Some biological aspects and life history strategies of Nile tilapia *Oreochromis niloticus* (L.) in Lake Victoria, Kenya

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Abstract

The life history characteristics of introduced Nile tilapia (*Oreochromis niloticus* L.) in Lake Victoria, including, sex ratio, fecundity, reproduction, weight-length relationship and body condition were studied and compared with those of other populations. Samples were collected by trawling and seining in the Kenyan sector of Lake Victoria between June 1998 and December 2000. Males predominated over females (sex ratio 1.42 : 1 : 00). *O. niloticus* spawned throughout the year but with a peak between December and June. Length at first maturity was (mean ± SD) 30.81 ± 0.09 for females and 34.5 ± 6 0.48 for males. There was little seasonal variation in relative condition, which ranged from 0.92 to 1.05 in males and 0.94 to 1.07 in females. Gonadosomatic index (GSI) was low during the postspawning period (July to October) and high during the protracted breeding period (December and June). Fecundity ranged from 905 to 7619 oocytes for fish of 28 to 51 cm total length (TL) respectively. The relationships between fecundity *(F)* and total length (*L*), weight (*W*) and ovary weight (OW) were: $F = 8.159L^{1.53}$, $F = 96.269W^{0.4504}$, $F = 1806 + 39.4OW$. The slope *b* of the weight-length relationship was 3.08–3.32 for males and 3.07–3.22 for females. Growth was allometric in both cases and was significantly different from the expected value of 3. The life history strategy of *O. niloticus* is discussed in context of environmental changes occurring in the lake.

Key words: condition, fecundity, introduction, overexploitation, weight-length

Résumé

Les caractéristiques de l'histoire de vie du tilapia du Nil (*Oreochromis niloticus* L.) introduit dans le lac Victoria, y compris la proportion des deux sexes, la fécondité, la reproduction, le rapport masse/longueur et la condition du corps furent étudiés et comparés à celles d'autres populations. Des échantillons furent pris par le chalutage et la pêche à la seine dans la partie kenyane du lac Victoria entre juin 1998 et décembre 2000. Les mâles prédominèrent sur les femelles (un sex-ratio de 1.42:1.00). La période de frai dura toute l'année, culminant entre les mois de décembre et juin. La longueur à la première maturité fut (en moyenne ± SD) 30.81 ± 0.09 pour les femelles et 34.5 ± 6 0.48 pour les mâles. Il y avait peu de fluctuation saisonnière dans la condition relative, qui allait de 0.92 à 1.05 chez les mâles et de 0.94 à 1.07 chez les femelles. L'indice gonadosomatique (GSI) fut bas dans la période après le frai (de juillet à octobre) et élevé dans la période de frai prolongée (de décembre à juin). La fécondité allait de 905 à 7619 oocytes pour les poissons de 28 à 51 cm TL respectivement. Le rapport entre la fécondité (F), la longueur totale (L), masse corporelle (W) et masse des ovaires (OW) fut: $F = 8.159L^{1.53}$, $F = 96.269W^{0.4504}$, $F = 1806 + 39.4OW$. Le gradient *b* du rapport masse/longueur fut 3.08–3.32 chez les mâles et 3.07–3.22 chez les femelles. La croissance fut allométrique dans les deux cas, et différa énormément de la valeur attendue de 3. La stratégie de l'histoire de vie de *O. niloticus* est ici traité dans le contexte de changements environnementaux qui se produisent dans le lac.

Introduction

The herbivorous tilapiine, the Nile tilapia, *Oreochromis niloticus* (L.) was introduced into Lake Victoria in the

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1950s and 1960s to boost the then declining fishery (Welcomme, 1967; Ogutu-Ohwayo, 1990). The native tilapiines of 1950s and 1960s were *Oreochromis esculentus* (Graham) and *Oreochromis variabilis* (Boulenger). Nile tilapia is now the commercially most important tilapiine in Lake Victoria and the third most important fishery in Lake Victoria, after Nile perch, *Lates niloticus* (L.) and a native cyprinid, *Rastrineobola argentea* (Pellegrin) (Witte & Van densen, 1995, Cowx *et al.*, 2003). Among the commercially important fish species of the lake, tilapia is the most desired by the lake community. The increase in importance of *O. niloticus* is attributed to overfishing of endemic tilapiines, thus reducing competition, while swamp clearance could have increased its spawning areas (Ogutu-Ohwayo, 1990; Balirwa, 1998). Nile tilapia can also survive a wide range of pH, resists low levels of dissolved oxygen and feeds on a variety of food items (Balirwa, 1998; Njiru *et al.*, 2002, 2004).

