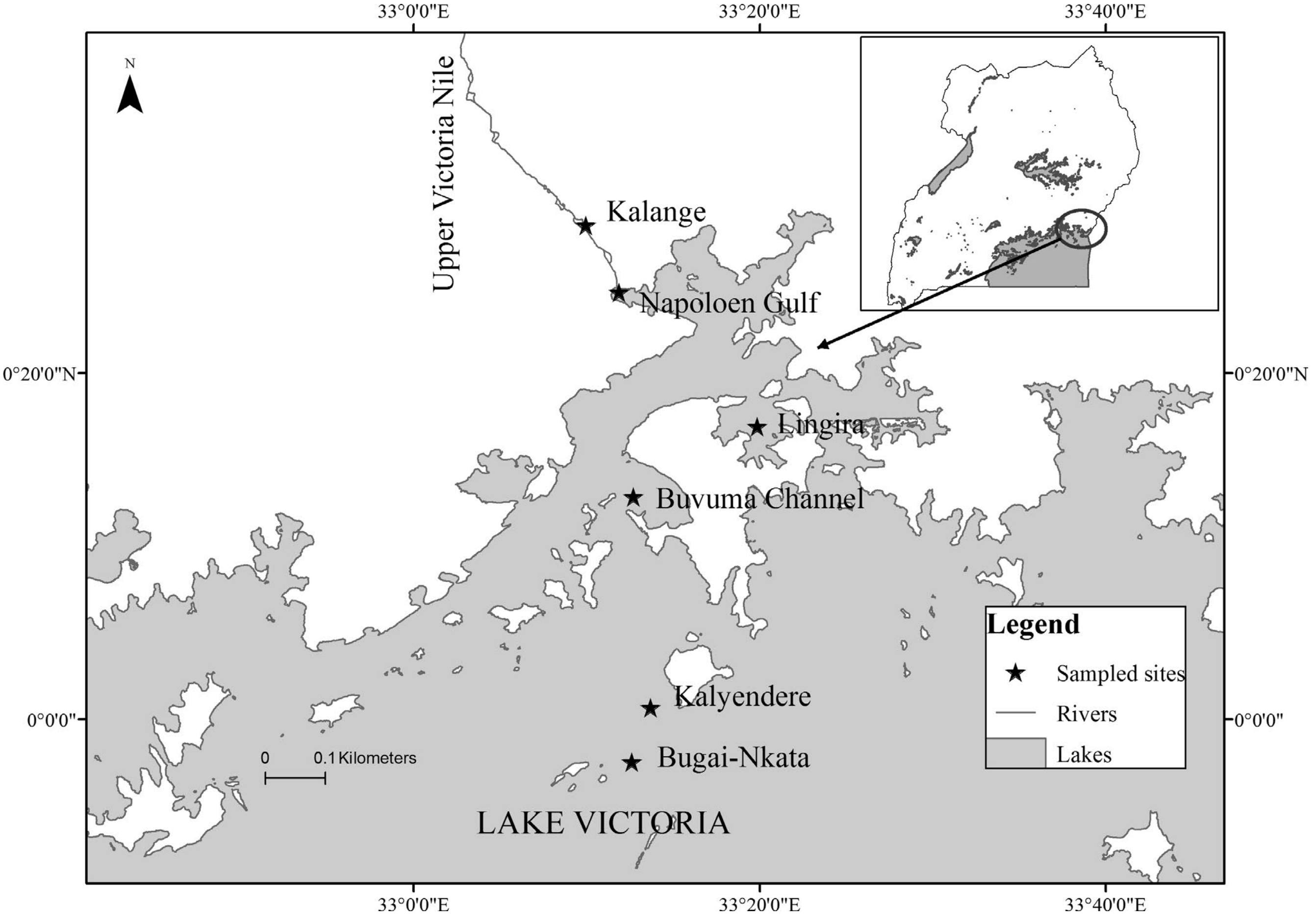

FIGURE 2 Location of sampling sites in the northern portion of Lake Victoria and Upper Victoria Nile

(LVFO, 2007) from August 2014 to February 2015 at different sites in the northern part of Lake Victoria and Upper Victoria Nile (UVN; Figure 2) using 5-mm mesh size nets, which are preferred by dagaa fishers. These data were compared with historical data collected between 1970 and 2010 from the archives of the National Fisheries Resources Research Institute (NaFIRRI).

