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Population Dynamics of Commercially Important Fish Species in Two Reservoirs of the Walawe River Basin, Sri Lanka

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Abstract

Population dynamics of dominant fish species in two lowland reservoirs of Sri Lanka were studied based on length-based stock assessment methodologies, as implemented in FiSAT II software. The estimated growth parameters of *Oreochromis mossambicus* in Udawalawe and Chandrikawewa reservoirs and those of *O. niloticus* and *Labeo dussumieri* in Udawalawe reservoir fall within the growth space of auximetric plots of cichlids and cyprinids indicating reliability of estimates. In the Chandrikawewa reservoir where *O. mossambicus* exhibited faster growth, increased fishing pressure might lead to push the population towards the extreme of 'r-selected' life strategy so that continuation of the fishery at the present exploitation level is advisable. Relative yield-per-recruit (Y'/R) analyses indicate that for *O. niloticus* and *L. dussumieri* in Udawalawe reservoir, exploitation levels can be increased to optimize Y'/R. However, since these two species and *O. mossambicus* are caught in the same fishing gear, exploitation rate for *O. niloticus* and *L. dussumieri* has to be increased to a level that would not lead to over-exploitation of *O. mossambicus* stock.

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Introduction

Sri Lanka has a long tradition of reservoir construction. The main purpose of these ancient and recently constructed lowland reservoirs is irrigation and a few upland reservoirs constructed during the second half of the last century are for the generation of hydroelectricity. Fisheries production is a secondary use of these reservoirs, which has been developed after the introduction of exotic cichlid species, Oreochromis mossambicus into Sri Lankan freshwaters in 1952 (Fernando and De Silva 1984). Several attempts have been made to define management strategies for the reservoir fisheries of the country such as development of empirical yield predictive models (Wijevaratne and Amarasinghe 1987; Moreau and De Silva 1991; Nissanka et al. 2000; Amarasinghe et al. 2002), determination of optimal fishing strategies using surplus yield models (De Silva et al. 1991) and dynamic pool models (Amarasinghe 1987, 2002; Amarasinghe and De Silva 1992). There are certain similarities among the characteristics of fisheries of individual reservoirs of Sri Lanka. They include, (1) single type of fishing craft, non-mechanized fibre-glass boat with out-rigger manned by two fishers, (2) uniformity of fishing gear, gillnet of 7.6 to 12.7 cm stretched mesh sizes with a panel length of about 300 m in each boat; and (3) dominance of two exotic cichlids, O. mossambicus and O. niloticus in the landings forming over 90% of the landings (De Silva 1988; Amarasinghe 1998). However, due to the inadequacy of information about the population dynamics of dominant fish species, scientific management of reservoir fisheries of the country is not yet fully realized (De Silva 1996; Amarasinghe 1998; Schiemer et al. 2008).

In the present study, an attempt is made to investigate the population dynamics of economically important fish species in two reservoirs in the Walawe river basin of Sri Lanka. These two reservoirs were selected because of the vast difference in the magnitude of their fisheries in spite of their close proximity to each other having similar limnological characteristics (Table 1).

Materials and Methods

The fisheries of Chandikawewa reservoir (6° 19' N; 80° 51' E) and Udawalawe reservoir (6° 27' N; 80° 50' E), situated in the Walawe river basin of Sri Lanka (Fig. 1), were investigated. In Chandrikawewa, sampling was carried out from January 1995 to August 1997 whereas in the Udawalawe reservoir, study period was from January 1995 to December 1997. Some physicochemical and biological characteristics of the two reservoirs are given in table 1 and abbreviations and symbols used in the text of this paper are given in table 2. The most dominant species were *Oreochromis mossambicus* in Chandrikawewa and *O. mossambicus, O. niloticus* and *Labeo dussumieri* in Udawalawe. The LFD of these dominant species were collected once or twice a month from randomly selected boats. Due to unavoidable circumstances however, monthly sampling could not be carried out in October 1995 in the Udawalawe reservoir and in three months in Chandrikawewa (October 1995, May 1997 and June 1997). Smaller (< 40 fish) samples were disregarded in the analysis. Nevertheless, results of the analyses of the present study were not compromised because there were 31 samples of *O. mossambicus*, 30 samples of *O. niloticus*, 35 samples of *L. dussumieri* from Udawalawe and 26 length frequency samples of *O. mossambicus* from Chandrikawewa. In Chandrikawewa, fishers use gillnets of stretched mesh sizes ranging from 7.0 cm to 25.4 cm. In Udawalawe, gillnet stretched mesh sizes range from 7.0 cm to 35.6 cm. In both reservoirs, gillnets of mesh sizes greater than 11.4 cm are used especially during rainy season when there are peak catches of Indian major carps.

