

Influence of Fishing Pressure and Water Level Fluctuations on the Reproductive Biology Traits of *Oreochromis niloticus* (Linnaeus 1758) in Irrigation Reservoirs of Sri Lanka

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Abstract

The reproductive biological characteristics of *Oreochromis niloticus* (Linnaeus 1758) were investigated in relation to fishing pressure and water level fluctuation in 10 irrigation reservoirs of Sri Lanka. It was found that matured larger sized male fish made larger and deeper nests. The negative relationship between gonado-somatic index (GSI) and size of maturity (L_m) of female indicates that more energy is utilised for gonadal growth of early matured fish. There were negative relationships of fishing intensity (FI) with egg diameter, L_m , GSI, and condition factor of *O. niloticus*, showing that heavy fishing pressure in the reservoir fisheries favoured r-selected life strategies. Based on daily water level data of reservoirs, an index to express water availability for a sufficient period, making it possible for the fish to construct nests, termed as water level fluctuation index (WLFI) was calculated. Nest density during peak spawning period was positively related to WLFI. Hence, it was concluded that two anthropogenic factors, FI and reservoir water level fluctuations, influenced reproductive biology attributes of reservoir populations of *O. niloticus*, which highlighted the necessity for coordination between fisheries and irrigation authorities for augmenting fish yields.

Keywords: altricial-precocial dichotomy, exotic cichlids, nesting behaviour, parental investment, reproductive effort

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Introduction

Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758) introduced to many tropical waters in the world for development of aquaculture and capture fisheries, has gained a reputation as a commercially important food fish species (Pullin and Lowe-McConnell 1982; Beveridge and McAndrew 2000; De Silva et al. 2004). The reproductive characteristics of *O. niloticus* are more or less similar to those of many nest building cichlid species which exhibit parental care. Male fish constructs nests or spawning pits in shallow areas of the water body and displays territorial defence against other adult male counterparts in the population. Mature females are attracted to these reproductive arenas and after a brief courtship, spawning takes place in the nests. Male partner then relinquishes the spawning arena and female partner keeps eggs and young in her mouth as part of parental care. Nest building as part of reproductive behaviour in members of the family Cichlidae is mostly associated with territoriality and courtship (Trewavas 1983), which can be treated as a parental investment. Also as life history attributes of this species are known to be related to the chaos of the habitats (Lowe-McConnell 1982; Noakes and Balon 1982; Lorenzen 2000), it is important to investigate interrelationships of reproductive characteristics and the influence of anthropogenic factors for shaping-up of life-history strategies.

Life history strategies are known to be closely related to the conditions of the environment that they inhabit. For example, altricial traits are those which are adapted to live in unpredictable environments and precocial traits are those which dominate more predictable environments (Balon 1981; Bruton 1990). As such, environmental factors which favour different life history strategies are needed to be understood for effective conservation and management of fish populations such as cichlid populations, which consist of wide ranges of life-history attributes (Philippart and Ruwet 1982; Lorenzen 2000). As *O. niloticus* is the mainstay of the reservoir fishery of Sri Lanka (Amarasinghe and Weerakoon 2009) and as irrigation requirements in the command areas of the reservoirs bring about environmental perturbations (Piet 1998; Piet and Vijverberg 1998), it can be hypothesized that these anthropogenic factors have some impacts on the life history strategies of this species. In the present study, an attempt was made to investigate whether reproductive biology traits of *O. niloticus* population in selected irrigation reservoirs of Sri Lanka showed divergent strategies in relation to fishing pressure and reservoir water level fluctuations due to irrigation demand.

Materials and methods

Studies were conducted in 10 irrigation reservoirs namely Angamuwa, Balaluwewa, Dewahuwa, Ibbankatuwa, Kalawewa, Kandalama, Katiyawa, Rajanganaya, Siyambalangamuwa and Usgala-Siyambalangamuwa in the Kala Oya river basin, Sri Lanka (Fig. 1; Table 1). The study was conducted from April 2014 to April 2016 by visiting each reservoir approximately once in 2 months. The inland fishery is essentially a secondary use of these reservoirs. The exotic cichlid species, *O. niloticus* is the dominant species in the fisheries of all 10 reservoirs, accounting for over 60 % of the landings.

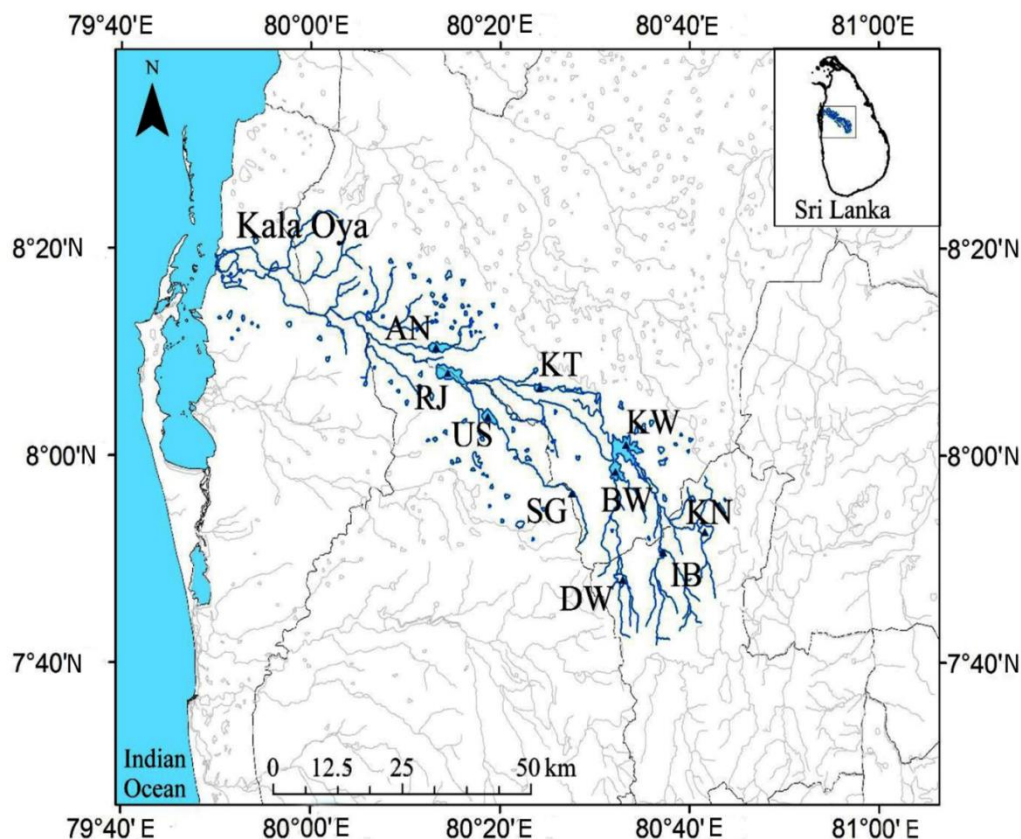


Fig. 1. Geographic locations of the 10 irrigation reservoirs studied at Kala Oya river basin of Sri Lanka. Inset shows the location of Kala Oya river basin in Sri Lanka. Abbreviations of reservoir names are as given in Table 1 (modified after Bandara and Amarasinghe 2017).