Knowledge of the life history strategies of fishes is essential for predicting population stability and fluctuations. Information on reproduction can also be used in to design fisheries management measures such as closed fish areas or seasons. For fish like Nile tilapia such knowledge is particularly important because of the species' dependency on shallow, nearshore areas. Aspects of biology and ecology of tilapia have been investigated in the past (review Lowe-McConnell, 1955, 1958; Welcomme, 1967; Lung'aiya, 1994; Balirwa, 1998; Njiru *et al.*, 2004), but here we present information on sex ratios, reproduction, fecundity, weight–length relationships and body condition for comparison with data from populations in its native habitats.

Materials and methods

Study area

The Kenyan part of Lake Victoria encompasses 6% of the lake area (68,000 km^2), and comprises the semi-enclosed Nyanza Gulf and part of the main lake (Fig. 1). The Gulf which constitutes the major part of the lake in Kenyan waters is shallow with an average depth of 6–8 m, and lies within the equatorial region between 34°13′ and 34°52′ east and 0°4′ and 0°32′ south of the equator. The main geographical, hydrological and physical characteristics of Lake Victoria were summarized by Bootsma & Hecky (1993) and Crul (1995). The Kenyan part has several inflowing rivers, mostly rising from the slopes of the western ridge of the East African Rift Valley. The main rivers are the Sio, Nzoia, Yala, Nyando, Sondu-Miriu and Kuja. The minimum air temperature ranges between 17.1 and 34.8°C. The hottest months are December to March. The water temperature and solar radiation are relatively constant throughout the year (mean $22 \pm 3^{\circ}C$ and 1200 ± 140 ME m^{-1} s^{-1}). Annual rainfall ranges from 400 to 800 mm with long rains occurring from March to May and the short rains from November to December. There are two types of winds, the east and south monsoon and the westerly air streams. Wind is the major factor determining the annual cycle of water mixing (Talling, 1966).

Samples collection

Fish samples were collected monthly by bottom trawling (head rope 22.6 m, coded mesh size 24.5 mm) and beach seining (coded mesh size 5 mm) from the Kenyan waters of Lake Victoria (Fig. 1) between June 1998 and December 2000. The sample sites were defined using a Global Positioning System (GPS), and depth (m) estimated by an echo sounder. Seining provided juveniles <10 cm TL. Stations 1, 2, 3, 6, 10 and 11 were <5 m deep, 4, 7 and 12 were between 5 and 10 m deep, stations 5 and 8 had depths >10 m and station 9 was 20 m deep. Immediately after capture the total length (TL) of individual fish was measured to the nearest cm and the fish weighed to the nearest gram. Each fish was dissected and sexed. Sex ratio, expressed as male:female, was analysed by depth and by 5 cm length classes, and deviations from the 1:1 null hypothesis were tested by the chi-square test. Maturity status was assigned as stage I–VI according to Witte & Van Densen (1995). Ovaries were removed, weighed (g) and preserved in Gilson's fluid. To determine the minimum size of fish at first maturity, females and males were grouped separately into 5 cm size-classes. Fish in maturity stages I, II, III were considered immature, while those in stages IV, V and VI were considered mature for the purpose of calculating the size at first maturity. The length at first maturity (Lm_{50}) is 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 the 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 &