Fig. 1. Map of study area showing locations of Udawalawe and Chandrikawewa reservoirs. Inset shows the location of study area in Sri Lanka. Arrows indicate inflows and outflows.



During each sampling visit, TLs of the commercially important species landed were measured to the nearest 0.5 cm below the actual length. The monthly samples of length measurements were grouped into 1cm intervals depending on the minimum and maximum lengths recorded for the landings of each species to result in 15-26 lengthclasses per species. During the monthly field visits, catch and effort data were also collected (Athukorala and Amarasinghe, in press) and total monthly fish production of each species was determined based on these data.

The LFD were analyzed for fitting the von Bertalanffy growth model for nonseasonalized growth described by the following equation.

$$L_{t} = L_{\infty} \left[1 - e^{-K(t - t_{o})} \right]$$
 (1)

For this purpose, an initial estimate of L_{∞} was obtained using the Powell-Wetherall method (Powell 1979; Wetherall 1986; Pauly 1986a) as implemented in the FiSAT II (version 1.2.2) software package (Gayanilo et al. 2006) and is given by the following relationship.

 $L_m - L_c = p + qL_c$ (2) where, $L_m = (L_{\infty} + L_c)/\{1 + (Z/K)\}$ and the slope and intercept of which gives $L_{\infty} = -p/q$ and Z/K = -(1+q)/q

Using this initial estimate of L_{∞} as the root value, preliminary estimates of L_{∞} and K were then determined by means of ELEFAN I routine of FiSAT II software. In ELEFAN I, von Bertalanffy growth model is fitted by a non-parametric method where the optimum growth curve that passes through the highest number of peaks in the length frequency samples which are

(4)

sequentially arranged with time as determined from the goodness of fit value, Rn. Here, restructuring of length frequencies i.e., dividing frequencies of each length class by moving average over five length-classes, followed by their transformation using average adjusted frequency value minus 1 as the denominator, allows the identification of peaks independent of their height.

Table 1. Some physico-chemical characteristics and fishing intensity in the two reservoirs studied. The parameters marked with asterisks were obtained from the Mahaweli Authority of Sri Lanka. The other values were measured during field studies. SE - Standard error of the mean.

Parameter	Chandrikawewa	Udawalawe
Water temperature \pm SE (°C)	28.7 ± 0.14	28.5 ± 0.20
$pH \pm SE$	7.5 ± 0.09	7.6 ± 0.06
Conductivity \pm SE (μ S cm ⁻¹)	198.1 ± 6.2	186.3 ± 6.7
Alkalinity \pm SE (mg l ⁻¹)	91.2 ± 3.9	97.2 ± 4.1
Full supply level (FSL) (m above mean sea level)*	61.00	88.39
Reservoir area at FSL (ha)*	439	3413
Reservoir capacity at FSL (km ³)*	0.028	0.269
Mean depth (m)*	6.38	7.88
Total number of fishing crafts	12	58
Fishing intensity (craft-days ha ⁻¹ yr ⁻¹)	5.25	3.37

Monthly LFD of fish species studied in the two reservoirs showed similar peak lengthclasses in the corresponding months of each year, possibly due to similar yearly patterns of growth and recruitment. As such, LFD of corresponding months in different years were pooled and a series of LFD samples from January to December of a 'mean, artificial year' was obtained for the analysis using ELEFAN I method, as adopted by Amarasinghe and De Silva (1992).