Table 1. Physical characteristics of the 10 reservoirs studied (Irrigation Department Sri Lanka, 1975; * Source - <http://www.damsafety.lk/?p=dswrpp-works-phase-1&locale=en&id=38>). MSL – Mean Sea Level; FSL - Full Supply Level. Abbreviations of reservoir names are given in parentheses.

Reservoir	Catchment (km ²)	Capacity at FSL (10 ⁶ m ³)	FSL (m above MSL)	Mean depth (m)	Area at FSL (ha)
Angamuwa (AN)	129.5	15.79	64.3	1.99	792
Balaluwewa (BW)	269.8	41.42	120.0	4.43	934
Dewahuwa (DW)	67.3	13.56	182.1	3.13	433
Ibbankatuwa (IB)	169.0*	11.72	162.1	2.89	405
Kandalama (KN)	98.0	33.74	162.1	4.58	736
Katiyawa (KT)	86.7	5.55	94.3	2.16	257
Kalawewa (KW)	572.0	87.81	128.1	4.43	1 980
Rajanganaya (RJ)	1 611.0	100.66	68.2	6.30	1 599
Siyambalangamuwa (SG)	46.6	2.6	35.4	1.78	146
Usgala-Siyambalangamuwa (US)	184.6	26.72	87.2	3.47	769

Nesting of Oreochromis niloticus

Details about factors influencing nesting sites of *O. niloticus* in the 10 reservoirs were described by Bandara and Amarasinghe (2017). For clarity, the approach adopted for studying nesting of *O. niloticus* is briefly mentioned here. In each reservoir, underwater observations were made using a snorkel and a diving mask in three 5 m × 5 m quadrats, fixed in the littoral area opposite to the dam site that was subjected to littoral exposure due to reservoir water level fluctuations. The positions of these quadrates were changed according to fluctuations in the water level. The number of nests, nest diameter, depth of nest and nesting water depth of *O. niloticus* was determined to the nearest 0.1 cm using a meter ruler and/or a measuring tape in each quadrat at different water depths ranging from 0.1 m to 2 m. Here, only freshly constructed nests, as determined by the appearance, (i.e., those which were not covered with silt and those which were not invaded by aquatic plants) were chosen. Nest density (ND) was expressed as number of nests per m².

Reproductive biology of Oreochromis niloticus

Samples of 15–25 fish were randomly collected from the commercial landings in the 10 reservoirs during each field visit. They were packed in ice and were brought to the laboratory. Total sample sizes in the 10 reservoirs ranged from 139 in Ibbankatuwa reservoir to 221 in Rajanganaya reservoir. In the laboratory, total length and body weight of each specimen were determined to the nearest 0.1 cm and 0.1 g respectively. Each specimen was dissected and the sex was determined. The maturity stages of males and females were determined through visual inspection of the appearance, size and texture following Duponchelle et al. (2000). There were seven maturity stages of fish in which the stages above III were considered as mature. Gonads were carefully removed and weighed to the nearest 0.1 g. Female gonads (ovaries) of Stage IV were preserved in Gilson's fluid, stored in the dark, and were shaken rigorously from time to time to facilitate separation of eggs from ovarian membranes. Percentage mature (Stage III and above) males and females in each length class were determined. From the plots of percentage maturity against length, mean sizes at maturity or lengths at 50% maturity (L_m) of *O. niloticus* were determined for the 10 reservoirs separately. A logistic curve fitted to the proportion (P) of sexually mature males and females using the following equation (King 2007) was used for the purpose.

$$P = 1/(1 + \exp[-r(L - L_m)])$$

where r is the slope of the curve of the curve, and L_m is the mean length at sexual maturity. L_m was estimated by transforming this equation to linear form as follows:

$$\ln [(1 - P) / P] = rL_m - rL$$

From the preserved gonads, diameter of each oocyte was determined using a stage micrometre under a light microscope. The number of oocytes belonging to the largest diameter modal group was considered as the absolute fecundity. From the oocytes of the same modal group, mean egg diameter was estimated. The relationship between absolute fecundity (F) and body weight (W) of fish in each reservoir was determined by a linear regression technique. From these regression relationships, relative fecundity (RF) of *O. niloticus* in each reservoir was determined as F for 200 g body weight of fish (Bagenal 1978). Fish of 200 g body weight was chosen because it represented the average landing weight of *O. niloticus* in Sri Lankan reservoirs. Similar estimates were used for comparative studies of relative fecundity of *Oreochromis mossambicus* (Peters 1852) in Sri Lankan reservoirs (De Silva 1986) and *O. niloticus* in three hydroelectric reservoirs in Cote d' Ivoire (Duponchelle et al. 2000). Gonado-somatic index (GSI) of each specimen of male and female *O. niloticus* separately was determined as,

$$GSI = \frac{\text{Gonad weight}}{\text{Somatic weight}} \times 100$$

where, somatic weight = [total weight – (gut weight + gonad weight)] (Strum 1978). GSI values of fish of both sexes in each reservoir were determined separately for each sampling. In each reservoir, the GSI values of both sexes were plotted against sampling occasions to determine the peak spawning seasons.

Condition factor

The condition factor (K) of was determined separately for males and females in each reservoir as follows;

$$K = \frac{100W}{TL^3}$$

where W is body weight in g; and TL is the total length in cm (Froese 2006).

Fishing intensity

In a parallel study on the status of the fisheries of the 10 reservoirs, fish production and fishing effort data were collected from the data-logs of fishers from January 2010 to December 2015. Based on these data, the fishing intensity was determined and expressed as number of boats ha⁻¹ yr⁻¹ (Sanders and Morgan 1976; Gulland 1983).

Water level fluctuation index

The optimum nesting depth (NDP_{opt}) in each reservoir was calculated using formula by Bandara and Amarasinghe (2017):

$$NDP_{opt} = \frac{\sum_{i=1}^n N_i * Z_i}{\sum_{i=1}^n N_i}$$

where, n_i = number of depth classes in the quadrat; N_i = number of nests in i^{th} depth; and Z_i = mean water depth of the depth class. Here, 50 % of the optimum nesting depth (NDP_{opt}) was considered as the minimum water depth required for nest building for fish.

Daily water level data in each reservoir were obtained from the Irrigation Department and Mahaweli Authority of Sri Lanka. Based on these data, an index to express water availability for a sufficient period making it possible for *O. niloticus* to construct nests, termed as water level fluctuation index (WLFI) was calculated on a monthly basis. A total number of days (N_{NB}) spent by male and female *O. niloticus* for the entire courtship behaviour from the beginning of nest construction to spawning was determined in a pond experiment at the state-owned Aquaculture Development Centre in the study area (Dambulla). Observations for nest building were made in three cement ponds (3.1 m × 4.6 m × 0.6 m) with sand filled bottom to provide substrate for nest building. Nine female and 3 male fish of more or less similar sizes were then introduced to the each of three tanks and were kept until they start building nests. Daily observations were then made to determine the total number of days that fish spent to complete spawning cycle.

