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Some aspects of the biology and life-history strategies of *Oreochromis variabilis* (Boulenger 1906) in the Lake Victoria Basin

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Abstract

Oreochromis variabilis (Boulenger), a fish species endemic to Lake Victoria, was abundant, forming an important component of the indigenous fisheries stocks before and up to the late-1950s. Catches declined drastically thereafter, and only sporadic catches are currently found in Lake Victoria. Remnants population of the species, however, are found in several small waterbodies (SWBs) within the lake basin. The life-history characteristics of *O. variabilis* in Lake Victoria, including, sex ratio, reproduction and length–weight relationship, were compared to those in selected three SWBs in the lake basin. Fish samples were collected by monofilament gillnets of 30–255 mm between 2001 and 2005. Males predominated over females from all the sampled sites (sex ratio 1.00:0.33). Length at first maturity (Lm_{50}) had mean (±SE) of 18.48 ± 1.50 cm TL for males, and 16.87 ± 0.95 cm TL for females, and did not exhibit any significant differences between habitats. Fecundity ranged between 73 and 14 800 eggs for fish of 13.5–18.6 cm TL, respectively. Absolute fecundity of *O. variabilis* was proportional to the body weight, but nearly proportional to the cube of the fish length. Egg diameter varied from 0.3 to 5.19 mm, with a mean (±SE) of 3.44 ± 0.08 mm. Growth was allometric in both male and female, being significantly different from the expected value of 3 ($P < 0.05$). The life-history strategy of *O. variabilis* is discussed within the context of changes in the lake and the SWBs.

Key words

endemic, Kenya, Lake Victoria, length–weight relationship, reproduction, sex ratio.

INTRODUCTION

Oreochromis variabilis (Boulenger) is an indigenous fish species of Lake Victoria and its affluent rivers, Kwania, Salisbury, Lake Nabugabo, Lakes Kyoga and Victoria Nile above Murchinson Falls (Trewavas 1983). The species exists mainly in waters <10 m deep and that has partly exposed shores (Kudhogania & Cordone 1974). This species, together with the native *Oreochromis esculentus* (Graham), provided a lucrative Lake Victoria shoreline fishery before and during the early-1960s (Fryer & Iles 1972; Ogutu-Ohwayo 1990). This species has since, however, become a rarity, with the decline in its stocks attributed to such factors as environmental degradation, competition and predation by introduced non-native species. The water quality of Lake Victoria also has deteriorated over the years because of increased nutrient loads leading to increased lake eutrophication (Lung'ayia *et al.* 2000). Eutrophication favours the proliferation of blue-green algae, which have replaced diatoms as the preferred diet of *O. variabilis* (Lung'ayia *et al.* 2000). To increase the declining fish catches in the 1960s, *Oreochromis niloticus* (L), *Oreochromis leucostictus* (Trewavas), *Tilapia rendalii* Boulenger and *Tilapia zillii* (Gervais) were introduced into the lake fishery (Ogutu-Ohwayo 1990). Introduced *Oreochromis niloticus* are competitively superior and have gradually replaced *O. variabilis* (Fryer & Iles 1972; Njiru *et al.* 2005). Predation by introduced Nile perch, *Lates niloticus* (L) (Ogutu-Ohwayo 1990), and indiscriminate fishing have further suppressed the species population (Cowx *et al.* 2003). Currently, *O. variabilis* rarely appears in fish catches in Lake Victoria (Witte *et al.* 1992; Njiru *et al.* 2010). The species is endangered, resulting in its being listed in the World Conservation Union Red Book of

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endangered species (Maithya 1998, 2008). Remnants of *O. variabilis* are found in several isolated small waterbodies (SWBs) within the Lake Victoria basin, however, where they were stocked during the early-1920s (Maithya 1998, 2008).

Knowledge of the life-history strategies of fishes is important for predicting the performance of a fish stock (Bagenal 1978; Cowx *et al.* 2003; Njiru *et al.* 2006). Aspects of the biology and ecology can be used for the conservation and propagation of specific fish species. To this end, there is little knowledge of the biology and ecology of the existing stocks of *O. variabilis* in Lake Victoria and the small waterbodies in its environs. Accordingly, this study investigated the sex ratio, size at first maturity, fecundity, egg diameter and length–weight relationships of the species in the Lake Victoria basin. These aspects of life history will be important in formulating stock mitigation and conservation programmes for this endangered fish species.