Monthly LFD samples were also converted into weight using the following formula, based on the unbiased estimator of mean weight of fish within a length class, presented by Beyer (1987).

$$W_{m} = \sum_{i=1}^{k} n_{i} \{ [\{ 1/(L_{i+1} - L_{i}) \} \{ a/(b+1) \}] (L_{i+1}^{b+1} - L_{i}^{b+1}) \}$$
(3)

The number of fish in the ith length class in the total catch of mth month was estimated by:

 $N_i = (n_i/W_m)C_m$

Length-structured VPA which allows the reconstruction of the population from total catch data by length was carried out to determine the array of F for each length class. As F is known to be proportional to probability of capture (Sparre and Venema 1998), the overall probabilities of capture for different length classes were determined by dividing the F values of individual length classes from the maximum value in the F-array. Using these probabilities of capture, LFD were corrected and thereafter final estimates of growth parameters (L_{∞} and K) were obtained from the LFD corrected using probabilities of capture. As LFD were collected from gillnet catches, correcting them for gear selection was thought to be necessary for more precise estimation of

growth parameters. Since L_{∞} and K are not species-specific but are inversely proportional, the following growth performance index (φ '), which is constant for a species (Moreau et al. 1986), was used to compare growth parameters of a given species in different localities.

$$\varphi' = \operatorname{Log}\left(\mathbf{K}\right) + 2\operatorname{Log}\left(\mathbf{L}_{\infty}\right) \tag{5}$$

The φ' index is sensitive to the units of measurement of L_{∞} and K and the expression of L_{∞} (i.e., TL, SL or any other measurement), so that comparable units and expressions of growth parameters were used in calculating φ' . Based on the L_{∞} and K of cichlid species and cyprinid species as reported in www.fishbase.org (Froese and Pauly 2007), auximetric plots (i.e., growth space shown in a scatter plot of log L_{∞} against log K; Pauly 1998) were prepared and the estimated L_{∞} and K values of the present study were superimposed. The L_{∞} values in www.fishbase.org are given as TL or SL. Hence, before preparing the auximetric plots, all SL values were converted to TL assuming TL≈SL*1.25. The unspecified values of L_{∞} were treated as TL. Total mortality (Z) was calculated using original LFD by the length-converted catch curve method (Pauly 1983a). In this method, the slope of the following linear regression line fitted to the right hand descending part of the catch curve, starting from the second highest data point, gives an estimate of Z.

$$Ln(C_i/\Delta t) = c - Zt_i$$
(6)

where, $\Delta t = (1/K)\ln[(L_{\infty} - L_i)/(L_{\infty} - L_{i+1})]$. As gillnets of a wide range of mesh sizes were used in both reservoirs, at least the regression line which fits the first portion of the descending part of the catch curve was considered to represent the exponential decay curve of the exploited phase of the fish stock. Natural mortality was estimated using the following empirical equation derived by Pauly (1980).

$$Log_{110} (M) = -0.0152 - 0.279 Log_{10} (L_{\infty}) + 0.6543 Log_{10} (K) + 0.4634 Log_{10} (T)$$
(7)

In this method, L_{∞} was expressed in TL in cm, K was on annual basis and T was in degrees Celsius. Fishing mortality (F) was estimated by subtracting M from Z and the exploitation rate (E) was estimated as F/Z.

Recruitment pulses per year and their relative strength were determined from the routine implemented in FiSAT II software, which involves backward projection of length frequencies onto time axis based on growth parameters. It must me noted that information on reproductive seasonality of fish species studied could be related to recruitment patterns for cross-checking the reliability of parameters of von Bertalanffy growth model, if the actual calendar months of recruitment pulses are determined using an approximate value of t_0 . Although it would be possible to obtain an approximate value of t_0 using the empirical relationship based on L_{∞} and K (Pauly 1983b), no attempts were made to determine the recruitment patterns in relation to real calendar months. This was due to the unavailability of information on reproductive seasonality of fish species studied. Length-structured VPA was performed once again using the final estimates of growth parameters and the length-wise probabilities of capture were determined from the F-array resulted from this analysis. Length at 50% retention in the probability curve was considered as the L_c.

