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# The effect of overfishing on the life-history strategies of Nile tilapia, *Oreochromis niloticus* (L.) in the Nyanza Gulf of Lake Victoria, Kenya

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*Studies were conducted on reproductive characteristics of Oreochromis niloticus from 1998 to 2000. The results were combined with published work on growth parameters of O. niloticus from 1985 to 1999 in order to establish the current survival strategies exhibited by O. niloticus in the Nyanza Gulf of Lake Victoria. The study revealed that size at maturity had decreased concurrently with increasing fishing mortality. Observations on reproductive effort point to a fish species under stress. It is observed that the behavioural change in O. niloticus is not due to size selective predation but due to size selective exploitation. Indications that O. niloticus in the Nyanza Gulf of Lake Victoria allocates more energy for reproduction than for somatic growth (i.e. increased turnover rate) are multiple. It is concluded that O. niloticus in the Nyanza Gulf exhibits an 'r'-selected life history strategy in order to survive stressful conditions.*

**Keywords:** Maturity, population parameters, reproductive strategy

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## Introduction

The Nile tilapia, *O. niloticus* (L.), is the most important cichlid of commercial interest in Lake Victoria. Introduced in the 1950s, together with other tilapiines such as *O. leucostictus* (Graham), *Tilapia zillii* (Gervais) and *Tilapia melanopleura* (Dumeril), it then quickly out competed the other endemic tilapiines, namely: *O. esculentus* (Graham) and *O. variabilis* (Boulenger). It subsequently became the dominant tilapiine in Lake Victoria (Welcomme, 1967; Trewavas, 1983). The success of this species has been attributed to, among other factors, its mouth-brooding reproduction system, feeding flexibility and its tolerance to a wide range of physico-chemical variables (Balirwa, 1998).

In the recent past, *O. niloticus* in the Nyanza Gulf of Lake Victoria has been under intense pressure as a result of over-fishing and other environmental factors (Getabu, 1992; Ojuok, 1999). Earlier studies also show that this species is not under predation pressure from the introduced Nile perch, *Lates niloticus* (L.) (Ogutu-Ohwayo, 1985; Mkumbo and Ligetvoet, 1992). The breeding characteristics of *O. niloticus* have changed in the recent past (Ojuok, 1999). The adaptability and plasticity of tilapias are well-known but, despite enormous research efforts (Fryer and Iles, 1972; Balarin, 1979), a clear understanding of their life histories still remains elusive. In stable lacustrine environments the selective pressures are normally associated with density-dependent mortalities. Intensive intra-specific and inter-specific competition, highly

specialised feeding and reproductive habits are considered to belong to the “*K*-selected” end of the *r*-*K* continuum (Pianka, 1970). In unstable environments, a more “*r*-selected” pattern characterised by high fecundities, fluctuating density-independent mortalities, fast generation overturn and more generalised feeding exist. It has been suggested (Noakes and Balon, 1982) that tilapias master “the best of both strategies” under different environmental conditions. This paper describes the current life-history strategy exhibited by *O. niloticus* in the Nyanza Gulf of Lake Victoria based on the observed breeding habits, population parameters and reviewed literature.

## Materials and methods

Fish samples were collected from 1998 to 2000 using bottom trawl nets from Nyanza Gulf, Lake Victoria (Figure 1). For each fish the total length, (TL, cm) and total weight (g) were measured to the nearest centimetre and gram respectively. Each fish was dissected, sexed and maturity status assigned using a modified Nikolski (1963) key, which has been described by Ntiba and Jaccarini (1990). Size at 50% maturity was estimated from fitting the size frequency of mature individuals by length class using the least square method by means of the ‘solver’ option in Excel. Estimates were compared statistically using student *t*-test (Zar, 1999). The sex ratio, expressed as number of male to female was analysed by 5 cm length class and deviation from 1:1 ratio statistically tested by Chi-square test ( $\chi^2$ ).

Size frequency distribution of intra-ovarian oocytes was determined by measuring the diame-

ter of oocytes contained in a cross section taken from the central part of the right and left lobes of the ovary earlier preserved in Gilson’s fixative. The mean ova diameter of mature gonads and fecundity were compared with those reported by other investigators. Data on fish growth parameters in the Nyanza Gulf were obtained from the literature.

## Results

### Size at first maturity

The smallest mature male *O. niloticus* was 21.0 cm TL while the smallest mature female was 22.7 cm TL recorded in the 5-10 m depth zone. The mean ( $\pm$  standard error) length at first maturity ( $L_{m50}$ ) for males was  $34.56 \pm 0.48$  cm TL and  $30.81 \pm 0.09$  cm TL for females. Application of the Student *t*-test revealed that the mean  $L_{m50}$  of females was significantly lower than that of males.