METHODS

Study area

The research sites of this study included the Oele Beach area of Lake Victoria (Kenya side) and three SWBs within its basin (Fig. 1). The locations of the sites were: Oele Beach [00°03′55″N; 034°08′13″E, 1138 m a.s.l.], Kalenyjuok Dam [00°04′23″N; 034°13′11″E, 1187 m a.s.l.], Komondi Dam [01°07′33″S; 034°26′12″E, 1406 m a.s.l.] and Mamboleo Dam [00°42′47″S; 035°02′46.1″E, 1842 m a.s.l.]. The maximum surface area and depth for Oele, Kalenyjuok, Komondi and Mamboleo dams were 1.5×5.3 m^2, 5.92 m; 340×118 m^2, 3.10 m; 345×182 m^2, 3.90 m; and 483×132 m^2, 3.5 m, respectively.

A reconnaissance survey was conducted prior to commencement of this study to characterize the refugia habitats. During the characterization exercise, Oele Beach was the only region of Lake Victoria harbouring stocks of *O. variabilis* that could provide representative samples

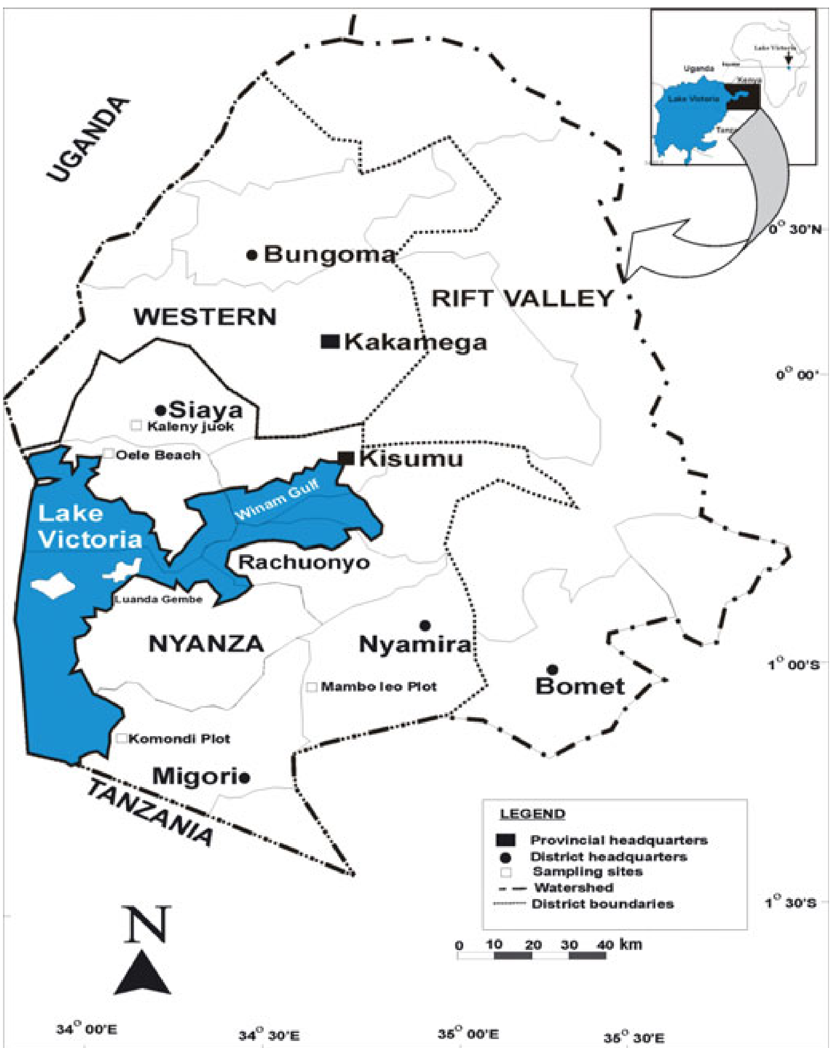

Fig. 1. Map of Lake Victoria basin, Kenya, showing study sites.

for the study. The dams were selected on the basis of the presence of *O. variabilis*.