The water level fluctuation index (WLFI) was defined as follows:

$$WLFI = \frac{N_{WL}}{N_{NB}}$$

where N_{WL} is the number of consecutive days with at least water depth $\geq 50\%$ of NDP_{opt} in the nesting site, which essentially has the maximum of 30 days. This index varies from 0 when $N_{WL} = 0$, to 1 when $N_{WL} = N_{NB}$. WLFI values corresponding to peak spawning seasons (generally April/May and December/January), as determined from the seasonal variation of GSI, were then calculated.

Interrelationships of reproductive attributes, fishing pressure and reservoir water level fluctuation

Interrelationships of the variable of nesting habits, those of reproductive biology and fishing intensity were determined using appropriate linear and logarithmic regression techniques. The relationship between nest diameter and depth of nest was determined using linear regression. Nest density was related to relative fecundity (RF) and GSI of female fish (GSI_F). With regard to interrelationships of reproductive biology variables, GSI_F was related to RF and length of maturity of female *O. niloticus* ($L_{m(F)}$). Also, the relationship of mean egg diameter (ED) of the fish in the 10 reservoirs was computed with $L_{m(F)}$. Fishing intensity (FI expressed as boats $ha^{-1} yr^{-1}$) was related to ED, L_m of female and male fish ($L_{m(F)}$ and $L_{m(M)}$ respectively), and condition factor (K) of both sexes (K_F for females and K_M for males) after appropriate data transformation.

Finally, from the plots of GSI of both sexes, the peak spawning seasons were determined in each reservoir, and monthly mean GSI during the peak spawning seasons in the 10 reservoirs were then related to corresponding WLF1.

Results

The diameters of the spawning pits (nests) varied from 5 cm to 95 cm in the 10 reservoirs (Fig. 2). Smaller (5–20 cm) nests were observed in Dewahuwa and the nests in Angamuwa, Ibbankatuwa, Rajanganaya and Usgala-Siyambalangamuwa reservoirs were much larger (90–95 cm). The majority of nests observed in the reservoirs were generally between 35 cm and 65 cm in diameter. The widest range of diameters of nests was observed in Usgala-Siyambalangamuwa (20–95 cm) (Fig. 2).

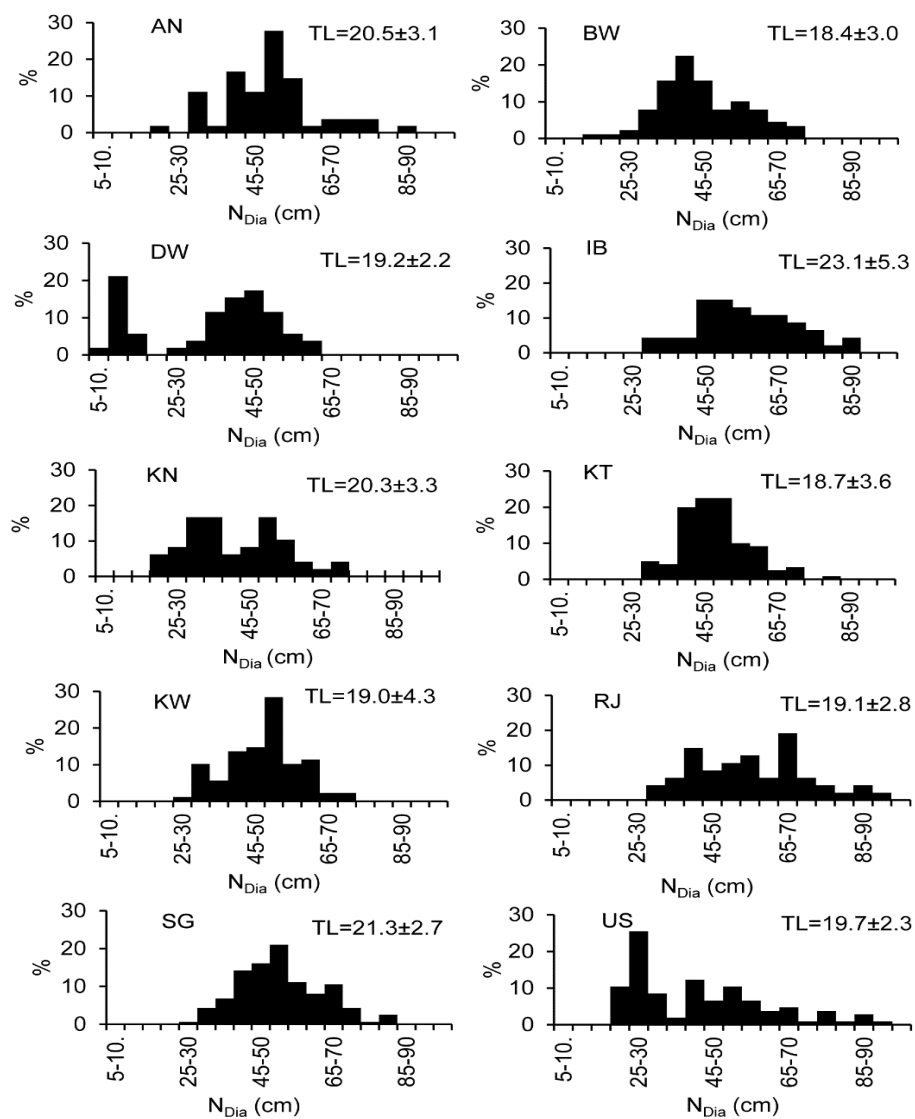


Fig. 2. The frequency distribution (%) of nest diameter (N_{Dia}) of *Oreochromis niloticus* in 10 reservoirs studied at Kala Oya river basin. The mean lengths \pm SD (TL in cm) of adult male *O. niloticus* sampled from each reservoir are also shown. Abbreviations of reservoir names are as given in Table 1.

Mean nest diameter ranged from 43.6 cm in Kandalama to 59.2 cm in Siyambalangamuwa, and the range of mean depth of nests was from 10.0 cm in Kandalama to 13.9 cm in Siyambalangamuwa (Table 2). Fishing intensity (FI) in the 10 reservoirs are also given in Table 2.

Table 2. Nesting characteristics (mean \pm SE) of *Oreochromis niloticus* and fishing intensity in 10 reservoirs studied. Abbreviations of reservoir names (Abbr.) are as given in Table 1.