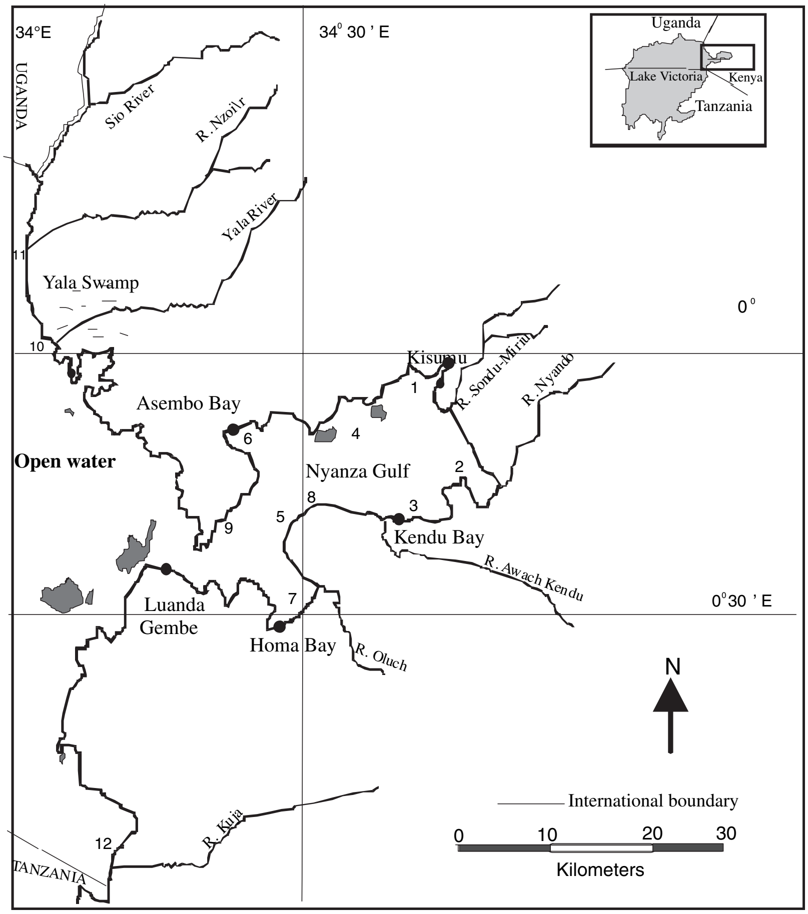

Fig 1 Map of Lake Victoria, Kenya showing sampling sites

Venema, 1998). Estimates were compared using a *t*-test (Zar, 1999).

The weight-length relationship was expressed as $\log_{10}W = \log_{10}\ a + b\ \log_{10}\mathrm{TL}$; where W is the body weight in gram, TL the total length centimetre, a the intercept and b the slope of the regression line (Wootton, 1990). Analysis of covariance (ANCOVA) was used to compare the slopes within depths and the Student–Newman–Keuls test (SNK) to evaluate which slopes were significantly different. Relative condition factor (Kn) was estimated using $\mathrm{Kn} = W/a\mathrm{TL}^b$ (LeCren, 1951), where Kn is the condition factor. Only fish of 15 cm TL and above (stage III–VI) were considered in the derivation of condition factor.

Fecundity was estimated from total counts of ova in the ovaries of fish in the most advanced state of development. The weight of the gonad relative to the body weight, i.e. Gonadosomatic Index (GSI), was calculated as: GSI = (weight of ovary/weight of fish) × 100.

Results

Sex ratio

Males were more abundant than females, and the sex ratio of the population was significantly different from 1:1 ($\chi^2 = 114.30$); males were significantly more abundant than females except in the 20–25, 25–30, 35–40 cm TL length groups ($P < 0.05$). The total numbers of males were significantly greater than females in all depth stations (Table 1; $P < 0.05$), but females of the 30–35 cm TL length group dominated in the 0–5 m and 5–10 m depth zone, and females of the 35–40 cm TL class length dominated in the 10–15 m depth zone.