Y'/R analysis was carried out incorporating probabilities of capture (Pauly and Soriano 1986; Gayanilo and Pauly 1997) as determined from the F-array of length-structured VPA. As it is a fact that the efficiency of fishing effort tends to increase in Sri Lankan reservoirs (Amarasinghe and Pitcher 1986; Amarasinghe 2002), the E value which corresponds to 10% of the maximum rate of Y'/R increase with increasing E, defined as $E_{0.1}$ was determined as an index of assessing status of the fishery (Gayanilo and Pauly 1997).

Abbreviation/Symbol	Definition
W	Total weight of fish in g
TL	Total length in cm
SL	Standard length in cm
LFD	Length frequency data
\mathbf{W}_{m}	Sample weight in the m th month in g
n _i	Number of fish in the i th length class in a monthly sample
Ni	Number of fish in the i th length class in the total monthly catch
L_i, L_{i+1}	Lower and upper limits of the i th length class
a, b	Constants in the length-weight relationship, $W = aTL^b$
К	Number of length classes in monthly sample
C _m	Total catch in the m th month
L_{∞}	Asymptotic total length in cm
Κ	Growth constant
Т	Age in years
to	Theoretical age at zero length (years)
Rn	Goodness-of-fit, $Rn = 10^{ESP/ASP}/10$, where $ESP = explained$ sum of
	peaks and ASP = available sum of peaks
φ'	Growth performance index
Z	Total mortality estimated by length-converted catch curve
Μ	Natural mortality coefficient
F	Fishing mortality coefficient
VPA	Virtual Population Analysis
L _c	Length at first capture in cm
C _i	Catch in numbers in i th length class.
E	Exploitation rate
E _{opt}	Optimum exploitation rate giving maximum Y'/R
E _{0.1}	E value which corresponds to 10% of the maximum rate of Y'/R
	increase with increasing E
Т	Mean annual water temperature in degrees Celsius
Y'/R	Relative yield-per-recruit
B/R	Relative biomass-per-recruit

Table 2. Abbreviations and symbols used in the text.

Results

The size ranges, ranges of monthly sample sizes and length-weight relationships of the individual species studied in the two reservoirs are given in table 3. Monthly LFD and raised length frequencies to the total monthly catches of *O. mossambicus* in Chandrikawewa and *O. mossambicus*, *O. niloticus* and *L. dussumieri* in Udawalawe are available from the authors upon request. Powell-Wetherall plots of the four species studied in the two reservoirs, which clearly indicate fully exploited phases of the fish stocks (Fig. 2), gave reasonable estimates of L_{∞} and Z/K. The growth curves which were determined by means of ELEFAN I, superimposed on LFD are shown in figure 3 for the same species.



Fig. 2. Powell-Wetherall plots for (A) *O. mossambicus*, (B) *O. niloticus*, (C) *L. dussumieri* in Udawalawe reservoir and (D) *O. mossambicus* in Chandrikawewa (L' = Cut off length in cm; Mean L = Mean length of fish bigger than L' in cm).

Table 3. Size ranges, ranges of monthly sample sizes, number of samples and length-weight relationships of the individual species studies in Udawalawe and Chandrikawewa. As the samples less than 40 fish were disregarded in the analyses, the minimum sample size was 40 for every species and the number of samples used for that analysis varied from species to species.