Sampling procedure

Fish samples were collected between 2001 and 2005, using monofilament gillnets of mesh sizes 30–255 mm nominal bar length. Three sets of nets were used in each treatment, each set comprising 10 nets of mesh sizes 30, 38, 48, 60, 77, 97, 124, 157, 199 and 255 mm. Fish sampling was conducted by creating 20 × 30 m random fishing transects in a randomized complete block design. Nets were set twice during daylight between 0800–1000 and 1400–1600 h. After retrieval from the nets, the total length (TL) of each *O. variabilis* was measured to the nearest 0.1 cm from the most anterior part of the head (with the mouth closed) to the farthest tip of the caudal fin, using a measuring board. The total wet weight was measured to the nearest 0.1 g with an electronic weighing balance (Scanvaegt Salter, model 323; Avery Weigh-Tronx Ltd, West Midlands, UK).

Fish were then dissected and sexed. Sex ratios were determined for only those fish whose gonads were identifiable as male and female. The sex ratio, expressed as male/female, was analysed by refugia area, and by 1 cm length classes, with deviations from the 1:1 null hypothesis tested with the use of chi-square test. The fish maturity status was assigned as stage I to VI, according to the method described by Witte and van Densen (1995). To determine the minimum size of fish at first maturity, females and males were grouped separately into 1 cm size-classes. Fish in maturity stage I, II and III were considered immature, while those in stage IV, V and VI were considered mature for the purpose of calculating the size at first maturity (Lm_{50}). The length at first maturity (Lm_{50}) in this study was defined as the mean length at which gonadal development had advanced to at least stage IV in 50% of individuals. The length at which 50% of individuals were fully mature was estimated by fitting frequency data of mature individuals by length class to a logistic curve using the least-square method (Sparre & Venema 1998). Estimates were compared using a *t*-test (Zar 1999).

The number of ripe eggs was taken as absolute fecundity (Bagenal 1978), while all other eggs, together with ripe ones, were used to determine the intra-ovarian oocyte size distribution. The size frequency distribution of intra-ovarian oocytes was calculated by measuring the diameter of 100 randomly selected ripe and developing eggs per female fish from preserved ovaries (Ekanem 2000). The measurement of egg diameter was taken with a calibrated eyepiece micrometer inserted on a compound microscope. Egg diameter was estimated by measuring the length and width of each egg to the nearest 0.1 nm. Estimates were compared using ANOVA, while the homogeneity of eggs was compared using coefficient of variation. The two measurements were added, and their sum divided by two. The result was then multiplied by 100 to convert nanometers to millimeters. All statistical test interpretations were at 95% confidence level.

The length–weight relationship was expressed as $\log_{10} W = \log_{10} a + b \log_{10} \mathrm{TL}$, where W = individual fish specimen wet weight (g); TL = total length (cm); a = intercept; and b = slope of the regression line. Fecundity–length and fecundity–weight relationships of *O. variabilis* from different refugia habitats were obtained after the log-transformation of individual mass data of these parameters, using the method of Witte and van Densen (1995). Analysis of covariance (ANCOVA) was used to compare the slopes between the habitats, and the Student-Newman test (SNK) was used to evaluate which slopes were significantly different (Zar 1999).

RESULTS

Sex ratios

Males were more abundant than females at all the sampled sites (Table 1). Kalenjouk Dam recorded the highest number of males and females, while the lowest number of males and females were recorded at Komondi and Mamboleo Dams, respectively. The sex ratio of the stocks was significantly different from 1:1 (χ^2 = 274.25). The highest number of males and females was found in the following class size: 12–20 cm TL, 16–24 cm TL, 12–22 cm TL and 12–20 cm TL at Mamboleo, Komondi, Kalenyjouk Dams and Lake Victoria, respectively. The total numbers of males were significantly different in most class sizes (Table 1).

Size at maturity

The distribution of ripe males and females in the sampled waterbodies is presented in Fig. 2. The smallest ripe female *O. variabilis* was 12.5 cm TL from Kalenyjuok Dam, while the smallest ripe male was 13.0 cm TL found in stocks from both Kalenyjuok Dam and Lake Victoria. The largest ripe male and female of 29.0 cm TL and 25.6 cm TL, respectively, were from Mamboleo Dam. The overall mean (±SE) size at maturity (Lm_{50}) size was 16.87 ± 0.95 cm TL for females, and 18.48 ± 1.50 cm TL for males. A *t*-test revealed no significant variations in size at first maturity between males and females ($P < 0.05$), although females had a much smaller size at Lm_{50} than males.