Abbr.	Nest diameter (cm)	Depth of nest (cm)	Nest density (Nos.m ⁻²)	Fishing intensity (boats ha ⁻¹ yr ⁻¹)
AN	54.0 \pm 1.3	13.6 \pm 0.42	0.46 \pm 0.18	26.78
BW	55.1 \pm 0.9	11.6 \pm 0.46	0.30 \pm 0.13	25.10
DW	45.5 \pm 1.5	10.3 \pm 0.67	0.18 \pm 0.09	18.00
IB	58.5 \pm 2.0	13.0 \pm 0.45	0.24 \pm 0.18	7.03
KN	43.6 \pm 1.8	10.0 \pm 0.61	0.28 \pm 0.23	16.32
KT	50.6 \pm 0.9	11.9 \pm 0.29	0.40 \pm 0.28	29.04
KW	56.9 \pm 0.8	13.1 \pm 0.28	0.32 \pm 0.01	26.91
RJ	57.5 \pm 2.1	13.5 \pm 0.56	0.26 \pm 0.16	21.55
SG	59.2 \pm 0.7	13.9 \pm 0.26	0.25 \pm 0.07	13.19
US	43.8 \pm 1.8	12.7 \pm 0.29	0.56 \pm 0.29	15.32

The fecundity (F) of *O. niloticus* in the 10 reservoirs varied from 234 to 2661 for fish of the body weight (W) ranged between 46–1011 g. In all 10 reservoirs, there were significant positive relationships between W and F (Fig. 3). Using these regression relationships (Fig. 3), relative fecundity (RF) that was estimated as fecundity of a female of 200 g in weight, varied from 607.3 in Kandalama to 877.2 in Usgala-Siyambalangamuwa (Fig. 3). From the plots of percentage maturity against total length (Fig. 4), length at 50 % maturity (i.e., mean size of maturity or L_m) was determined.

Mean size of maturity (L_m), mean egg diameter and condition factor (K) of *O. niloticus* in the 10 reservoirs are given in Table 3. Mean egg diameter (ED) of the fish in the 10 reservoirs ranged from 1.39 mm in Rajanganaya to 1.72 mm in Usgala-Siyambalangamuwa (Table 3). The relationship of the depth of the nest (N_{Dep}) to the diameter of the nest (N_{Dia}) (Fig. 5a) indicates that nest of larger diameter are often deeper. Relative fecundity (RF) was found to be significantly related to ND (Fig. 5b). Although not significant at 0.05 probability level, increasing trends are evident for mean size of maturity of males (L_{m(M)}) with nest diameter (Fig. 5c) and depth of nest (Fig. 5d) indicating that larger males construct larger and deeper nests.

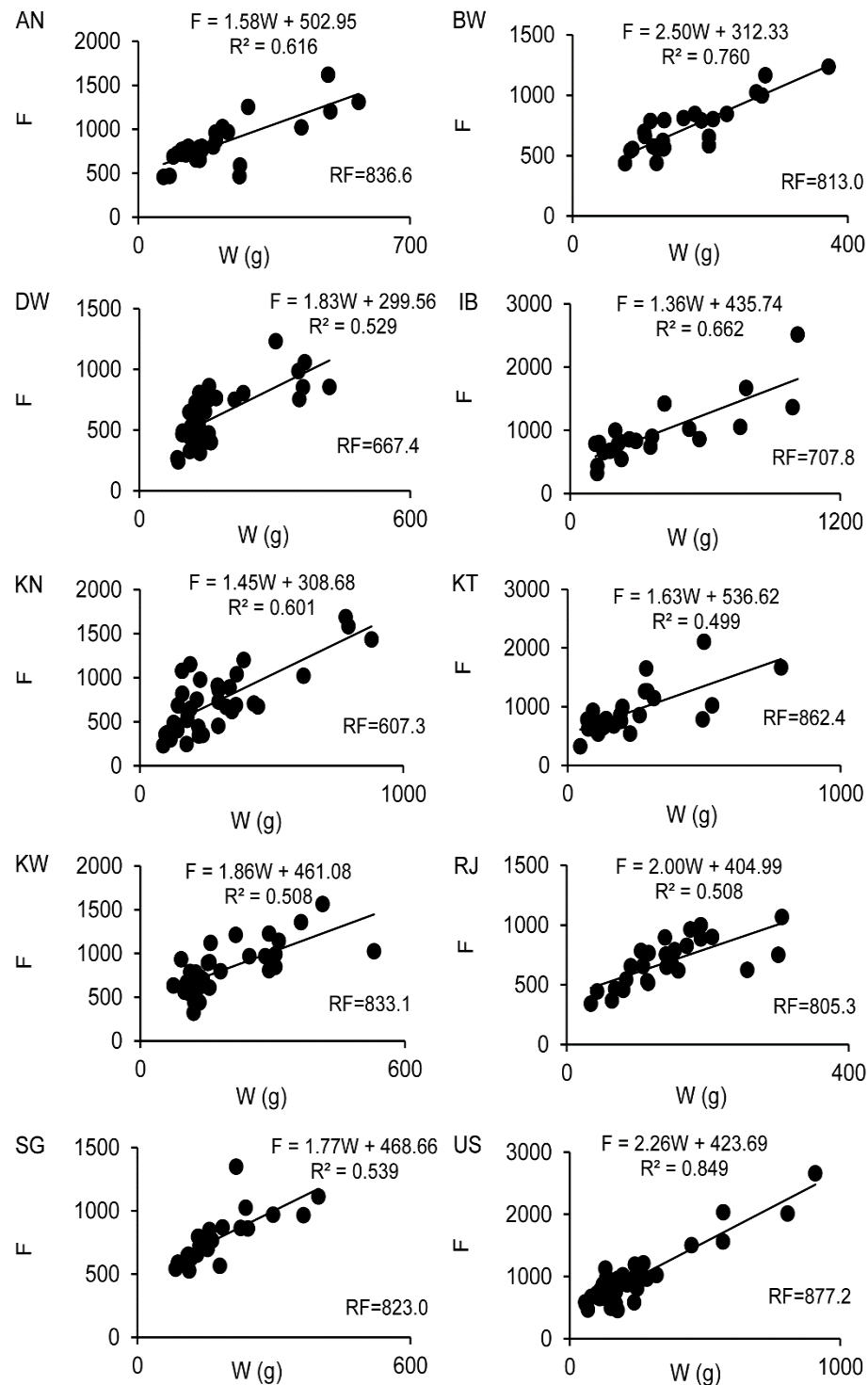


Fig. 3. The relationship between fecundity (F) and body weight (W) of *Oreochromis niloticus* in the 10 reservoirs studied at Kala Oya river basin. Relative fecundity (RF) of *O. niloticus* in 10 reservoirs studied estimated from the regression relationships are also given here. R^2 = Coefficient of determination. All relationships are significant at least at 0.01 probability level. Abbreviations of reservoir names are as given in Table 1.