Reservoir/Species	Size (TL) range in cm	Range of monthly sample sizes	Number of samples	Length-weight relationship
Udawalawe				
O. mossambicus	14.5 - 32.0	40 - 1484	31	$W = 0.059 TL^{2.59}$
O. niloticus	14.0 - 39.0	40 - 975	30	$W = 0.037 TL^{2.76}$
L. dussumieri	17.0 - 38.0	40 - 531	35	$W = 0.010 TL^{3.02}$
Chandrikawewa				
O. mossambicus	14.0 - 28.0	40 - 358	26	$W = 0.061 TL^{2.56}$

Here, a reasonably good fit is apparent, even though the growth curves based on the L_{∞} and K obtained from the LFD that were corrected using probabilities of capture, were superimposed on the uncorrected LFD. Length-structured VPA plots of *O. mossambicus*, *O. niloticus* and *L. dussumieri* in Udawalawe and *O. mossambicus* in Chandrikawewa, the F-arrays of which were used for correcting LFD for probabilities of capture, are shown in figure 4. The probabilities of capture estimated using F-arrays of all four species (Fig. 5) indicate non-sigmoid selection ogives justifying the need for correcting LFD using probabilities of capture. The growth parameters estimated by Powell-Wetherall method and ELEFAN I method are in close agreement (Table 4). The φ ' values estimated for the species in different localities are given in table 5. As the φ ' values of the species investigated in the present study fall within the same range of those recorded elsewhere, the estimates of growth parameters of fish species in the present study are biologically reasonable. The estimated L_{∞} and K values of the present study were superimposed on the auximetric plots of cichlids and cyprinids (Fig. 6) indicate that the estimates of growth parameters of the four fish stocks in the present study are reliable.

Length-converted catch curves of the four species are shown in figure 7. The regression relationships are highly significant (Coefficient of determination (r^2) ranged from 0.995 in *L. dussumieri* in Udawalawe to 0.979 in *O. mossambicus* in Udawalawe; p < 0.001), indicating that the effect of gillnet selection on the data points of the first portions of descending parts of catch curves were minimal. Estimated mortality parameters of four species studied in the two reservoirs are given in table 6. The recruitment patterns of fish stocks studied indicate that in all four fish stocks, recruitment was continuous with two prominent peaks of different magnitudes (Fig. 8), which might have resulted low Rn values associated with the fitted growth curves. Y'/R of the four species in the two reservoirs as a function of E at the present L_c are shown in figure 9. Y'/R analyses indicate that at the present L_c for the 4 stocks investigated (Table 6), although *O. mossambicus* in Chandrikawewa and Udawalawe registered only slightly higher E_{opt} than the present E in the magnitude of 5.6 to 9.3%, in *O. niloticus* and *L. dussumieri* respectively, E_{opt} were 29% and 48% higher than the present E. As we recommend the E_{0.1} as the appropriate level of E in order to allow a provision to increase the efficiency of fishing to a level not exceeding the optimal fishing mortality, comparison was made between the E_{0.1} and present E of the four stocks

studied. They indicate that *O. mossambicus* in both reservoirs are exploited beyond the $E_{0.1}$ level whereas E can be further increased for *O. niloticus* and *L. dussumieri* in Udawalawe. Also, at these levels of E in all four stocks, B/R are predicted to be around 25% of the maximum (Fig. 9) ensuring safe levels.





Fig. 4. Results of length-structured VPA for (A) *O. mossambicus*, (B) *O. niloticus*, (C) *L. dussumieri* in Udawalawe reservoir and (D) *O. mossambicus* in Chandrikawewa.

Resservoir/Species	Powell-Wetherall		ELEFAN I			
	L_{∞}	Z/K	L_{∞}	Κ	Rn	
Udawalawe						
O. mossambicus	34.1	3.56	34.3	0.58	0.186	
O. niloticus	40.7	2.71	41.3	0.78	0.188	
L. dussumieri	41.4	5.80	41.7	0.52	0.174	
Chandrikawewa						
O. mossambicus	29.6	2.24	28.9	0.54	0.248	

Table 4. Growth parameters of commercially important fish species in two Sri Lankan reservoirs. Abbreviations and units are as given in table 2.



