



Life-History Strategies of Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758) (Teleostei, Cichlidae), in Irrigation Reservoirs of Sri Lanka

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Abstract

As in many tropical countries, reservoir fishery of Sri Lanka is dominated by the exotic cichlid, *Oreochromis niloticus* (Linnaeus, 1758). *Oreochromis niloticus* populations in irrigation reservoirs are expected to be under the influence of various disturbances such as changes in hydrological regimes, trophic conditions and fishing pressure. In the present study, an attempt was made to investigate the effect of biological productivity and fishing pressure on life history patterns of *O. niloticus* populations in 10 irrigation reservoirs of Sri Lanka. *Oreochromis niloticus* populations in environmentally stressed reservoirs, exhibited low age at maturity than those inhabiting reservoirs with relatively low biological productivity. Hydraulic retention time (HRT) in reservoirs also had negative influence on size and age at maturity of *O. niloticus*. As length at first capture of *O. niloticus* is positively related to mean length at maturity, these attributes have significant implications on the optimal fishing. Fishing intensity (FI) in *O. niloticus* populations also had negative influences on mean length and age at maturity. Hence, the present study supports the opinion that altricial or opportunistic traits having faster growth and achieving maturity early in the life dominate disturbed environments and that precocial or equilibrium traits exhibiting delayed maturity occur in more stable environments. Possible shifting of life history strategies of *O. niloticus* to opportunistic traits due to disturbance events could be manipulated by increasing FI for smaller individuals in the population.

Keywords: Cichlidae, Nile tilapia, r- and K- selection, stunting, tropical reservoirs

Introduction

The life history strategy of an organism is defined as the trade-off among energetic investments in growth, reproduction, and survivorship to solve particular ecological problems (Stearns, 1992), and is usually vibrant between continuum of r- (small-bodied, short-lived individuals with high fecundity and low per capita investment per offspring) and K- (large-bodied, long-lived individuals with low fecundity and high per capita investment per offspring) strategies (MacArthur and Wilson, 1967; Pianka, 1970; Stearns, 1976). In the rapidly changing environment, the species would be likely to favour rapid growth and early reproduction referred to as 'opportunistic' population. The populations in more constant environment commonly behave as 'equilibrium' ones with slower growth and delayed reproduction (Winemiller, 1989; Winemiller and Rose, 1992).

In animals such as fishes, amphibians and reptiles that continue to grow following sexual maturation, energy in excess of immediate metabolic requirements for maintenance is allocated to somatic growth and reproduction (Charnov, 1993; Heino and Kaitala, 1999). In teleost fish populations, a trade-off is achieved between energy allocation for reproduction and growth. This enables defining reproductive effort in that the proportion of energy that fishes spend for reproduction as opposed to growth, is influenced by the disturbances of the natural environment (Roff, 1983; Gunderson and Dygert, 1988; Gunderson, 1997). Based on the reproductive investment, organisms are suggested to be placed in the continuum from 'capital breeding', a situation in which reproduction is performed by stored energy, to 'income breeding', where concurrent energy is used for reproduction (Stephens et al., 2009; McBride et al., 2015). This phenomenon has important implications in the

fisheries and aquaculture because faster growth of fish is favoured in aquaculture systems to achieve marketable size of harvest within a short duration. In tilapia populations, phenotypic variations are reported to occur in that feral populations are characterised by slow growth with high maximum body size (Moreau et al., 1986) as opposed to those in aquaculture systems having faster growth in small maximum body size (Pauly et al., 1988). Iles (1973) argued that in tilapia populations under adverse environmental conditions, maturation at an earlier age and increased relative fecundity enable fish to withstand high mortality rates. Hence, life history strategies of fish in changing environments that are vibrant between the traits favouring rapid growth and early reproduction and those supporting slower growth and delayed reproduction, are important attributes to be explored for effective management of the fishery resources.

The inland fishery of Sri Lanka is almost entirely dependent on the multitude of reservoirs. As the primary use of most ancient reservoirs is irrigation of agricultural lands, fisheries production is essentially a secondary use of reservoir resources and is supported by the introduced populations of *Oreochromis niloticus* (Linnaeus, 1758) (Amarasinghe and Weerakoon, 2009). There are various disturbance events in irrigation reservoirs such as changes in hydrological regimes, trophic conditions and fishing pressure (Nadarajah et al., 2018a, 2019), and as such, life history patterns of *O.*

niloticus populations are hypothesised to be under the influence of such disturbances. In the present study, an attempt was made to investigate factors influencing life history patterns of *O. niloticus* populations in irrigation reservoirs of Sri Lanka in relation to biological productivity, hydraulic retention time and fishing pressure.