### Population structure

Males were more abundant than females and the overall sex ratio of the population was significantly different from the expected 1:1 ratio ( $\chi^2 = 99.06$ ) (Table 1). Males were predominant in populations of older fish ( $> 40$  cm TL). The proportion of females declined significantly ( $P < 0.05$ ) above 40 cm TL and no female *O. niloticus* exceeding 55 cm TL were caught.

### Ova frequency distribution and fecundity

The egg diameter frequencies of ovary developmental stages (excluding stage I) are shown in

**Table 1.** Occurrence of males and females of *O. niloticus* by size groups in Lake Victoria, Kenya. Values with asterisk show no significant difference at 0.05 level.

Size group (cm)	n	males	females	Ratio	$\chi^2$
10–15	195	125	70	1.8:1	15.51
15–20	289	165	124	1.3:1	5.82
20–25	358	184	174	1.1:1	0.28*
25–30	298	139	159	0.9:1	1.34*
30–35	357	146	211	0.7:1	7.24
35–40	587	294	293	1.0:1	0.002*
40–45	595	421	174	2.4:1	102.54
45–50	356	300	56	5.4:1	169.04
50–55	101	92	9	7.1:1	29.72
55–60	3	3	0		
Total	3177	1869	1308	1.4:1	99.06

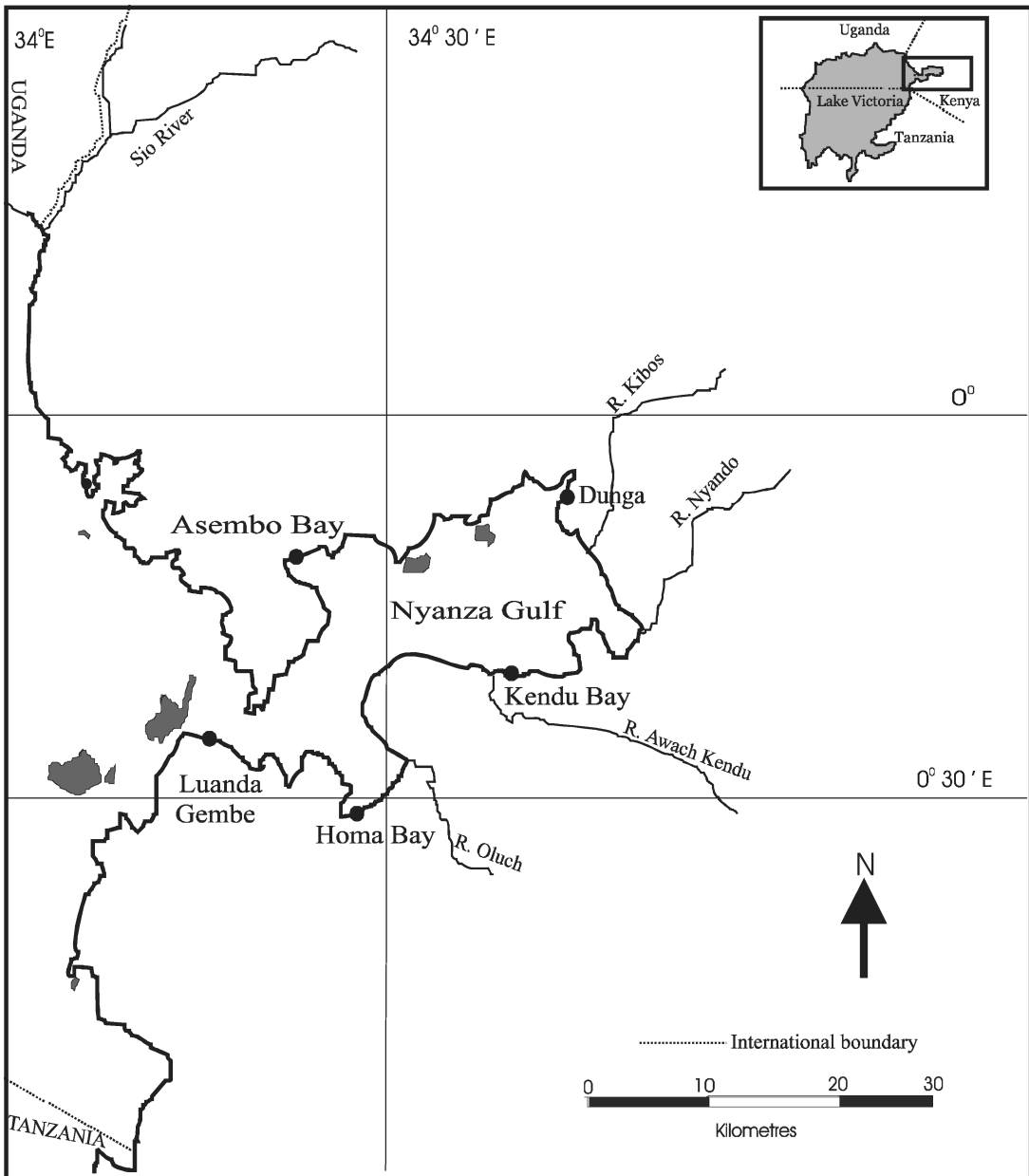


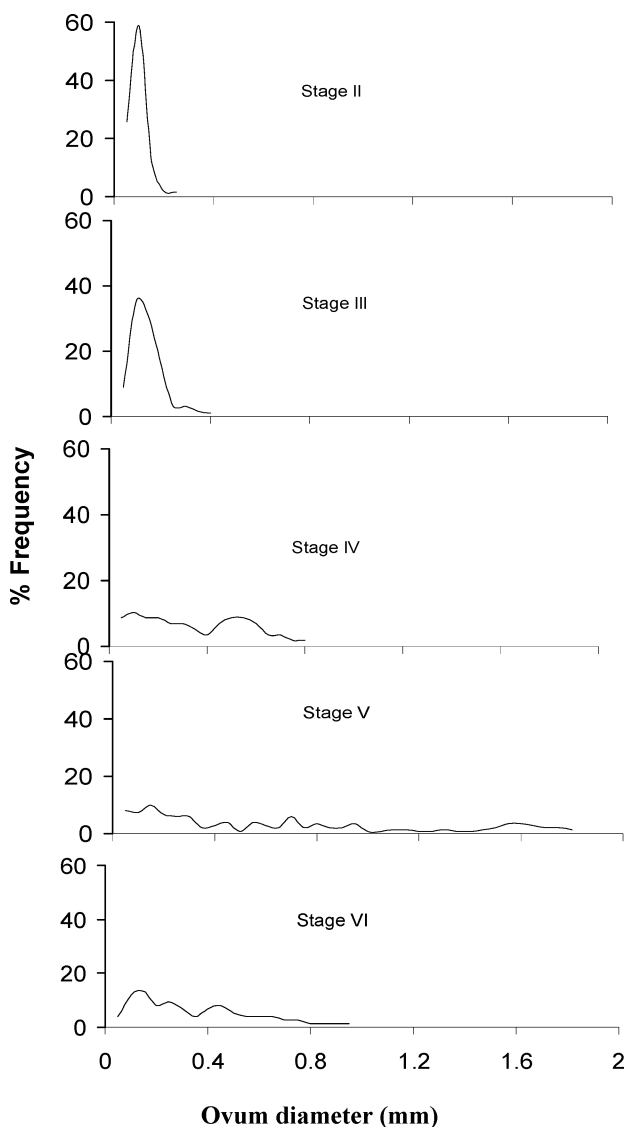
Figure 1. Map showing the study area, Nyanza Gulf of Lake Victoria, Kenya.

Figure 2. The size distribution of oocytes was from 0.05 to 1.80 mm. Stages II and III (immature) had single modes while the mature stages (IV-VI) had more than one mode. The progressive maturation to spawning condition (Stage II-V) was evident from the increasing egg diameters of the most advanced mode at each stage. The advanced mode of stage V with the egg diameter range of 1.5–1.8 mm was the ultimate egg development stage when spawning

is imminent (Figure 2). The largest egg recorded in this study was 2.0 mm. The fecundity range for *O. niloticus* was 461–7619 ova for fish of 29.0–52.0 cm TL.

### Discussion

The study shows that the size at first maturity ( $Lm_{50}$ ) of *O niloticus* in the Nyanza Gulf of Lake



**Figure 2.** Size frequency distribution of oocytes in each stage of development of the ovary (II-VI) of *O. niloticus* in the Nyanza Gulf of Lake Victoria

Victoria has reduced since the late 1980s when it was reported to mature for the first time at an average length of 35 cm TL (Getabu, 1992). The fecundity of *O. niloticus* has 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 (Lungayia, 1994), to 461–7619 eggs for fish of 26–52 cm TL. The intra-ovarian oocyte distribution of ripe fish shows that more than three cohorts of oocytes are present, which confirms that the species is a batch spawner and able to spawn more than once in a breeding season. Furthermore it has been reported

elsewhere that *O. niloticus* in the Nyanza Gulf has a protracted breeding period lasting several months (Ojuok, 1999). The population structure is dominated by males and there is a dearth of females in the larger size classes suggesting the females could be diverting energy away from somatic growth for reproduction purposes.