Table 1. Ratio of male (M) to female (F) *O. variabilis* in Lake Victoria and several small waterbodies (SWBs)

	Site											
	Mamboleo Dam			Komondi Dam			Kalenyjouk Dam			Lake Victoria		
Class size (cm)	M	F	χ^2	M	F	χ^2	M	F	χ^2	M	F	χ^2
4–6	4	0	4.00*	0	0	0.00	0	0	0.00	0	0	0.00
6–8	2	1	0.33	0	0	0.00	0	0	0.00	5	4	0.11
8–10	5	1	2.67	0	0	0.00	2	2	0.00	9	6	0.60
10–12	6	0	6.00*	1	0	1.00	4	1	1.80	4	2	0.67
12–14	30	8	12.74*	4	0	4.00*	65	28	14.72*	41	13	14.52*
14–16	30	6	16.00*	17	7	4.17*	51	27	7.38*	39	16	9.62*
16–18	29	4	18.94*	43	16	12.36*	78	32	19.24*	29	12	7.05*
18–20	34	13	9.38*	33	11	11.00*	71	23	24.51*	26	2	20.57*
20–22	24	2	18.62*	25	9	7.53*	22	11	3.67	7	0	7.00*
22–24	8	2	3.60*	27	6	13.36*	0	0	0.00	0	0	0.00
24–26	22	1	19.17*	1	0	1.00	2	2	0.00	0	0	0.00
26–28	13	1	10.29*	2	0	2.00	0	0	0.00	0	0	0.00
28–30	1	0	1.00	0	0	0.00	0	0	0.00	0	0	0.00
Total	208	39	115.63*	153	49	53.54*	295	126	66.89*	160	55	51.28*

*Indicates a significant difference between male and female ratios.

Fecundity

Absolute fecundity varied from 73 to 14 880 eggs (Table 2). Lake Victoria stocks were the most fecund, with a mean (±SD) of 3780.05 ± 2865.00 eggs, while Mamboleo Dam stocks, with a mean of 396.05 ± 234.40 eggs, were the least fecund. Stocks from Komondi Dam and Kalenyjouk Dam recorded a mean of 798.65 ± 211.47 and 624.93 ± 194.26 eggs, respectively. Fecundity–length and fecundity–weight relationships of *O. variabilis* from different habitats are presented in Table 3. One-factor ANOVA revealed significant differences in fecundity among gravid fish stocks from the sampled sites ($P < 0.05$). Fecundity of *O. variabilis* was proportional to the body weight, but nearly proportional to the cube of the fish length (Table 3).

Egg diameter

Egg diameters were found to vary from 0.30 mm in the Lake Victoria habitat to 5.19 mm in Kalenyjouk Dam (Fig. 3). The largest egg did not belong to the biggest fish, nor was the smallest egg found in the smallest fish. The majority of the eggs from Lake Victoria, and Mamboleo and Kamondi Dams varied between 0.65 and 2.04 mm in diameter, while those in Kalenyjouk Dam had a size range of 2.05–3.79 mm (Fig. 3). The mean diameter of eggs from Komondi Dam, Lake Victoria and Kalenjouk Dam was not significantly different. Fish stocks in Kalenyjouk Dam had larger egg sizes significantly different from those of other habitats ($P < 0.05$). Eggs from Kalenyjouk Dam also exhibited a higher homogeneity in egg size (Coefficient of variation = 34.04%), compared to the other waterbodies. Eggs from Lake Victoria had a higher heterogeneity in diameter (CV = 72.99%), compared to eggs from other waterbodies.

Length–weight relationship

The weight–length relationship for *O. variabilis* from the habitats is summarized in Table 4. The highest male and female b coefficient was from fish in Lake Victoria and Kalenjouk Dam, while the lowest was from fish from Komondi Dam and Lake Victoria. Overall, the *O. variabilis* growth patterns in the Kalenyjuok Dam exhibited a better b coefficient than the other waterbodies. The *O. variabilis* stocks in all the habitats exhibited a slight negative allometric growth ($b < 3$) of the stocks in all habitats. There was significant difference ($P < 0.05$) between the regression slopes of the fish stocks from Lake Victoria and Kalenyjuok Dam, compared to Kamondi and Mamboleo Dams, in terms of length and weight (Table 4).