Materials and Methods

In the present analysis, attempts were made to investigate the effect of some environmental perturbations associated with hydrological regimes and fishing pressure on selected life history parameters of *O. niloticus* in 10 irrigation reservoirs in a major river basin (the Kala oya river basin) in Sri Lanka. *Oreochromis niloticus* populations in the 10 reservoirs are self-sustaining feral populations, which feed on natural food resources in the reservoir ecosystems. Morphometric and physico-chemical characteristics, map of the Kala oya river basin depicting geographical locations of 10 reservoirs are given elsewhere (Bandara and Amarasinghe, 2018; Nadarajah et al., 2018a). For clarity, geographic coordinates of the 10 reservoirs studied and some of their morphometric and edaphic characteristics are given in Table 1. The reservoir extent at full supply level ranged from 146 ha (Siyambalangamuwa) to 1980 ha (Kalawewa).

Table 1. Geographic coordinates, and some of their morphometric and edaphic characteristics of the 10 reservoirs in the Kala oya river basin, Sri Lanka.

Reservoir(Abb)	Geographic coordinates	CA (km ²)	RA at FSL (ha)	Mean depth (m)	Temp ± SE (°C)	Cond. (µS.cm ⁻¹)	Alk. (m. equiv.L ⁻¹)
Angamuwa (AN)	80°14'E; 8°10'N	129.5	792	1.99	27.91 ± 0.28	407.2	170.7
Balaluwewa (BW)	80°32'E; 7°58'N	269.8	934	4.43	27.44 ± 0.28	244.8	115.5
Dewahuwa (DW)	80°33'E; 7°48'N	67.3	433	3.13	27.66 ± 0.59	275.6	130.7
Ibbankatuwa (IB)	80°41'E; 7°52'N	169.0	405	2.89	27.07 ± 0.55	169.0	100.0
Kandalama (KN)	80°41'E; 7°53'N	98.0	736	4.58	27.87 ± 0.61	200.8	111.9
Katiyawa (KT)	80°24'E; 8°7'N	86.7	257	2.16	27.81 ± 0.35	377.9	153.8
Kalawewa (KW)	80°32'E; 8°1'N	572.0	1980	4.43	27.46 ± 0.32	207.2	98.2
Rajanganaya (RJ)	80°14'E; 8°9'N	1611.0	1599	6.30	28.00 ± 0.35	380.1	153.2
Siyambalangamuwa (SG)	80°28'E; 7°57'N	46.6	146	1.78	28.26 ± 0.51	384.2	138.4
Usgala Siyambalangamuwa (US)	80°18'E; 8°4'N	184.6	769	3.47	27.88 ± 0.38	448.1	148.4

Abb. – abbreviations of reservoir names; CA – catchment area in km²; RA – reservoir area; FSL – full supply level; Temp – water temperature; Cond. – electrical conductivity; Alk. – total alkalinity.

Mean lengths at maturity of female *O. niloticus* of the 10 reservoirs used in the present analysis were obtained from Bandara and Amarasinghe (2018). Asymptotic total length (L_{∞}), fishing mortality (M) and mean length at first capture or length at 50 % retention in the fishing gear (L_c) of 10 *O. niloticus* populations, estimated by mean of FiSAT II (version 2.1.1) software package (Gayanilo et al., 2005) in a parallel study (Bandara et al., 2020), were also used in this analysis. Daily water level data in individual

reservoirs and data on reservoir outflow, depending on the availability, were obtained for 3 to 6 years between 2010 and 2015, from the databases of the Irrigation Department and the Mahaweli Authority of Sri Lanka. In a parallel study on the status of the fisheries of 10 reservoirs, fish production and fishing effort data were collected from the data-logs of fishers from January 2010 to December 2015 (Nadarajah et al., 2018a). Based on these data, mean annual fishing intensity (FI) was determined and was

expressed as the number of boats ha⁻¹.yr⁻¹ (Sanders and Morgan, 1976; Gulland, 1983). Also, chlorophyll-*a* content (Chl-*a*), and two measures of morpho-edaphic indices (MEI), determined as ratio of total alkalinity to mean depth (MEI_o) and ratio of electrical conductivity to mean depth (MEI_c) given by Nadarajah et al. (2018b) were used in this analysis.