Size at maturity

The smallest ripe male *O. niloticus* was 21.0 cm TL, while the smallest ripe female was 22.7 cm TL, both recorded in

Table 1 Ratio of male (M) to female (F) *O. niloticus* by depth zone in Lake Victoria, Kenya. Values with asterisks indicate significance difference between male and female ratios

	Depth stratum (m)											
	0–5			5–10			10–15			15–20		
Length group (cm)	M	F	χ2	M	F	χ2	M	F	χ2	M	F	χ2
10–15	40	16	10.29*	42	34	0.84	43	20	8.40*	0	0	0.00
15–20	64	51	1.47	56	59	0.08	45	50	0.26	5	4	0.11
20–25	94	87	0.27	71	66	0.18	19	21	0.10	0	1	1.00
25–30	69	73	0.11	46	60	1.80	24	25	0.02	0	3	3.00
30–35	51	92	11.76*	62	92	5.84*	29	26	0.16	5	5	1.80
35–40	113	93	1.94	124	108	1.10	49	86	10.14*	21	19	0.01
40–45	121	51	28.48*	191	67	59.60*	102	50	17.79*	22	11	3.67
45–50	93	19	48.89*	128	16	87.11*	76	15	40.89*	15	6	3.86*
50–55	31	5	18.78*	32	1	29.12*	26	6	12.50*	6	1	5.57*
55–60	1	0	1.00	0	0	0.00	2	0	2.00	0	0	0.00
Total	677	487	31.01*	752	503	49.40*	415	299	18.85*	74	50	4.65*

the 5–10 m depth zone. The mean size at maturity (Lm_{50}) size was 34.56 ± 0.48 cm TL for males and 30.81 ± 0.09 cm TL for females. Males and females matured at a slightly larger size than average, 35.45 cm TL and 31.18 cm TL for males and females, respectively, in the 10–15 m depth zone, whilst the smallest size at maturity 33.23 cm TL and 30.58 cm TL, for males and females, respectively, was in the 5–10 m depth zone. The mean Lm_{50} of females was significantly lower than that of males [$t_{0.05}$ (2),5 = 6.304, $P = 0.05$].

Seasonal reproductive cycles

Seasonal variation in the GSI was found in male and female *O. niloticus* (Fig. 2). The main reproductive period for males, based on the GSI analysis was between January and April,

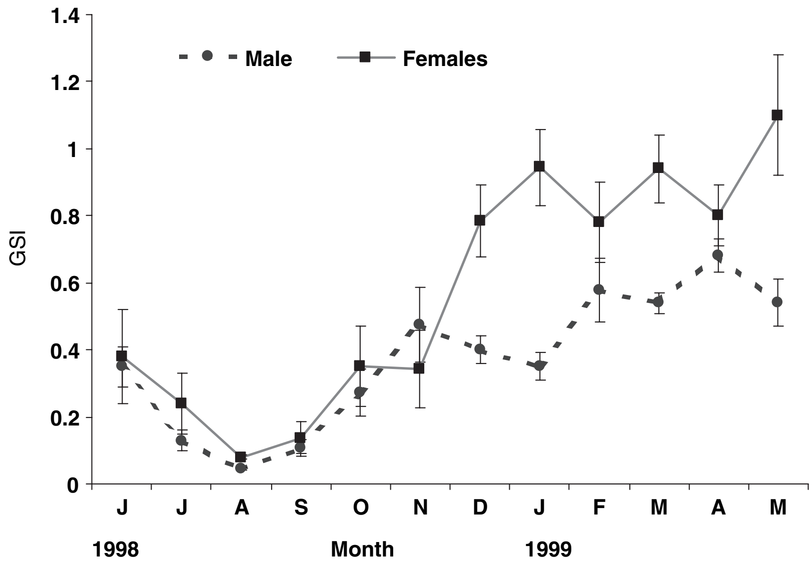

Fig 2 Monthly variation in gonodosomatic index (GSI) of *O. niloticus* in Kenyan waters of Lake Victoria. Vertical bars are standard deviations

which was followed by a reproductively quiescent period between July and October. Females followed a similar trend except the peak occurred later, between January and May.