Current data (2014–2015) were collected from four sites (Figure 2) comprising: Kalange located on UVN (<10 m deep), Napoleon Gulf (<20 m deep), Buvuma channel (20–40 m deep), and Bugaia-Nkata (>40 m deep). Unpublished Frame Survey data of 2014 showed Napoleon Gulf with 120 active fishing canoes whilst Buvuma channel had >200. However, in terms of the area available for fishing, which is larger for Buvuma channel than Napoleon Gulf, the former was considered to have low fishing pressure compared with the later. The deep open site of Bugaia-Nkata, which was less accessible to dagaa fishing due to long distance and high water turbulence, and Kalange, where commercial fishing for dagaa (<10 active fishing canoes) started after 2010, were also considered to have a low fishing intensity. It was hypothesised that biological aspects of dagaa would vary between the sites with varying fishing intensities, as judged by the number of active dagaa fishing canoes relative to fishing area.

Fish specimens were measured and grouped into 1-mm length classes and the percentage frequency in different length classes calculated. Length frequency distributions of dagaa in the four study sites, for the period 2014–2015, were generated to determine the mean length of the fish that was harvested in different sites. Mean lengths of dagaa from Napoleon Gulf, for which historical data (collected using 10-mm mesh size) were available, were also calculated and compared for the different time periods. The condition factor for the period 2014–2015 in Napoleon Gulf was calculated according to Le Cren (1951) and compared across years. The length at 50% maturity was determined by plotting the proportion of mature individuals against standard length and fitting a logistic regression curve (Sparre & Venema, 1998). Absolute fecundity was determined as the total number of ripe eggs in the left and right gonad of fish in stages V and VI. Relative fecundity, calculated as the total number of eggs per unit weight, (weight (g) calculated from the length-weight relationship equation obtained in this study), was compared across years to find out whether the reproductive potential of fish had changed. The proportion of mature dagaa retained by nets of 3, 5, 6, 8 and 10-mm mesh sizes was determined using experimental data collected previously from three sites of Napoleon Gulf (<20 m deep), Lingira (20–40 m deep),

TABLE 1 Mean standard length (SL), length at 50% maturity (Lm_{50}), condition factor (K), absolute (AF) and relative (RF) fecundity of dagaa in different habitats of Lake Victoria

Parameter	Napoleon Gulf	Buvuma channel	Bugaia-Nkata	UVN
Mean SL (±*SD*)	31.3 ± 6.5^a (*n* = 5,486)	32.0 ± 6.3^b (*n* = 5,117)	44.1 ± 3.4^c (*n* = 967)	33.2 ± 8.6^d (*n* = 4,689)
Lm_{50} (Males)	36 (*n* = 354)	35 (*n* = 560)	38 (*n* = 217)	36 (*n* = 575)
Lm_{50} (Females)	36 (*n* = 232)	35 (*n* = 605)	37 (*n* = 140)	37 (*n* = 488)
K (±*SD*)	0.95 ± 0.15^a (*n* = 3,184)	1.00 ± 0.10^a (*n* = 1,947)		0.93 ± 0.13^a (*n* = 2,271)
Mean AF (±*SD*)	554 ± 228^a (*n* = 16)	492 ± 86^b (*n* = 18)	482 ± 119^b (*n* = 27)	507 ± 133^b (*n* = 19)
Mean RF (g^{-1})	1,325 (*n* = 16)	1,253 (*n* = 18)		1,090 (*n* = 19)

Condition factor and relative fecundity were not determined for Bugaia-Nkata due to lack of data. Different letters in the same parameter in varying habitats indicate significant differences at $p < 0.05$.

and Kalyendere (>40 m deep) by LVFO in 2005 (June and July). These sites were comparable (in terms of depth) to the stations investigated in this study.

A one-way ANOVA was performed to test the effect of habitat on standard length and condition factor. Normal distribution and homogeneity of variance assumptions were checked using Normal Q-Q and residual plots as well as Levene's test, and in cases where one of the assumptions were violated, a Brown-Forsythe test was conducted on non-transformed data to avoid Type I error. Spatial differences in lengths at 50% maturity were investigated using a generalised linear model with maturity status (mature or immature) as a binomial response variable and fish length and site as predictor variables. Temporal variations in lengths at 50% maturity, on the other hand, were investigated by running Spearman's rank correlation between lengths at 50% maturity and year. Inter-site differences in absolute fecundity were compared by Analysis of covariance (ANCOVA) using absolute fecundity as dependent variable, site as fixed factor, and fish size as covariate. All tests were statistically significant at $p < 0.05$.

3 | RESULTS

Selected life history aspects of dagaa (mean standard length, length at 50% maturity, condition factor, and fecundity) in different habitats of Lake Victoria and UVN are presented in Table 1. Generally, these attributes were higher, with exception of absolute fecundity that was lowest, in Bugaia-Nkata than other sites. Post hoc analyses using the Games-Howell post hoc criterion for significance indicated that the mean standard length deferred significantly among all the sites ($p < 0.05$), although similar differences were not observed for condition factor ($p > 0.05$, Table 1). From the results of the generalised linear model, there was evidence that both habitat and size are significant predictors of maturity ($p < 0.05$). The predicted main effect of habitat on fecundity was significant, although there was also a significant interaction between habitat and size of fish. In terms of inter-site variations, absolute fecundity did not differ significantly between Buvuma channel, Upper Victoria Nile, and Bugaia-Nkata, but these three were significantly different from Napoleon Gulf, which had the highest fecundity (Table 1).