As age and length in fish are not linearly related, for comparative analysis of the growth of *O. niloticus* population in 10 reservoirs, absolute age of maturity and absolute age at first capture were used for the analysis, in addition, to mean lengths at maturity of female *O. niloticus* population and mean length at first capture. For this purpose, the theoretical age at zero length (*t*₀) was calculated using the following empirical formula (Pauly, 1979).

$$\text{Log}_{10}(-t_0) = -0.3922 - 0.275 \log_{10} L_\infty - 1.038 \log_{10} K \quad (1)$$

Using growth parameters (*L*_∞, *K* and *t*₀) of *O. niloticus* population in 10 reservoirs, age of maturity (*t*_m) of each population was estimated from inverse von Bertalanffy growth formula (VBGF) given below (Gulland, 1983).

$$t_m = \frac{1}{K} \ln \frac{L_\infty}{L_\infty - L_m} + t_0 \quad (2)$$

where *L*_m is the length of maturity of female *O. niloticus*. Similarly, age at first capture (*t*_c) was also estimated using the following form of the same equation.

$$t_c = \frac{1}{K} \ln \frac{L_\infty}{L_\infty - L_c} + t_0 \quad (3)$$

Mean annual hydraulic retention time (HRT in yr) of each reservoir was determined by the following equation (Dillon, 1975).

$$\text{HRT} = \frac{\text{Reservoir volume in million cubic metres (MCM)}}{\text{Annual outflow (MCM yr}^{-1}\text{)}} \quad (4)$$

The possible relationships between life history parameters and environmental factors pertaining to biological productivity, hydrological changes and fishing intensities were explored to investigate the effect of environmental factors on life history strategies of *O. niloticus*. Here, productivity-related variables such as Chl-*a* and MEI, fishery-related variables such as fishing intensity, fishing mortality, mean length and age at first capture, and the hydrological variable, HRT, were related to life history strategies of *O. niloticus*. Life history-related variables considered in the regression treatments were VBGF parameters and length and age of maturity. The ratio of *L*_m/*L*_∞ was also determined to investigate whether there was a consistency across the 10 populations of *O. niloticus*, which was postulated by Pauly (1984) to explain 'precocious' spawning.

Results

Von Bertalanffy growth parameters (*L*_∞, *K* and *t*₀), mortality rates (*Z*, *M* and *F*), length and age of maturity (*L*_m and *t*_m), length and age at first capture (*L*_c and *t*_c) and *L*_m/*L*_∞ ratio of *O. niloticus* population in 10 irrigation reservoirs are given in Table 2. The ratio of *L*_m/*L*_∞ in the 10 *O. niloticus* populations was in fair consistency ranging from 0.34 in Kalawewa to 0.56 in Ibbankaruwa.

The growth curves drawn from the von Bertalanffy growth formula (VBGF), *L*_t = *L*_∞[-exp{-*K*(*t* - *t*₀)}], where *L*_t is the length at age *t*, are shown in Figure 1. Also shown in Figure 1 is the plot of Ln *L*_∞ against Ln *K*, indicating that VBGF parameters of 10 *O. niloticus* populations fall within the "growth space" of the species (Pauly, 1998).

The attributes that were thought to be affecting life history strategies of *O. niloticus* populations, included fishery-related parameters (FI and fishing mortality), biological productivity-related parameters (Chl-*a*, MEI_o and MEI_c) and a hydrology-related parameter, HRT (Table 3).

Table 2. Von Bertalanffy growth parameters (*L*_∞ and *K*) of *Oreochromis niloticus* population in 10 irrigation reservoirs, estimated by means of ELEFAN technique as implemented in FiSAT software (Bandara et al., 2020). Also given are the values of *t*₀ of the 10 *O. niloticus* populations as an estimate from Equation 1.

Reservoir	<i>L</i> _∞ (cm)	<i>K</i> (yr ⁻¹)	<i>t</i> ₀ (yr)	<i>Z</i> (yr ⁻¹)	<i>M</i> (yr ⁻¹)	<i>F</i> (yr ⁻¹)	<i>L</i> _m (cm)	<i>t</i> _m (yr)	<i>L</i> _c (cm)	<i>t</i> _c (yr)	<i>L</i> _m / <i>L</i> _∞
Angamuwa	42.8	0.31	-0.27	1.83	0.74	1.09	19.9	1.75	17.88	1.47	0.46
Balaluwewa	48.5	0.24	-0.20	1.34	0.60	0.74	19.5	1.94	16.11	1.48	0.40
Dewahuwa	48.8	0.42	-0.34	1.88	0.87	1.01	19.0	0.83	15.75	0.59	0.39
Ibbankatuwa	46.2	0.24	-0.20	0.71	0.61	0.10	25.7	3.19	19.30	2.05	0.56
Kandalama	51.3	0.28	-0.53	1.25	0.66	0.59	20.7	1.32	16.89	0.90	0.40
Katiyawa	48.4	0.52	-0.22	2.87	1.00	1.87	20.2	0.82	14.35	0.46	0.42
Kalawewa	51.5	0.27	-0.54	2.06	0.64	1.42	17.7	1.02	16.68	0.91	0.34
Rajanganaya	53.4	0.49	-0.29	3.84	0.94	2.90	20.9	0.72	17.25	0.51	0.39
Siyambalangamuwa	45.1	0.23	-0.66	0.80	0.60	0.20	22.5	2.34	18.20	1.59	0.50
Usgala Siyambalangamuwa	49.9	0.2	-0.16	1.83	0.53	1.30	21.7	2.69	15.80	1.74	0.43