DISCUSSION

Catches were dominated by males, possibly attributable to differential migration of sexes (Rinne & Wanjala 1982;

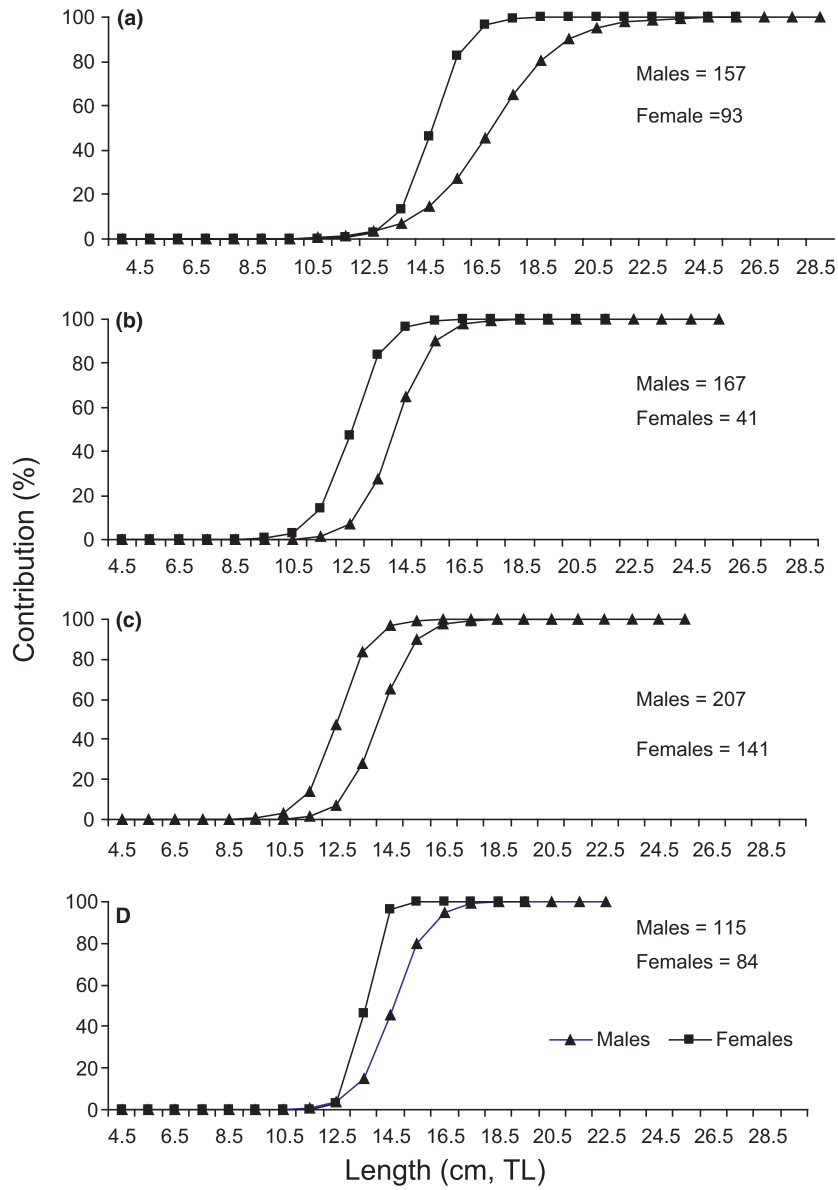

Fig. 2. Maturity ogives for *O. variabilis* in Lake Victoria basin (a = Mamboleo Dam; b = Komondi Dam; c = Kalenyjouk Dam; d = Oele beach, Lake Victoria).