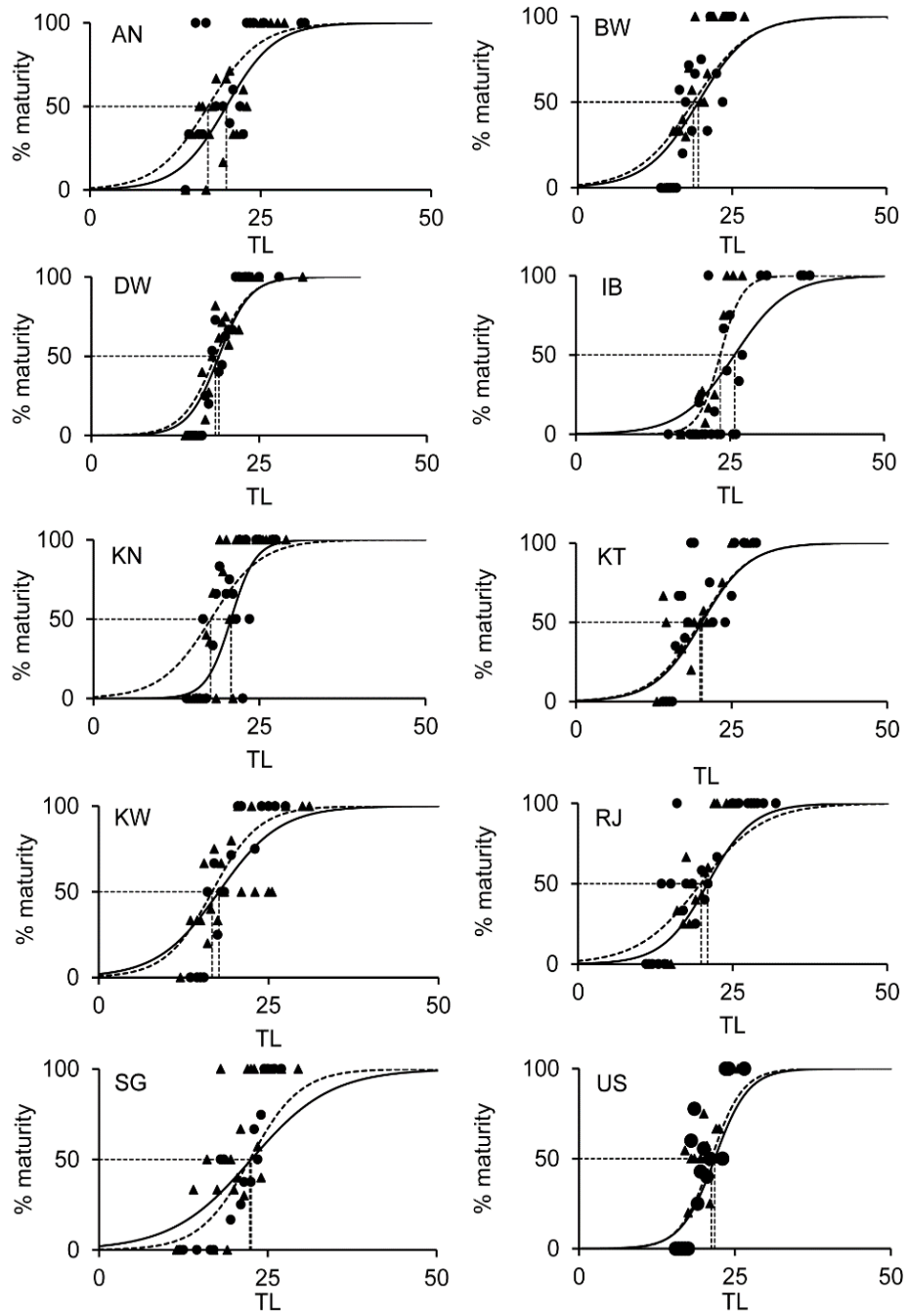


Fig. 4. Percentage maturity of female and male *Oreochromis niloticus* against total body length (TL) in 10 reservoirs studied at Kala Oya river basin. Females: solid line with circular markers; Males: dash line with triangular markers. Abbreviations of reservoir names are as given in Table 1.

Table 3. Length at 50 % maturity or mean length of maturity (L_m) of females and males, mean (\pm SE) egg diameter (ED) and mean (\pm SE) condition factor (K) of females and males *Oreochromis niloticus* in the 10 reservoirs studied. Abbreviation of reservoir names (Abbr.) are as given in Table 1.

Abbr.	L_m (cm)		ED (mm)	K (100g cm ⁻³)	
	Female	Male		Female	Male
AN	19.9	17.3	1.58 \pm 0.10	1.9 \pm 0.031	1.0 \pm 0.024
BW	19.5	18.7	1.46 \pm 0.15	2.1 \pm 0.043	2.1 \pm 0.058
DW	19	18.5	1.46 \pm 0.11	1.0 \pm 0.036	1.1 \pm 0.04
IB	25.7	23.4	1.64 \pm 0.21	1.0 \pm 0.037	1.9 \pm 0.03
KN	20.7	17.7	1.62 \pm 0.08	2.0 \pm 0.031	2.1 \pm 0.029
KT	20.2	19.9	1.42 \pm 0.08	2.1 \pm 0.034	2.0 \pm 0.07
KW	17.7	16.7	1.50 \pm 0.10	1.9 \pm 0.031	1.9 \pm 0.028
RJ	20.9	19.9	1.39 \pm 0.14	1.9 \pm 0.021	1.9 \pm 0.026
SG	22.5	22.3	1.67 \pm 0.22	2.1 \pm 0.035	2.0 \pm 0.035
US	21.7	21.2	1.72 \pm 0.12	1.9 \pm 0.036	1.9 \pm 0.034