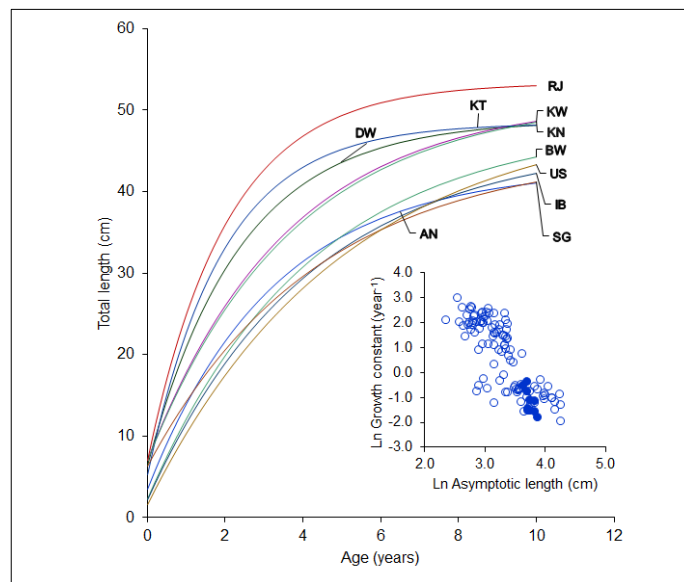


Fig. 1. Growth curves of 10 reservoir populations of *Oreochromis niloticus*. Inset shows the positions of the 10 populations in the “growth space” of *O. niloticus* as reported in www.fishbase.org. AN: Angamuwa; BW: Balaluwewa; DW: Dewahuwa; IB: Ibbankatuwa; KN: Kandalama; KT: Katiyawa; KW: Kalawewa; RJ: Rajanganaya; SG: Siyambalangamuwa; US: Usgala Siyambalangamuwa.

Table 3. Two morpho-edaphic indices (MEI_o and MEI_c), mean annual hydraulic retention time (HRT), chlorophyll-a content (Chl-a), mean annual fishing intensity (FI) and trophic state index (Carlson and Simpson, 1996) in 10 irrigation reservoirs studied.

Reservoir	MEI_o	MEI_c	HRT (yr)	Chl-a ($\mu\text{g}\cdot\text{L}^{-1}$)	FI (boat-days $\cdot\text{yr}^{-1}$)	Fish yield ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	TSI*
Angamuwa	85.6	204.2	0.315	17.96	26.8	175.4	63.56
Balaluwewa	26.0	55.2	0.149	24.48	25.1	160.5	64.14
Dewahuwa	41.7	88.0	1.476	20.58	18.0	102.9	60.76
Ibbankatuwa	34.6	58.4	0.012	8.00	7.0	94.5	60.25
Kandalama	71.2	175.0	0.748	22.43	10.3	43.9	63.21
Katiyawa	22.2	46.7	0.388	25.21	9.0	76.5	62.40
Kalawewa	24.4	43.8	0.149	25.12	26.9	120.4	63.46
Rajanganaya	24.3	60.4	0.448	19.80	21.6	114.6	60.86
Siyambalangamuwa	77.7	215.7	0.156	8.22	13.2	175.6	57.78
Usgala Siyambalangamuwa	42.2	128.9	0.191	17.62	15.3	134.1	59.41

*Nadarajah, 2019.

(Sources: Nadarajah et al., 2018a, 2018b).

Asymptotic length of *O. niloticus* in 10 reservoir populations was negatively related to MEI_c (Fig. 2a) and MEI_o (Fig. 2b), showing that in biologically productive reservoirs, maximum size of *O. niloticus* was smaller than in less productive reservoirs. Although not significant at 5 % probability level, asymptotic length of *O. niloticus* was positively related to reservoir extent (Fig. 2c).