Table 2. Fecundity of *Oreochromis variabilis* from Lake Victoria basin (F_{min} and F_{max} = minimum and maximum fecundity, respectively; L_{min} and L_{max}, = minimum and maximum length, respectively; W_{min} and W_{max} = minimum and maximum weight, respectively, recorded for fecund individuals)

Habitat	F_{min}	F_{max}	L_{min} cm TL	L_{max}, cm TL	W_{min} (g)	W_{max} (g)
Lake Victoria	1192	14 880	13.5	18.6	45	135
Kalenyjuok Dam	98	1846	12.5	24.5	38	295
Komondi Dam	105	1207	13.0	20.5	40	160
Mamboleo Dam	73	942	13.5	25.6	40	237

Njiru *et al.* 2006). Tilapia males establish nesting arenas in the shallow waters, aggregating there during the spawning period. In contrast, females visit the arena to spawn, but leave quickly and disperse thereafter. Consequently, the fishing methods used for the nesting areas could have resulted in the catch being biased towards males. Balirwa (1998) considering *O. niloticus* caught by gill nets in Lake Victoria found different habitats to favour one sex over the other. Vegetated habitats (*Cyperus papyrus*), for example, had a higher proportion of males. Most of habitats in this study were shallow (3–6 m) and had high vegetation cover, possibly contributing to the bias in sex ratios. Further, the faster

Table 3. Relationships between fecundity (*F*), total length (L) and body weight (W) of *O. variabilis* in habitats within Lake Victoria basin (values with same superscripts indicate no significant differences in fecundity)

Habitat	Relationship	Sample size (*n*)	r^2
Lake Victoria	$F = 0.068\ L^{3.893a}$	20	0.68
	$F = 9.594\ W^{1.311d}$	20	0.72
Kalenyjuok Dam	$F = 0.024\ L^{3.534a}$	58	0.79
	$F = 2.873\ W^{1.169d}$	58	0.81
Komondi Dam	$F = 0.169\ L^{2.915b}$	32	0.64
	$F = 9.384\ W^{0.934e}$	32	0.64
Mamboleo Dam	$F = 0.041\ L^{3.145b}$	20	0.69
	$F = 2.704\ W^{1.0776e}$	20	0.68

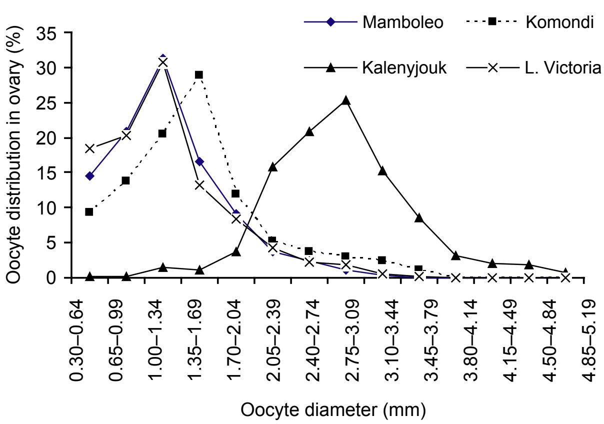

Fig. 3. Intra-ovarian oocyte distribution in *O. variabilis* from Lake Victoria basin.

Table 4. Correlation between log TL (cm) and log W (g) of *O. variabilis* stocks in refugia habitats of the Lake Victoria basin (similar superscripts letters indicate no significant difference)

Habitat	Weight-length relationship	Sample size (*n*)	r^2
Lake Victoria	Male[a]: $\log W = 2.95 \log TL$-0.03	115	0.98
	Female[b]: $\log W = 2.77 \log TL$-0.02	84	0.84
Kalenyjuok Dam	Male[a]: $\log W = 2.92 \log TL$-0.02	207	0.91
	Female[a]: $\log W = 2.97 \log TL$-0.02	141	0.93
Komondi Dam	Male[c]: $\log W = 2.67 \log TL$-0.03	153	0.96
	Female[a]: $\log W = 2.91 \log TL$-0.02	81	0.96
Mamboleo Dam	Male[d]: $\log W = 2.74 \log TL$-0.04	167	0.95
	Female[e]: $\log W = 2.81 \log TL$-0.03	41	0.98

growth rate of males, and higher mortality of females (Trewavas 1983), might mean the male *O. variablis* reach bigger sizes and survive longer.