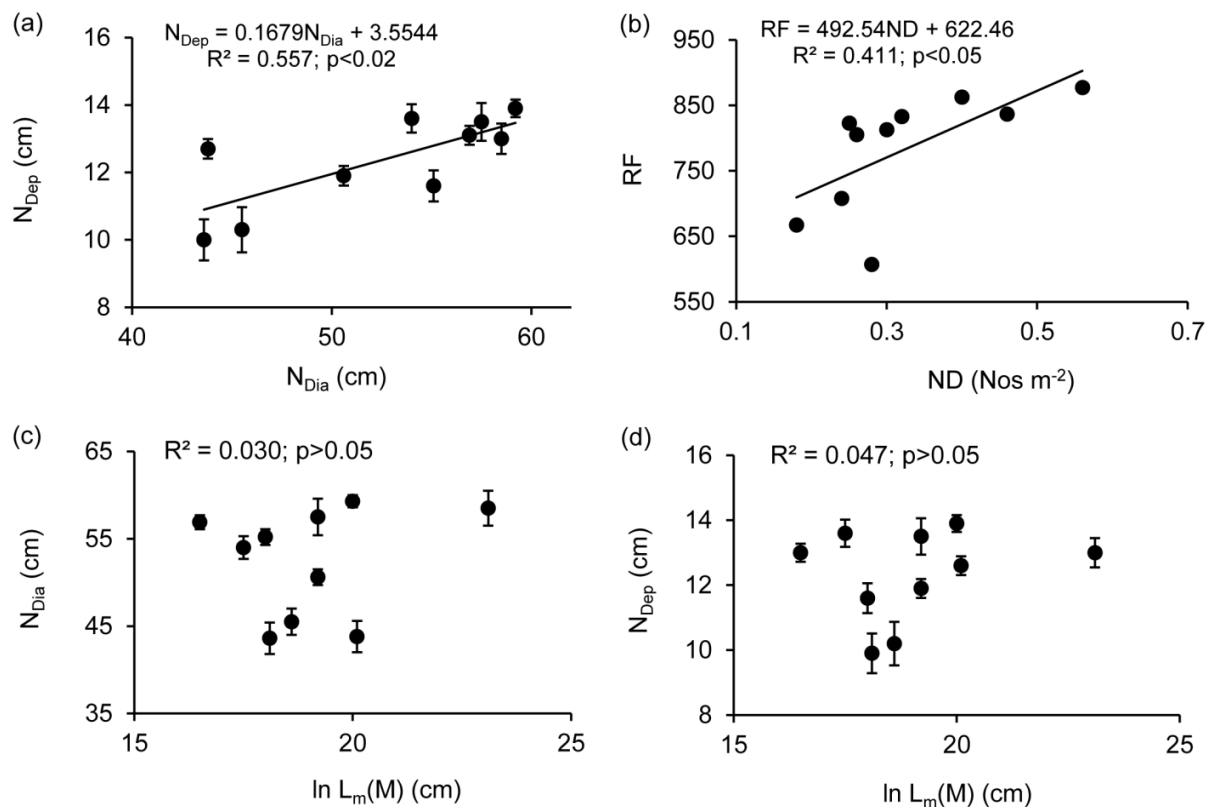


Fig. 5. The relationships of (a) nest diameter against depth of the nest ($N_{Dep} \pm SE$); (b) nest density (ND) against relative fecundity (RF); (c) nest diameter ($N_{Dia} \pm SE$) against male size of maturity ($L_{m(M)}$); and (d) depth of nest ($N_{Dep} \pm SE$) against $L_{m(M)}$ of *Oreochromis niloticus* in 10 reservoirs studied at Kala Oya river basin. GSI – Gonado-somatic index; L_m – Size of maturity. R^2 = Coefficient of determination. p - Probability level.

The positive linear relationship between RF and GSI_F (Fig. 6a) and the positive relationship between ED and $L_{m(F)}$ (Fig. 6b) indicate that the populations with higher GSI_F are more fecund and produce larger eggs. There was also a positive linear relationship of female GSI (GSI_F) with ND (Fig. 6c) indicating that nest site availability would govern fecundity in *O. niloticus*. RF of the fish was positively related to N_{Dep} (Fig. 6d). Although not significant at 0.05 probability level, RF was also positively related to N_{Dia} (Fig. 6e) showing that female fish were attracted to larger and deeper nests. The negative log-linear relationship between GSI_F and size of maturity ($L_{m(F)}$) of female (Fig. 6f) perhaps indicates reduced body condition.

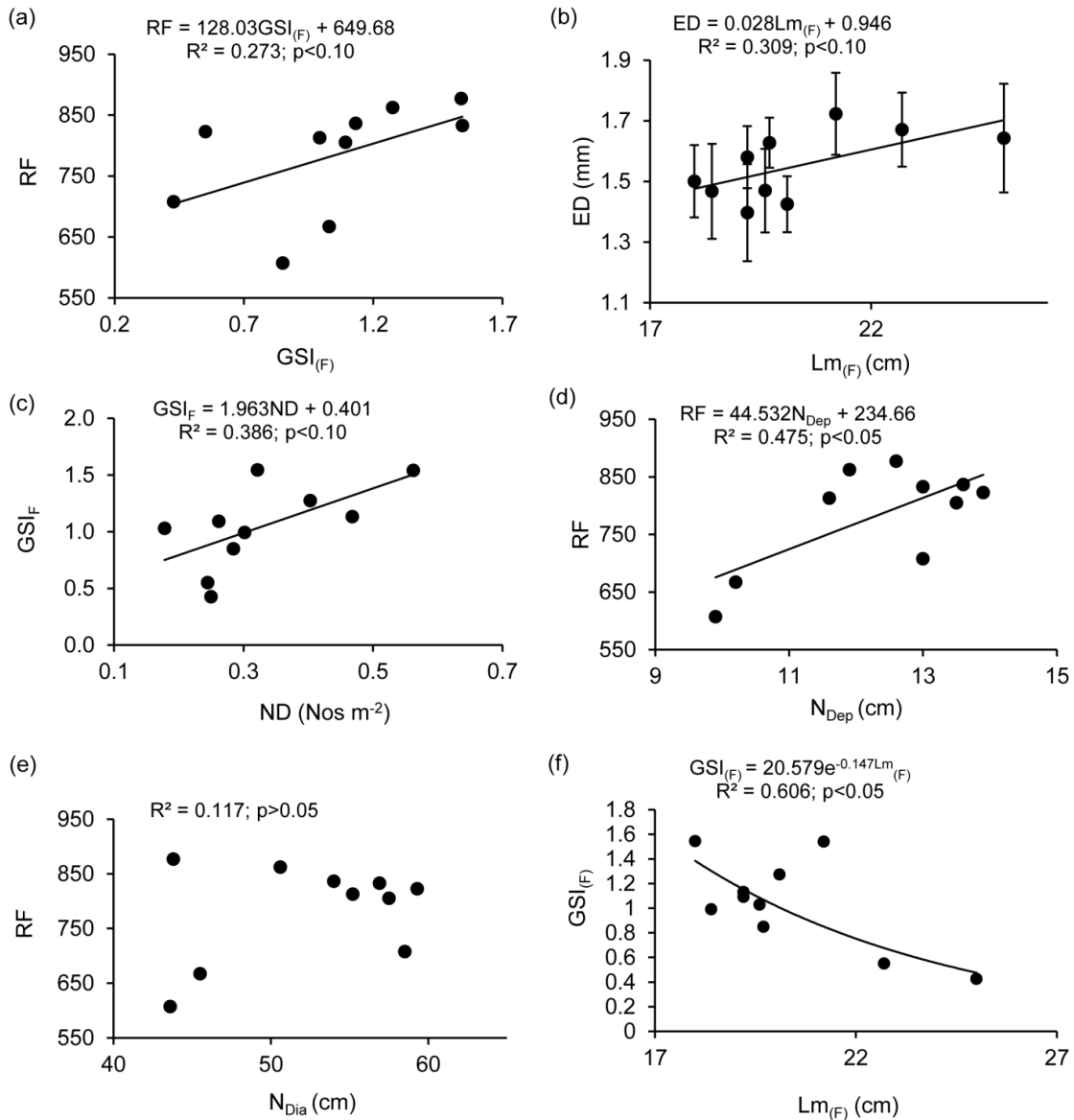


Fig. 6. The relationships of (a) relative fecundity (RF) against female gonado-somatic index (GSI_F); (b) egg diameter (ED) against $L_{m(F)}$; (c) nest density (ND) against female GSI (GSI_F); (d) relative fecundity (RF) against depth of nest (N_{Dep}); (e) RF against nest diameter (N_{Dia}); and (f) GSI_F against length at first maturity of female ($L_{m(F)}$) of *Oreochromis niloticus* in 10 reservoirs studied at Kala Oya river basin. R^2 = Coefficient of determination. p - Probability level.

Influence of FI on the reproductive biology of *O. niloticus* was evident from the negative relationship between ED and FI (Fig. 7a) and negative log-linear relationships of L_m of both females and males with FI (Fig. 7b). There were also negative linear relationships between FI and condition factor of both sexes of the fish populations in the 10 reservoirs (Fig. 7c).