There were negative logarithmic relationships of mean length of maturity of female *O. niloticus* in the 10 irrigation reservoirs with fishing intensity (Fig. 3a) and fishing mortality (Fig. 3b). Age at maturity of female *O. niloticus* in the 10 reservoirs was also negative logarithmically related to fishing mortality (Fig. 3c). Mean length of maturity of female *O. niloticus* 10 reservoir populations had positive linear relationships

with mean length at first capture (Fig. 3d) and mean age at first capture (Fig. 3e).

Chlorophyll-a (Chl-a) content in the 10 reservoirs was negative linearly related to mean length of maturity (Fig. 4a) and age of maturity (Fig. 4b) of female *O. niloticus* indicating that in biologically productive reservoirs, *O. niloticus* attains maturity early. There was a positive ln-ln relationship between HRT and Chl-a (Fig. 4c) indicating that the reservoirs with high HRT were biologically more productive than those with low HRT. Negative ln-linear relationships between HRT and mean length of maturity (Fig. 4d) and age of maturity (Fig. 4e) of female *O. niloticus* also substantiated the perception that early maturity of *O. niloticus* was experienced in biologically more productive irrigation reservoirs.

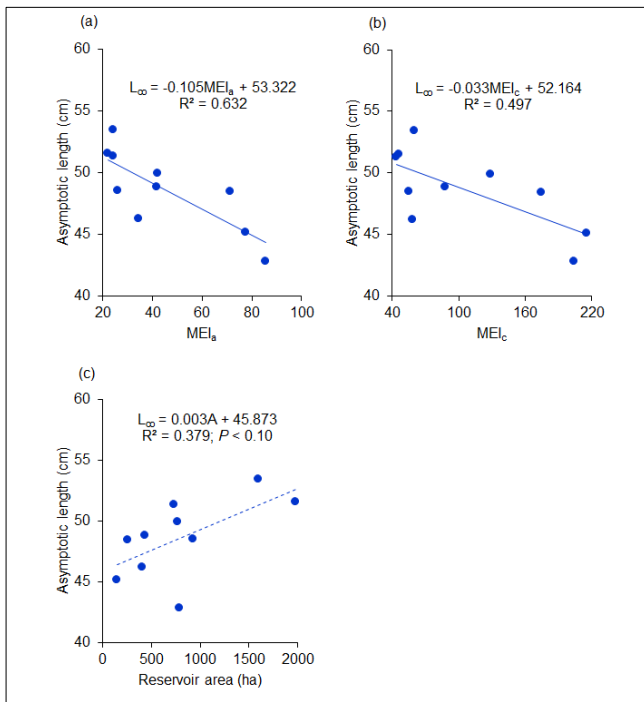


Fig. 2. Relationship of asymptotic length (L_{∞}) of *Oreochromis niloticus* in 10 reservoir populations with morpho-edaphic indices (MEI) (a) based on alkalinity (MEI_a); (b) based on conductivity (MEI_c); and (c) reservoir area (A).

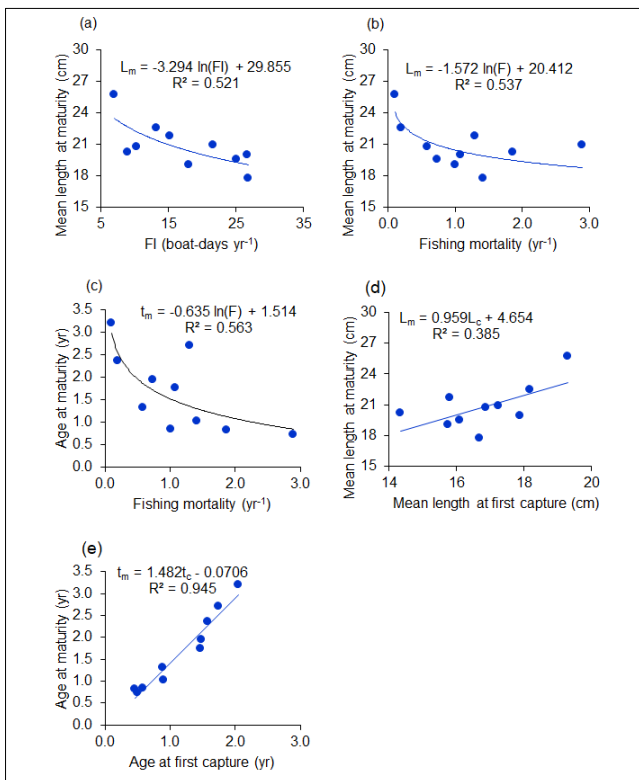


Fig. 3. Relationships of attributes of reproductive biology of 10 *Oreochromis niloticus* populations with fishery-related parameters. L_m = mean length at maturity; t_m = age at maturity; L_c = mean length at first capture; t_c = age at first capture; FI = fishing intensity; F = fishing mortality.