Fig. 5. Selection curves of (A) *O. mossambicus*, (B) *O. niloticus*, (C) *L. dussumieri* in Udawalawe reservoir and (D) *O. mossambicus* in Chandrikawewa. The L_c (i.e., length at 50% retention) values are also indicated here.

Table 5. Growth performance indices (ϕ ') of fish species studied and those recorded for the same or closely related species in other localities. For comparison, ϕ ' values of the species in the present study were calculated for SL assuming SL \approx 0.8 TL. L $_{\infty}$ measured in cm and K expressed on annual basis are used here. * – Sri Lankan reservoirs. PS – Present study; A – Amarasinghe (1987); B – Amarasinghe et al. (1989); C – Amarasinghe and De Silva (1992); D – Amarasinghe (2002); E – Froese and Pauly (2007); F - Moreau et al. (1986).

Species	Locality	(Source	
-	-	Based on TL_{∞}	Based on SL_{∞}	_
O. mossambicus	Chandrikawewa*	2.65	2.46	PS
	Udawalawe*	2.83	2.64	PS
	Pimburettewa*	2.72	2.53	А
	Parakrama Samudra*	2.56-2.78	2.36-2.58	В
	Minneriya*	2.96	2.77	С
	Kaudulla*	3.00	2.80	С
	Tabbowa*	2.86	2.67	D
	African lakes/reservoirs	2.21-2.42	2.01-2.22	E, F
	Asian lakes/reservoirs	2.56-3.17	2.36-2.97	E, F
O. niloticus	Udawalawe*	3.09	2.89	PS
	Minneriya*	3.11	2.91	С
	Kaudulla*	3.00	2.81	С
	Tabbowa*	3.22	3.02	D
	African lakes/reservoirs	2.49-3.44	2.29-3.25	E, F
	Asian lakes/reservoirs	2.78-3.56	2.58-3.37	E, F
	European lakes/reservoirs	3.36-3.77	3.16-3.58	E
L. dussumieri	Udawalawe*	2.96	2.76	PS
L. calabasu	Rivers - India	3.10-3.20	2.90-3.01	E
L. coubie	African lakes	2.69-3.38	2.85-3.19	E
L. dussumieri	Pampa river - India	3.19-3.26	3.00-3.07	E
L. fimbriatus	Rivers - India	2.98-3.23	2.78-3.03	E
L. niloticus	Lakes/hydrodrome - India	3.28-3.31	3.09-3.12	E
L. rohita	Lakes - India	3.46-3.50	3.26-3.31	E
L. senegalensis	African lakes/rivers	2.61-3.12	2.41-2.92	E

Table 6. Mortality parameters of commercially important fish species in two Sri Lankan reservoirs. Abbreviations and units are as given in table 2.

Resservoir/Species	Ζ	М	F	L _c	Е	E _{opt}	E _{0.1}
Udawalawe							
O. mossambicus	2.55	1.21	1.34	18.3	0.53	0.75	0.62
O. niloticus	3.12	1.40	1.72	26.8	0.55	0.80	0.67
L. dussumieri	2.93	1.07	1.86	29.1	0.63	0.80	0.65
Chandrikawewa							
O. mossambicus	3.67	1.21	2.46	17.5	0.67	0.75	0.61



Fig. 6. The estimated L_{∞} and K values of the present study, superimposed on the auximetric plots of (A) cichlids and (B) cyprinids, based on the data reported in www.fishbase.org (Froese and Pauly 2007). The black circles indicate the data point corresponding to the four fish populations studied.



Fig. 7. Length-converted catch curves for (A) O. mossambicus, (B) O. niloticus, (C) L. dussumieri in Udawalawe reservoir and (D) O. mossambicus in Chandrikawewa.



Fig. 8. Recruitment patterns for (A) *O. mossambicus*, (B) *O. niloticus*, (C) *L. dussumieri* in Udawalawe reservoir and (D) *O. mossambicus* in Chandrikawewa.