Fecundity

The size and weight of ripe females ranged from 28 to 51 cm TL and 480 to 2850 g, respectively. The number of oocytes ranged from 905 to 7619, with a mean fecundity of 2715 oocytes. Fecundity in relation to total length (*L*, cm; Fig. 3a), body weight (*W*, g; Fig. 3b) and ovary weight (OW, g; Fig. 3c) were described by:

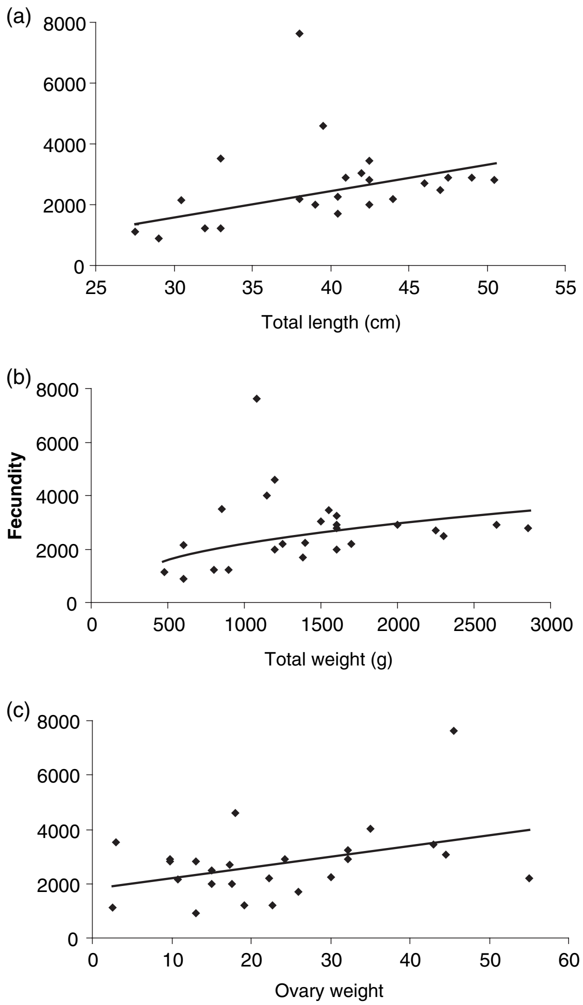

Fig 3 Diagrams showing relationship between fecundity and total length (a), fecundity and ovary weight (b), and fecundity and gonad weight (c). The curves and lines were fitted by calculated regressions

Table 2 Correlation between log TL (cm) and log *W* (g) of *O. niloticus* by depth in Lake Victoria. Similar superscript letters indicate no significance difference

Depth zone	Weight-length relationship	sample size (n)	r^2
Juveniles			
0–5 m[a]	log W = 3.04 log TL−1.75	152	0.99
5–10 m[a]	log W = 3.08 log TL−1.81	83	0.99
10–15 m[a]	log W = 3.06 log TL−1.78	38	0.99
Males			
0–5 m[b]	log W = 3.08 log TL−1.81	1371	0.99
5–10 m[b]	log W = 3.09 log TL−1.82	1229	0.99
10–15 m[c]	log W = 3.16 log TL−1.91	358	0.98
15–20 m[c]	log W = 3.32 log TL−2.17	74	0.99
Females			
0–5 m[d]	log W = 3.07 log TL−1.79	967	0.98
5–10 m[d]	log W = 3.12 log TL−1.85	779	0.99
10–15 m[e]	log W = 3.22 log TL−2.02	222	0.98
15–20 m[e]	log W = 3.19 log TL−1.97	50	0.99

$$F = 8.159L^{1.53}$$

$$F = 96.269W^{0.4504}$$

$$F = 1806 + 39.40\mathrm{W}$$

The length-weight relationship

The weight–length relationships for *O. niloticus* from each depth zones are presented in Table 2. Significant difference ($P < 0.05$) was found between the slopes of the regression lines (ANCOVA), but these differences were not significant for the juvenile life stages (SNK test). The major differences in slope were between depth zones 0–5 m and 15–20 m and 15–20 m, while for females it was between depth zones 0–5 m, 10–15 m and 15–20 m. The slopes of the regressions were significantly different from isometry 3 ($P < 0.05$), except in juveniles from the 0–5 m and 10–15 m depth zones.