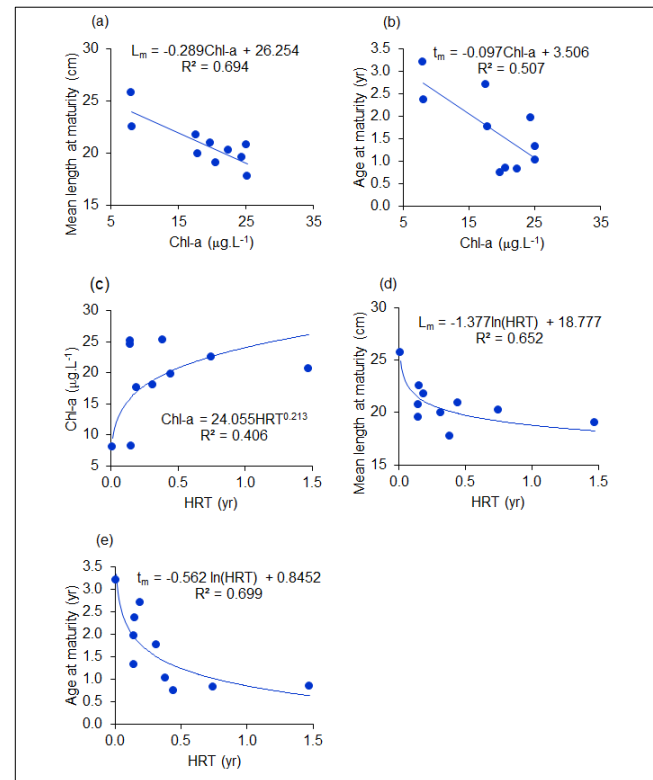


Fig. 4. Relationships of reproductive biology attributes of 10 *Oreochromis niloticus* populations with chlorophyll-a content (Chl-a) (Figs. a and b); relationship of Chl-a and hydraulic retention time (HRT) (Fig. c); and relationships reproductive biology attributes of 10 *O. niloticus* populations with HRT (Figs. d and e). L_m = mean length at maturity; t_m = age at maturity.

Discussion

The growth curves determined from the analysis of length frequency data of *O. niloticus* in 10 reservoirs (Bandara et al., 2020) indicated that across the reservoirs in the same river basin, there was considerable difference of growth pattern. As growth performance index ($\phi' = \log_{10} K + 2 \text{Log}_{10} L_{\infty}$, where K is growth constant and L_{∞} is asymptotic length) estimated for each *O. niloticus* population (Bandara et al., 2020) was within the range reported elsewhere (range: 1.56 - 3.72; mean: 2.97; Froese and Pauly, 2019), it could be established that the estimated VBGF parameters were biologically reasonable. From the present analysis, it was evident that L_{∞} of *O. niloticus* was positively related to habitat size (Fig. 2c). It is generally accepted that smaller, shallower lentic water bodies are biologically more productive than larger, deeper ones (Wetzel, 2001). The non-significant positive relationship between L_{∞} of *O. niloticus* and habitat size (Fig. 2c) might be due to narrow range of L_{∞} of the 10 populations of fish in reservoirs of the same river basin. The mean trophic state indices (TSI) in all 10 reservoirs were greater than 50 (Table 3) so that all these reservoirs can be treated as eutrophic with anoxic hypolimnia (Carlson and Simpson, 1996). Although estimated VBGF parameters fall within narrow ranges, present analysis permitted to explore factors influencing life history features of *O. niloticus* populations.