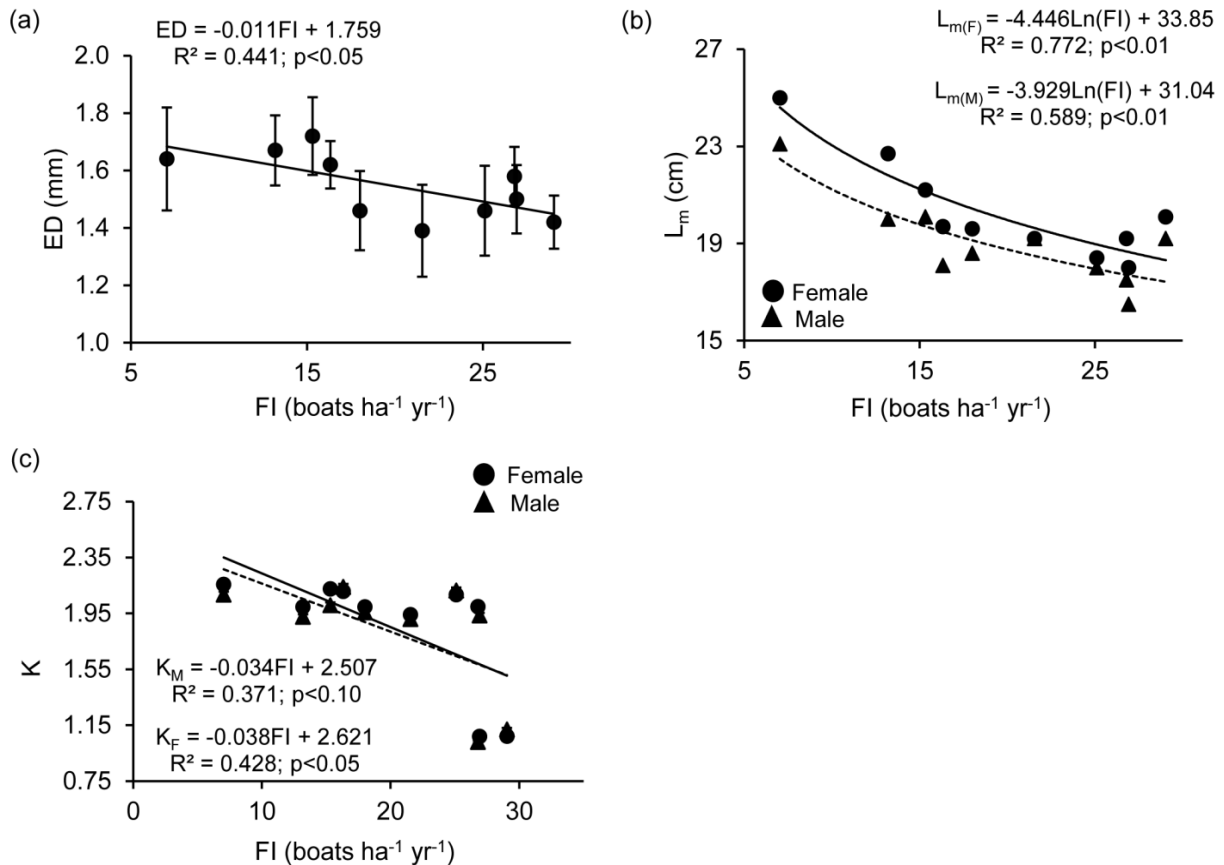


Fig. 7. The relationships of (a) egg diameter (ED) against fishing intensity (FI); (b) female and male L_m against FI; and (c) female and male condition factor (K) against FI. R^2 = Coefficient of determination. p - Probability level.

GSI values of both sexes plotted against sampling intervals in the 10 reservoirs are shown in Fig. 8, which indicate that mean spawning seasons occur roughly during December-January and April-May in all reservoirs. According to the observations made at the state-owned Aquaculture Development Centre, the nest building adult fish spend 8–12 days for nest excavation and territorial behaviour, 12–16 days for courtship and spawning, and 5–7 days for mouth egg incubation by females. Based on these observations, it was considered that on average, reservoir populations of *O. niloticus* also spend about 30 days to complete spawning cycle. WLF_I estimated on the basis of this value had significant positive log-linear relationship with nest density during the peak spawning seasons (ND_{PS} in Nos m⁻²) in the 10 reservoirs ($ND_{PS} = 0.144e^{1.072WLF_I}$; $R^2 = 0.552$; Fig. 9), showing that water level fluctuations in reservoirs studied had obvious effect on nesting of *O. niloticus*.

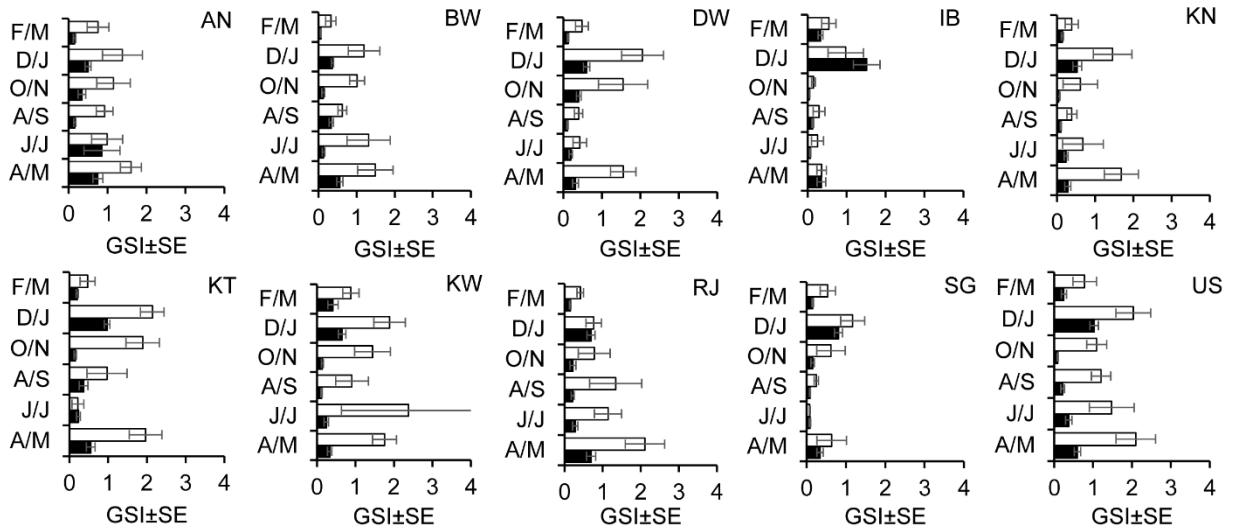


Fig. 8. Seasonal fluctuation of Gonadosomatic index (GSI) ± SE in female (open bars) and male (solid bars) *Oreochromis niloticus*. Abbreviations of reservoir names are as given in Table 1.