Relative condition factor

The monthly mean (±SD) Kn for males and females ranged from 0.92 ± 0.07 to 1.05 ± 0.10 and 0.94 ± 0.08 to 1.07 ± 0.14, respectively (Fig. 4). No appreciable change in the condition of males and females in the 15–55 cm TL size range was found, for depth or season, but there was a

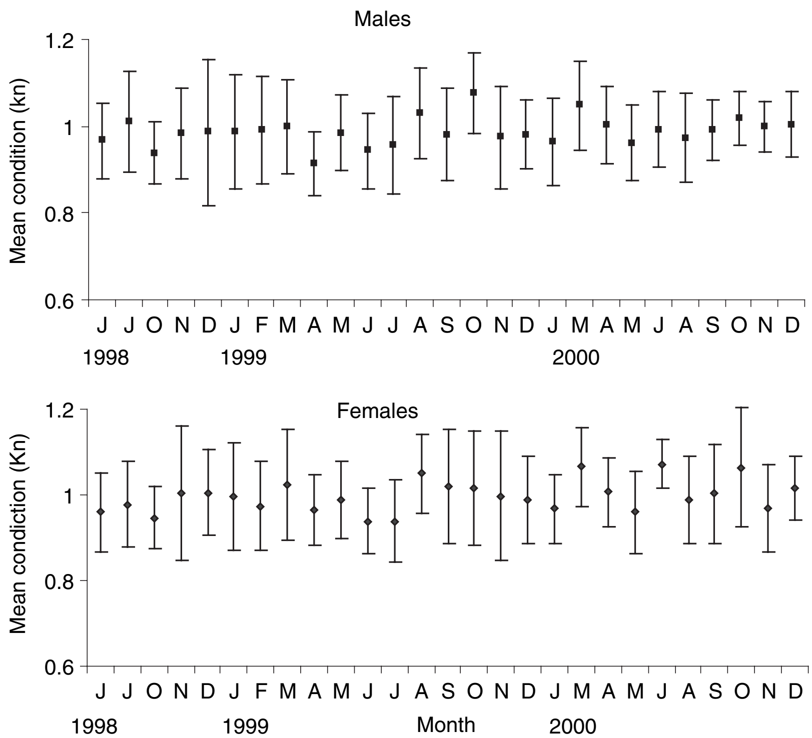

Fig 4 Monthly changes in relative condition factor in male and female *O. niloticus* size in Lake Victoria. Vertical bars are standard deviations

slight increase in Kn for 15–40 cm TL and 15–35 cm TL males and females, respectively. The slight increase corresponded with the stage at which 50% of males and females in the population attain sexual maturity.

Discussion

Nile tilapia in Lake Victoria shows a well-defined reproductive strategy, which has probably contributed to its success in the lake. The species has a protracted spawning period confirming the species is a multiple spawner, and probably able to rear several broods in any one spawning period. Multiple spawning behaviour has advantages in highly stressed environments like Lake Victoria (Ogutu-Ohwayo, 1990; Njiru *et al.*, 2004). To spawn on more than one occasion reduces the risk of wiping out a reproductive run. There has also been a reduction in size at first maturity (ripe male 21.0 cm TL, female 22.7 cm TL) since early in the 1990s, when *O. niloticus* was reported to mature for the first time at an average length of 35 cm TL in the Kenyan waters (Getabu, 1992). The fecundity of *O. niloticus* has also increased from 340–3706 eggs for fish of 17–57 cm TL (Lowe-McConnell, 1955), to 864–6316 eggs for fish of 28–56 cm TL (Lung'aiya, 1994) and to 905–7619 eggs for fish of 28–51 cm TL in this study. This earlier maturation of tilapia, protracted reproductive period and increased fecundity could be tactics to maximize reproductive success (Charlesworth & Leon, 1976; Stearns, 1976), possibly linked to a population response to overfishing (Van der Knaap, Ntiba & Cowx, 2002; Cowx *et al.*, 2003). These are common responses in fish populations and are used as indicators of overfishing (Caddy & Mahon, 1995). Overexploitation attributed to increase in boats, gears and fishers in the lake has been on the rise (Njiru *et al.*, 2002; Van der Knaap *et al.*, 2002; Cowx *et al.*, 2003). The number of boats on the lake has increased from 4000 in 1950s to over 40,000 in 2000 supporting 12,000 and 120,000 fishers, respectively (Van der Knaap *et al.*, 2002). There is also a substantial amount of illegal and undersized nets in the lake, which mostly target juveniles fishes all the species (Cowx *et al.*, 2003).