The negative relationships of L_{∞} of *O. niloticus* with two biological productivity-related indices, MEI_r (Fig. 2a) and MEI_c (Fig. 2b) indicated that fish populations inhabiting reservoirs with high biological productivity appeared to possess smaller maximum body sizes. Reservoirs, being the semi-fluvial environments that fall between rivers and lakes on a continuum of aquatic ecosystems, there is a considerable spatial and temporal heterogeneity of biological productivity (Kimmel and Groeger, 1984) making them environmentally unstable. It has been shown that stress factors in the aquatic environments cause elevated maintenance metabolism in fish populations to grow to smaller ultimate body sizes and mature at smaller body size (Pauly, 1984). Noakes and Balon (1982) indicated that tilapia populations with early maturity dominate the productive aquatic systems because fish allocate energy for reproduction and mentioned that this was a characteristic feature of altricial traits. As it was evident from the present analysis that length at first capture and age at first capture were positively related to length of maturity and age of maturity respectively, it could be apprehended that optimal fishing strategies of *O. niloticus* populations are influenced by life history strategies. The consistency of L_m/L_{∞} ratios in the 10 *O. niloticus* populations support the hypothesis of Pauly (1984) that stress factors cause elevated maintenance metabolism in fish populations to grow to smaller ultimate body sizes and mature at smaller body size.

The negative influence of fishing intensity on mean size of maturity and fishing mortality was evident from the present analysis. This was further substantiated by the negative relationships of fishing mortality with the length of maturity (Fig. 3b) and age at maturity (Fig. 3c). De Silva and Amarasinghe (1989) and Moreau (1999) have also shown negative influences of fishing pressure on the size of maturity of *Oreochromis mossambicus* (Peters, 1852) populations in Sri Lankan reservoirs. Based on the analysis of a broad database (www.fishbase.org), Froese and Binohlan (2000) have shown that optimal fishing strategies of fish stocks are influenced by life history strategies, who presented empirical relationships estimate L_{∞} from maximum observed length (L_{max}), length at first maturity (L_m) from L_{∞} , life span (t_{max}) from age at first maturity (t_m), and length at maximum possible yield per recruit (L_{opt}) from L_{∞} and from L_m , respectively. The degree of fishing pressure, expressed as fishing intensity (FI), is essentially a disturbance agent in the habitats of reservoir populations of *O. niloticus*. Organisms are known to exhibit life history patterns ranging from r-selection to K-selection (Pianka, 1970). According to MacArthur and Wilson (1967), r-selected species having early maturity and allocating energy for reproduction, dominate disturbed environments, as opposed to K-selected counterparts of the same species and/or other species with late maturity allocating more resources for somatic growth in relatively undisturbed environments. According to Noakes and Balon (1982), these r- and K-selected life strategies are analogous to altricial-precocial dichotomy, where altricial traits dominate unpredictable environments and precocial traits occur in more predictable environments.

In the *O. niloticus* populations in the 10 irrigation reservoirs, Chl-*a* was found to negatively influence mean size of maturity and mean age at maturity, further indicating that high biological productivity in the habitat brings about early maturity of fish. Hydraulic retention time (HRT) is known to be a factor influencing biological productivity in reservoirs (Kimmel and Groeger, 1984; Straškraba et al., 1993; Kawara et al., 1998). From the hydrological point of view, reservoirs characterised with higher HRT can be treated as more 'stable'. However, they are relatively stagnant, and generally allow the release of bioavailable nutrients from the sediment such as phosphorus and dissolved inorganic nitrogen as well as a shift in nitrogen species from nitrate to ammonium (Chen et al., 2020) making them environmentally perturbed. In the present study too, ln-transformed Chl-*a* and HRT were positively related (Fig. 4c). The negative ln-linear relationship of HRT with L_m and t_m of *O. niloticus* in the 10 irrigation reservoirs, as found in the present study, therefore further confirms that fish tend to mature early in their life in biologically productive habitats, perhaps due to allocation of dietary energy for reproduction.