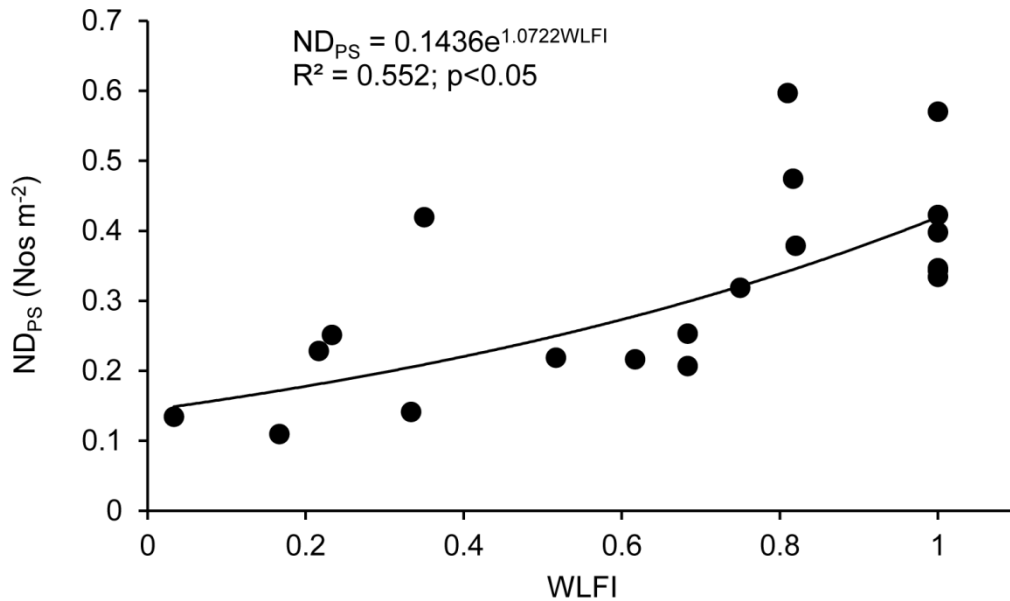


Fig. 9. Relationship of nest density during peak spawning periods (ND_{PS}) against WLF I in 10 reservoirs studied at Kala Oya river basin.

Discussion

The present study showed that larger matured male *O. niloticus*, which make larger and deeper nests have higher L_m (Fig. 5c and 5d). Also, females that were attracted to larger and deeper nest were more fecund and produced larger eggs (Fig. 6).

This implies that larger males spend more energy for nest construction and for the attraction of larger females which are more fecund producing larger eggs. In animal populations, mate selection is prominently related to the ability of females to choose the most suitable male (Candolin 2003). As such, it can be postulated that male *O. niloticus* invests energy to construct larger and deeper nests to attract larger females. In many animal taxa, mate selection by males is preferentially for larger, more fecund females (Katvala and Kaitala 2001; Kolm 2001; Wong and Jennions 2003). As evident from the present analysis, *O. niloticus* populations with higher GSI are more fecund (Fig. 6a) and those with larger L_m produce larger eggs (Fig. 6c), which indicate that reproductive investment during nest construction and courtship is perhaps optimised for the future survival of offspring. It has been reported that in a mating system of poeciliid fish, *Gambusia holbrooki* Girard 1859, the female mate choice is dominated by male sexual coercion (Bisazza et al. 2001), which can perhaps be similar to reproductive investment during nest building and courtship of male *O. niloticus*, as found in the present study.

The negative relationship between GSI and L_m of female *O. niloticus* (Fig. 6b) perhaps reflects the early maturity of females due to utilising more energy for gonadal growth. According to the life-history theory of organisms, when there are diminishing prospects of future reproduction, the situations favour increased current reproductive effort (Stearns 1992). Many life-history strategies such as r- and K-continuum (MacArthur and Wilson 1967; Pianka 1970) are related to a trade-off between reproduction and growth, especially in animal populations. In fish populations, high energy consumption for reproduction often results in early maturation and reduced body size (Renzick et al. 1990), which essentially reflects r-selected life strategies (Pianka 1970) or altricial traits (Bruton 1990).

It is also accepted that organisms in their communities place themselves in the continuum of r- and K-life strategies (MacArthur and Wilson 1967). The degree of fishing pressure, expressed as fishing intensity (FI), is essentially a disturbance agent (Iles 1973) in the habitats of reservoir populations of *O. niloticus*. Such r-selected species with early maturity and allocation of resources for reproduction dominate disturbed environments with high fishing pressure as opposed to favouring of K-selected counterparts of the same species and/or other species with late maturity allocating more resources for somatic growth in relatively undisturbed environments. Noakes and Balon (1982) equated r-selected and K-selected life strategies in cichlid populations to altricial-precocial dichotomy where altricial traits are those in unpredictable environments and precocial traits are those in more predictable environments (Balon 1981; Bruton 1990). From the present analysis, it was evident that FI was negatively related to ED of mature females, L_m and K of both sexes of *O. niloticus* in the 10 reservoirs studied. Smaller egg diameter, low L_m and low body condition are characteristic features of r-selected species or altricial traits which become dominant in unstable environments. As such, heavy fishing pressure in the reservoir fisheries favours r-selected life strategies.

According to Iles (1973), unstable environmental conditions caused by heavy predation and high fishing pressure are the driving forces to push tilapia populations towards r-selected life strategies. De Silva and Amarasinghe (1989) and Moreau (1999) have also shown that in *O. mossambicus* populations in Sri Lankan reservoirs, fishing pressure was negatively related to the length of maturity.

It was also evident from the positive log-linear relationship between nest density and WLFI (Fig. 9) that having the peripheral areas of reservoirs inundated for a sufficient duration is necessary for *O. niloticus* to complete the spawning cycle from nest construction to courtship and spawning. Reservoir water level fluctuations in Sri Lanka are predominantly governed by the irrigation demand in the command areas (Schiemer 1983; Renwick 2001). Nest density of *O. niloticus* in the 10 reservoirs studied showed positive relationships with relative fecundity and gonado-somatic index of fish and as such, it can be postulated that reservoir water level fluctuations due to irrigation demand have noteworthy effects on reproductive attributes of fish populations.

Hence, the present study highlighted that two anthropogenic factors, fishing intensity and reservoir water level fluctuations, influence life history patterns of reservoir populations of *O. niloticus*. As management of many biological populations often is not based on their life history strategies, the present analysis provides insight into profound management implications. Through effective coordination between irrigation authorities and fisheries authorities responsible for water management and fisheries management respectively, conditions in the reservoir environments can be manipulated to favour K-selected or precocial counterparts of *O. niloticus* populations to establish sustainable fisheries production.

Conclusion

Life history strategies in fish are known to be closely related to the conditions of the environment that they inhabit. Life history attributes of *O. niloticus*, an exotic fish species in many tropical countries including Sri Lanka, are known to be related to the chaos of the habitats. In the present analysis, reproductive biology traits of *O. niloticus* populations in selected irrigation reservoirs of Sri Lanka which contribute significantly to the reservoir capture fisheries were investigated in relation to fishing pressure and reservoir water level fluctuations due to irrigation demand. It is evident that larger male fish spend more energy for nest construction and for the attraction of larger females which are more fecund producing larger eggs. From the interrelationships of reproductive biology attributes, it can be postulated that high energy consumption for reproduction often results in early maturation and reduced body size, which essentially reflects r-selected life strategies or altricial traits. Unstable environmental conditions in irrigation reservoirs studied, caused by drastic water level fluctuations and high fishing pressure might be the driving forces to favour r-selected life strategies in reservoir populations of *O. niloticus*.

As such, it appears to be possible that through effective coordination between irrigation authorities and fisheries authorities responsible for water management and fisheries management respectively, conditions in the reservoir environments can be manipulated to favour K-selected or precocial counterparts of *O. niloticus* populations to establish sustainable fisheries production.

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