Catches were dominated by males, possibly because of differential migration of the sexes (Lowe-McConnell, 1958; Rinne & Wanjala, 1982). Tilapia males establish nesting arenas in the shallow waters and aggregate there during the spawning period, whilst ripe females visit the arena to spawn but leave quickly and disperse. Consequently, active fishing methods, such as trawls, used on nesting areas could result in the catch being biased towards males. This is a frequent occurrence in the cichlid trawl fisheries on Lake Malawi (D. Tweddle, personal communication). Furthermore, the faster growth of males (Fryer & Iles, 1972) may mean that they achieve the size at which they are caught in the trawl more quickly, again causing selection of males against the smaller females. This argument is supported by findings from Ugandan waters of Lake Victoria where the male:female sex ratios in populations of Nile tilapia caught by gillnets, which exhibit less selective sex discrimination, were close to 1:1, although different habitats may favour one sex over the other (Balirwa, 1998). For example, vegetated habitats (*Cyperus papyrus*, *Eichornia crassipes*) dominated habitats had a higher proportion of males (Balirwa, 1998).

No great variation in relative condition factor (Kn) was observed for *O. niloticus* throughout the year or by depth, although there was a slight increase in the rainy seasons. Lowe-McConnell (1958) found a similar relationship in *O. niloticus* in Lake Turkana and Moriarty & Moriarty (1973) in Lake George. Fish species in Lake Victoria have been known to have peak breeding time during the rainy periods (Witte & Van Densen, 1995). The observed increase in condition around on set of rainy seasons could be attributed to development of gonad material just prior to the breeding seasons. This peak in breeding is not well exhibited because of protracted period when fish are in a state of maturity (October to May), and good feeding resources (Njiru *et al.*, 2004). Changes in relative condition have been used as indicators of breeding periods of various fish species (Dadzie, Abou-Seedo & Manyala, 2000), but in the absence of conclusive evidence of variation in condition factor of *O. niloticus* in Lake Victoria, the use of this index in delineating breeding seasons should be approached with caution.

Nile tilapia appear to exhibit allometric growth (growth which does not comply to cube rule) as opposed to the assumed isometric growth (LeCren, 1951; Dadzie *et al.*, 2000). For weight-length relationship, there are cases in which the slope was typically below or above the expected value of three for fish growth in general to be assumed to be isometric. Different exponents could also suggest the fish we are dealing with are of different stocks. Although no values are available for direct comparison, the length–weight relationships derived by this study can form the basis of future work on this species. The higher gradient in stations with deeper waters could be because of the fatter mature fish moving offshore after spawning and to avoid competition for food in the inshore areas. The 0–10 m depth zone stations are intensively fished and use of illegal methods, such as seine nets and trawlers, was rampant during the study possibly leading to reduction in size. According to Tesch (1971), the slope is often nearly constant throughout the year or throughout a series of different environments for the same species. The intercepts, by contrast vary seasonally and between habitats. The slope therefore offers a more objective method for analysing growth and production in fishes.

In conclusion, there is evidence to suggest that Nile tilapia in the Kenyan part of the lake displays a '*r*'-selected life history strategy (Pianka, 1970; Mann & Mills, 1985) to survive the stressful conditions prevalent. The more intensive reproductive effort employed by females fits the theories of life history strategy expounded by Pianka (1970) and Stearns (1976), where natural selection has caused different fish forms to adapt to maximize fitness in specific habitats/environments. It could also be a mechanism to compensate for the intensive fishing pressure in the area.

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