There were no significant variations in size at first maturity between the males and females of *O. variabilis* in the different refugia, although females exhibited a much smaller size at fifty percent maturity (Lm_{50}) than males. Females invest more energy on gonadal development, compared to somatic growth, resulting in their maturing at smaller sizes (Bagenal 1978). Fecundity, and therefore brood size, of *O. variabilis* was found to be higher than that reported by Lowe-McConnell (1955). Lowe-McConnell (1955) reported *O. variabilis* fecundity in Lake Victoria to range between 323 and 547 eggs. This study found absolute fecundity to vary between 73 and 14 880 eggs, with Lake Victoria stocks exhibiting the highest mean (3780.05 ± 2865.00 eggs), and the lowest egg diameter (0.3 mm). The high number and smaller-sized eggs of *O. variabilis* from Lake Victoria stocks could be an ecological adaptation to survive in its changing environment. Lake Victoria water quality, for example, has deteriorated, with diatoms, the major food for *O. variabilis*, having shifted to unpalatable blue-green algae (Lung'ayia *et al.* 2000; Maithya 2008). The fishing pressure also has increased (Njiru *et al.* 2010), and the introduction of *O. niloticus* and predatory Nile perch have changed the trophic dynamics of the lake (Ogutu-Ohwayo 1990; Balirwa 1998; Njiru *et al.* 2010). Similar tactical changes were observed for *O. niloticus* in Lake Victoria that grew faster, was more fecund and attained maturity at lower sizes than previously reported (Balirwa 1998; Njiru *et al.* 2006).

Kalenyjouk Dam stocks were less fecund and had bigger-sized eggs, compared to Lake Victoria stocks within the same altitude range. This might be attributed to fishing and physical factors in the two habitats. There is little fishing in Kalenjuok Dam, with its waters being surrounded by thick macrophytes fringes, probably providing more feeding, breeding and nursery grounds. Further, studies by Maithya (2008) found a higher diatom concentration in Kalenyjouk Dam than Lake Victoria. Diatoms are the preferred food of *O. variabilis* (Fryer 1961). Larger eggs enhanced fry and larval viability (Hulata *et al.* 1974; Bagenal 1978). Thus, it can be argued that eggs produced by *O. variabilis* stocks from the Kalenyjouk Dam are superior, and of better quality than those in Lake Victoria, where the fish is endemic. Thus, the waterbody could be a better repository for obtaining broodstock for the propagation of the species.

This study also established that fecundity is proportional to fish size, when length is considered, but not so when weight is considered, confirming the findings of Bagenal (1978) on *Tilapia* species and other freshwater fishes. In the exponential formula linking fecundity to TL, the exponent (slope-*b*) numerical value obtained was between 2.91 and 3.90, which is within the range of 2.3–5.3 calculated for a variety of warm water fishes by Bagenal (1978). The *O. variabilis* stocks exhibited a slight negative allometric growth (growth that does not comply to cube rule), as opposite to isometric growth (LeCren 1951). For the length–weight relationship, all the slopes ranged from 2.67 to 2.97, all being below the expected value of 3 for isometric growth. The stocks of Kalenyjuok Dam exhibited higher *b* coefficients, probably indicating better living conditions, which might be attributed to less fishing pressures and the availability of a better diet. Similar exponents could suggest the fish are of the same stocks. Although no values are available for direct comparison, the length–weight relationship derived from this study could form the basis for the future work on this species. According to Tesch (1971), the slope is often nearly constant throughout the year, or throughout a series of different environments for the same species. In contrast, the intercepts vary seasonally and between habitats. Thus, the slope provides a more objective method for the analysis of growth and production in fishes.

In conclusion, there is evidence to suggest that *O. variabilis* in the different habitats of Lake Victoria basin displays different life-history strategies as a means of surviving the changing environment of the habitats. The strategy seems to exploit variations in the quality of habitats to enhance juvenile survival and growth (Winemiller 1989). Winemiller (1989), for example, found that females from environments with greater threats of predation for adult guppies matured at smaller size, had shorter interbrood intervals and allocated larger fractions of tissue to reproduction. The endemic stocks of Lake Victoria seem to have adapted more to the changes than those in the introduced SWBs. The more intensive reproduction effort employed by females fits the theories of life-history strategy as expounded by Pianka (1970) and Stearns (1976), wherein natural selection has caused different fish forms to adapt to maximize their fitness specific to each environment. This could also be a mechanism to compensate for the intensive fishing pressure and changes in environmental conditions in the habitats.

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