Mean standard length of dagaa in Napoleon Gulf halved between 1970s and 2015, whilst length at 50% maturity declined by 27% over the same period (Figure 3). There was a strong and significant negative correlation ($p < 0.05$, $r = -1$) between year and length at 50% maturity, although the decline in length at 50% maturity was not uniform for both males and females. The length at 50% maturity for females remained relatively stable at approximately 44 mm SL from 1970s through 1990s, after which it slightly declined to 40 mm SL in 2005 and 37 mm SL in 2015. By contrast, the length at 50% maturity for males declined steadily over the entire period. Despite a reduction in mean standard length and length at 50% maturity, the condition factor remained relatively stable at about 1 from 1960s through 2014–2015 (Table 2). Absolute fecundity decreased by almost fourfold, having declined from 2,282 ± 1,065 eggs in 1970s

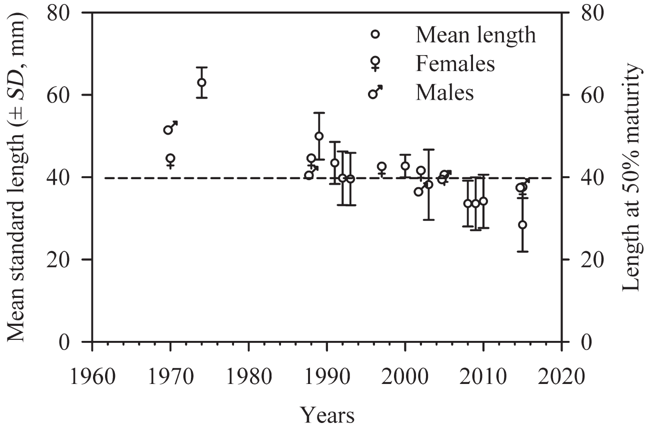

FIGURE 3 Changes in mean standard length (±*SD*, mm) of dagaa in Napoleon Gulf (Data for the period 1974–2010 adopted from NaFIRRI archives), and length at 50% maturity of dagaa in the Ugandan part of Lake Victoria (Data from Okedi, 1974; Wandera, 1992; NaFIRRI, 2005; Taabu-Munyaho, 2004) between 1974 and 2015. The horizontal dotted line indicates length at 50% maturity, which was used to set the minimum mesh size at 10 mm

TABLE 2 Changes in condition factor (±standard deviation) of dagaa in Napoleon Gulf between 1966 and 2015 (Data for 1966, 2009 and 2010 adopted from NaFIRRI, unpublished data)

Year	Condition factor	Sample size (*n*)
1966	1.02 ± 0.09	72
2009	0.92 ± 0.11	195
2010	0.97 ± 0.10	225
2015	0.95 ± 0.15	3,183

to 554 ± 228 eggs in fish of 40 ± 2 mm SL in 2015, whilst relative fecundity doubled from 611 to 1,325 eggs/g over the same period.

The proportion of immature dagaa harvested by different gear sizes varied across different habitats (Table 3). With the exception of Bugaia-Nkata and UVN, where the proportions of immature fish harvested by the 5-mm nets were 3% (low) and 39% (moderately low), respectively, in 2014–2015, >80% of dagaa harvested in other habitats were immature. However, comparison of data from samples retained by different gear sizes in 2005 showed that the 3, 5 and 6-mm mesh nets harvested higher proportions of immature fish in all the sites than the 8 and 10-mm mesh size nets.

4 | DISCUSSION

The study revealed that dagaa from the highly fished habitats (shallow inshore sites) were significantly smaller, and matured at smaller sizes, than those from the least fished habitats (deep open sites). These differences can be attributed to varying levels of fishing pressure between the habitats as manifested by the number of boats. This has also been suggested in previous studies for example Wandera (1992) and Taabu-Munyaho (2004) in the Ugandan part of Lake Victoria, Manyala and Ojuok (2007) in the Kenyan portion of Lake Victoria, Wanink (1998) in the Tanzanian part of Lake Victoria, and Sharpe et al. (2012) in lakes Victoria, Kyoga and Nabugabo. However, in shoaling pelagic species, such as dagaa, the populations are expected to be more or less the same size throughout the entire lake as they can move around the lake (Tumwebaze, Cowx, Ridgway, Getabu & MacLennan, 2007). The difference observed in this study where dagaa is larger in offshore sites than inshore areas, is therefore counter-intuitive, and suggests unexpected localised populations. This might be fully understood by examining the sizes of dagaa in deep open waters, where there is probably no fishing, but such sampling was not performed in this study.