Benefits of increased fecundity are believed to be offset by an increase in adult mortality (Stearns, 1977). The energetic cost of reproduction is high, and the increase in fecundity is accompanied by increased parental mortality. The increase in fecundity

**Table 2.** Growth parameters ( $K$  yr<sup>-1</sup>,  $L_{\infty}$  cm), mortality ( $Z$ ,  $M$ ,  $F$  yr<sup>-1</sup>), and exploitation rate ( $E$ ) of *O. niloticus* from Nyanza Gulf of Lake Victoria, Kenya

$L_{\infty}$	$K$	$Z$	$F$	$E$	Data collection and source
64.60	0.25	0.82	0.28	0.34	1985–1986 (Getabu, 1992)
63.10	0.35	1.71	0.99	0.58	1989–1990 (Dache, 1994)
56.70	0.59	2.12	1.12	0.55	1998–1999 (Present study)

could also be a mechanism to compensate for the intensive fishing pressure in the lake. Resource or energy limitations are common in nature, where trade-offs occur between current reproductive effort and somatic growth on the one hand and current reproductive effort and future reproductive probability on the other (Reznick, 1983; Stearns, 1992; Berg et al., 1998). The main reason for this is that excessive diversion of resources to reproduction at the expense of somatic activity exerts a cost in terms of the chance of survival (Calow, 1979).

*O. niloticus* in the Nyanza Gulf has been reported to be under intense fishing pressure (Njiru et al., 2007). Population parameters of *O. niloticus* have changed over the years (Table 2). The asymptotic length ( $L_{\infty}$ ) has decreased in the past two decades from 64.6 cm TL in 1986 (Getabu, 1992) to 56.7 cm TL in 1999 (Njiru et al., 2000). The growth rate ( $K$ ) has increased with a concomitant increase in fishing mortality ( $F$ ) and total mortality ( $Z$ ). The exploitation rate ( $E$ ) is relatively high (55%). There is evidence of over-fishing and this may explain why the size at first maturity has decreased concurrently with increasing total mortality.

*O. niloticus* segregates spatially from its potential predator, *Lates niloticus*, by inhabiting shallower areas in Lake Victoria (Ogutu-Ohwayo, 1985). Tilapias, especially the young, can withstand not only low dissolved oxygen (DO as low as 0.1 ppm is tolerated), but also very high levels of CO<sub>2</sub> (Fryer and Iles, 1972; Balarin, 1979; Philippart and Ruwet, 1982), conditions that cannot be tolerated by *L. niloticus*. Stomach analysis has also confirmed that *L. niloticus* from Lake Victoria rarely feed on Nile tilapia (Mkumbo and Ligtoet, 1992). It is, therefore, reasonable to suggest that the life-history strategy being displayed by *O. niloticus* in the Nyanza Gulf of Lake Victoria is not due to predation pressure.

According to the  $r$ - $K$  selection theory as a function of relative size-specific mortalities (Schaffer, 1974; Stearns, 1977; Horn, 1978), the balance between reproduction and growth, in an optimal situ-

ation, is determined from the relation between adult and juvenile survival. As a mouthbrooder, *O. niloticus* has reached a very advanced evolutionary state maximizing survival of its offspring; this feature is considered to belong within the 'K-selected end' of the  $r$ - $K$  continuum (Pianka, 1970). The reproductive strategy seen above contradicts this theory. Exploitation by man is usually strongly size selective for the larger individuals, and Estes (1979) considered this to artificially impose  $r$ -selection on animals originally evolved through K-selection. Following the argument that  $r$ - $K$  selection is mainly a function of size-specific mortalities, then theoretically, even for 'K-selected' species, a compensatory strategy (i.e. evolved adaptation) against increased mortality on the adult stages would be to increase the turnover rate by reducing the generation time (Kolding, 1993). In fact significant reduction in age at maturity for heavily fished stocks has been documented (Pitt, 1975; Jørgensen, 1990). Noakes and Balon (1982) also reported that under naturally fluctuating size-specific mortalities, tilapias are apparently able to adjust their mean generation time.

## Conclusions

Observations from this study have shown that *O. niloticus* from the Nyanza Gulf, Lake Victoria are under intense fishing pressure and currently display an  $r$ -selected life history style as opposed to the expected K-selection. From the population parameter and size at maturity studies, we recommend that a ban should be imposed on the use of beach seines and a reduction made on the number of licensed boats targeting this species.

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