The results of the present analysis corroborate another important life history strategy in *O. niloticus* populations. In the feral populations, tilapias are frequently observed to mature early, especially in small water bodies (Kolding, 1993). This phenomenon of plasticity in growth and maturity is generally referred to as "stunting" (El-Sayed, 2006), but the reasons for stunting in tilapias remain rather controversial. Eyeson (1983) mentioned that in pond aquaculture of *Sarotherodon melanotheron* Rüppell, 1852 due to prolific breeding, ponds became overcrowded and that as a result, there would be food shortage and slowing down of growth. Bhujel et al. (2007) mentioned that stunting in tilapia in experimental ponds as well as natural water bodies was due to overcrowding, limited food supply and other environmental stresses. This implies that the phenomenon of stunting would be due to poor nutrition caused by overcrowding. According to Iles (1973), on the other hand, stunting in tilapias is not due to overcrowding, but due to pre-adaptation of counterparts in the population to mature early in unstable environmental conditions such as predation. One can postulate that the positive relationship between L_{∞} and reservoir size (Fig. 2c) also reflects overcrowding and/or resource competition, making maximum body size of *O. niloticus* populations smaller in small water bodies. However, our contention is that early maturity and smaller maximum body size of *O. niloticus* populations was due to their response to unstable environmental conditions supporting the view point of Iles (1973). Kolding (1993) based on Pauly's (1984) hypothesis on the relationship of available oxygen and metabolism, postulated that stunting of *O. niloticus* in small water bodies was attributed to fluctuating oxygen content. Lorenzen (2000) has also discussed the phenomenon of stunting in the context of life history strategies in cichlids. It was shown that population densities were not responsible for stunted body size of *Lepomis microchirus* Rafinesque, 1819 (Aday et al., 2002). Kolding et al. (2008), based on the evidence from aquarium experiments, have shown that it was phenotypic plasticity of length at maturity of *O. niloticus*, which varied at different environmental conditions, but not age at maturity. From the present analysis, however, it was evident that in biologically more productive reservoirs, *O. niloticus* mature early in their life. It was also evident that heavy fishing pressure in reservoir fisheries, causing unstable environmental conditions has also brought about early maturity of *O. niloticus*. Hence, the present study supports the opinion with regard to life history strategies of tilapias, presented by Noakes and Balon (1982), who stated that altricial traits having faster growth and early maturity dominate unpredictable environments and precocial traits exhibiting delayed maturity occur in more predictable environments. However, as the present analysis dealt with the investigation of variable life history traits of 10 *O. niloticus* populations in relation to environmental perturbation, it is more appropriate to refer to populations which would be likely to favour rapid

growth and early reproduction as 'opportunistic' populations, and those in more constant environments as 'equilibrium' populations with slower growth and delayed reproduction (Winemiller, 1989; Winemiller and Rose, 1992).

A comprehensive review of fishes and fisheries of Asian inland lacustrine waters (Amarasinghe and De Silva, 2015) has revealed that most studies on population dynamics of reservoir fish populations have been reported from Sri Lanka. Jutagate and Krudpan (2004) studied population dynamics of a cyprinid, *Morulius* (= *Labeo*) *chrysophekadion* (Bleeker, 1849) in a Thai reservoir. Jutagate et al. (2010) investigated changes in the environmental conditions and fish assemblages due to dam construction in the Pak Mung River, Thailand and recommended sluice regulation to allow fish to move between the river and the estuary. Lorenzen (1995) has developed a population dynamics model for culture-based fisheries (CBF) that can be used to address the key management problems of CBF in small reservoirs.

Reservoirs in Sri Lanka have been constructed in the past for irrigation purposes, and fisheries development is essentially a secondary use. As such, strategies for management of reservoir fisheries should be viewed within the constraints of multiple uses of reservoir resources. Water demand for irrigation greatly influences HRT. On the other hand, FI is an attribute that can be managed by the fisheries authorities. As FI and HRT are shown to be important factors affecting life history strategies of *O. niloticus* in irrigation reservoirs, strategies for the management of reservoir fisheries that are dominated by exotic cichlids, as is the case of the Sri Lankan context, should be based on trade-off between multiple uses of reservoir resources. This is of particular importance because variable life history strategies of *O. niloticus* across reservoirs might have significant impacts on the optimal fishing strategies, especially on the optimal length of first capture for long-term sustainability of the fisheries.

Conclusion

Reservoir fishery of Sri Lanka is essentially a secondary use of reservoir resources, which were constructed in the past for irrigating agricultural lands. The exotic species, *Oreochromis niloticus*, is the mainstay in the fishery. Investigation of the effect of biological productivity and fishing pressure on life history patterns of *O. niloticus* populations in 10 irrigation reservoirs of Sri Lanka indicated that populations in biologically more productive reservoirs, exhibited low age at maturity than those inhabiting reservoirs with relatively low biological productivity. Hence, high biological productivity in reservoir ecosystems provides appropriate habitats for altricial or opportunistic life strategies favouring better growth of *O. niloticus* but with a tendency to mature early their life. On the other hand, precocial or

equilibrium traits exhibiting delayed maturity occur in more predictable environments. Life history strategies of *O. niloticus* are therefore influenced by disturbance events such as changing HRT and FI, which are attributes that can be managed by the irrigation and fisheries authorities, respectively. As such, strategies for the management of reservoir fisheries that are dominated by exotic cichlids such as Sri Lankan reservoir fisheries should be based on the trade-off between multiple uses of reservoir resources. Furthermore, possible shifting of life history strategies of *O. niloticus* to opportunistic traits due to disturbance events could be manipulated by increasing FI for smaller individuals in the population.

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