Nonetheless, the effect of fishing pressure is also manifested in the temporal variations in mean length and length at 50% maturity of dagaa on Lake Victoria between 1970s and 2015. The number of small seines targeting dagaa increased more than threefold from 8,000 in 2004 to >22,000 nets in 2014 (LVFO, 2015b). Most of these were dominated by nets <6-mm mesh sizes, especially on the Ugandan portion of the lake, which harvest high proportions of immature individuals especially from the shallow inshore/littoral sites (example shown in Table 3) that are known breeding and nursery grounds for dagaa and other commercially important fish species such as Nile perch and Nile tilapia (Balirwa et al., 2003; Manyala & Ojuok, 2007; Taabu-Munyaho, 2004; Wandera, 2005a; Wanink, 1999).

It should be noted that, in addition to fishing pressure, previous studies attributed the changes in size structure of dagaa to predation by Nile perch, parasitism and environmental factors. For instance, Sharpe et al. (2012) attributed a reduction in mean size and length at 50% maturity of dagaa in lakes Victoria and Kyoga to an evolutionary response to selection imposed by fishing and/or Nile perch predation, whilst Tumwebaze (2003) and Wandera (2005b) showed that a cestode parasite, *Ligula intestinalis*, (L.) that impairs its reproductive organs, tends to target fish >40 mm in length resulting in majority of dagaa being small. In the Kenyan waters of the lake, Manyala and Ojuok (2007) showed a significant relationship between larval density of dagaa and electrical conductivity, ambient water temperature, Secchi depth, and dissolved oxygen. Whereas the changes in size and length at maturity of dagaa in Lake Victoria are consistent with the effects of intensive fishing, the effect of predation, parasitism and environmental factors cannot be ignored.

Despite a reduction in mean length and length at 50% maturity of dagaa on Lake Victoria, the condition factor of dagaa in the Napoleon Gulf remained relatively stable at about 1 between 1966 and 2015 indicating that the fish was in good condition. This could be due to the availability of the abundant food (zooplankton) in their environment (Mwebaza-Ndawula, 1994; Vincent, Makanga & Nachuha, 2012).

TABLE 3 Percentage proportion of immature dagaa retained by the 10, 8, 6, 5 and 3 mm lampara nets in the Napoleon Gulf (shallow inshore), Lingira (mid-island) and Kalyendere (deep open) waters of Lake Victoria, Uganda in 2005. Data for 2005 adopted from LVFO (2005)

Year/period	Gear size (mm)	Napoleon gulf	Lingira	Kalyendere	Buvuma channel	Bugaia-Nkata	Upper Victoria Nile
2014–15	5	89 (*N* = 5,486)			80 (*N* = 5,117)	3 (*N* = 967)	39 (*N* = 4,689)
2005	3	77 (*N* = 4,585)	60 (*N* = 2,590)	59 (*N* = 3,407)			
	5	75 (*N* = 4,729)	38 (*N* = 3,475)	51 (*N* = 3,629)			
	6	60 (*N* = 4,276)	39 (*N* = 2,526)	52 (*N* = 3,078)			
	8	19 (*N* = 3,029)	60 (*N* = 2,590)	24 (*N* = 4,220)			
	10	28 (*N* = 1,944)	24 (*N* = 2,035)	13 (*N* = 3,456)			

The spatial variation in fecundity of dagaa observed in this study can be attributed to the size differences in different habitats. Sharpe et al. (2012) attributed a shift in the reproductive effort of dagaa in Lake Victoria to an evolutionary response to selection for increased reproductive investment, resulting from increased per capita food availability. In this study, smaller dagaa (found in highly fished sites) produced more eggs (which are small in size) than big ones, and this may reflect a strategy that ensures their survival in a stressful environment. Similar trends have been observed in Nyanza Gulf (with high fishing intensity) and Mwanza Gulf (low fishing intensity) (Manyala, Nyawade & Rabuor, 1992).

The spatial and temporal shifts in mean standard length and length at 50% maturity of dagaa are attributed, principally, to localised fishing pressure and gears. These changes have implications for long-term sustainability of dagaa fishery on Lake Victoria. The 8 and 10-mm mesh nets harvested high proportions of mature dagaa, nets of 5 and 6-mm mesh retained some mature fish when operated in the open waters whilst dagaa harvested in all habitats using the 3-mm mesh nets were immature. It is recommended that the minimum mesh size for harvesting dagaa should be adjusted from 10 to 8 mm. The restriction of fishing for dagaa within a distance of 2 km from the shoreline should be enforced to avoid harvesting juveniles and distressing fish breeding and nursery grounds.

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