Fig. 9. Relative yield per recruit and biomass per recruit as a function of exploitation ratio at the present levels of L_c for (A) *O. mossambicus*, (B) *O. niloticus*, (C) *L. dussumieri* in Udawalawe reservoir and (D) *O. mossambicus* in Chandrikawewa.

Discussion

As King (1995) mentioned that fish stock assessment employing computer software without a sound knowledge on the theoretical background of methodologies is a real disaster in fisheries science, in the present analysis, we attempted to illustrate the overall applicability of length-based fish stock assessment methodologies in analyzing our data. Due to the availability of user-friendly stock assessment software, it is hard to prevent unwary users from misinterpreting assessment methodologies through incompetent software application.

The LFD from the catch samples of fisheries are invariably influenced by the gear selection and as such, it is imperative that they should be corrected for gear selection especially due to the reason that accuracy of the shape of the growth curve is essentially determined by the relative abundance of smaller size classes of fish (Pauly 1986b). In the present analysis, the overall selection pattern as determined y the F-array of length structured-VPA was considered to a reasonable approach to correcting LFD of catch samples.

A method of authenticating growth parameters involves the comparison of growth performance indices in terms of growth in length or weight with other estimates obtained for the same or similar species. The φ' obtained here (Table 5) compares well with those of www.fishbase.org for the two cichlid species and for *Labeo* spp. The estimated growth parameters of the 4 fish stocks in the two reservoirs fall within the growth space of auximetric plots of cichlids and cyprinids so that they provide further evidence on the reliability of estimates of growth parameters. However, when the φ' values of cichlids and cyprinids studies here and their positions in the growth space of auximetric plots are compared with those reported elsewhere, it is evident that the Sri Lankan populations perform better than those in other localities. This is perhaps due to the fact that the trophic conditions in Sri lankan reservoirs favour better growth of these species than in other tropical regions. De Silva and Senaratne (1988) have also shown that *O. mossambicus* in Sri Lankan reservoirs exhibit better growth performance than in African lakes and reservoirs.

The annual instantaneous rate of total mortality (Z) may have been overestimated if larger fish were less vulnerable to the fishing gear or if adult fish underwent migrations. In the catch samples of the multi-mesh gillnet fisheries of the present study, as evident from F-array of length-structured VPA (Fig. 4) and from the selection patterns based on them (Fig. 5), it appeared that large fishes were less vulnerable for the fishing gear. We have therefore used data points of the first portions of descending parts of length-converted catch curves for the determination of Z so that the estimates were considered to be reasonably accurate. However, the estimates of Z are considerably high for all populations studied (Table 6). In Sri Lankan reservoirs, predatory pressure by piscivorous birds such as cormorants is reported to be very high (Winkler 1983). High estimates of Z may therefore be due to bird predation on reservoir fish populations. Heavy predation by fish-eating birds had also been recorded elsewhere (e.g. Moreau et al. (1993) in Lake George, Uganda; Mavuti et al. (1996) in Lake Ihema, Rwanda; and Moreau et al. (1997) in Lake Kariba, Zimbabwe).

As a whole, the optimal exploitation rates predicted by Y'/R analyses are quite high in all populations studied. The life history data of *O. mossambicus* which are available in the present study for both two reservoirs, indicate that the two populations are characterized by smaller body size and faster growth. The higher fishing intensities (Table 1) and high Z (Table 6) perhaps due to heavy predatory pressure might have brought about unstable environmental conditions in the two reservoirs which favoured "r-selected" life strategy for *O. mossambicus* populations. Iles (1973) has shown that early maturity and accelerated growth and life cycles in tilapias under unstable environmental condition such as heavy predatory pressure were a unique recruitment mechanism. According to Moreau (1999), size of maturity of *O. mossambicus* tends to decrease

with fishing pressure. It is also known that under unstable environmental conditions, the phenomenon of switching from somatic growth to reproduction is common in tilapias (Noakes and Balon 1982; Kolding 1993). Although Y'/R analyses predicted high values of E_{opt} for O. mossambicus populations in the two reservoirs, increased fishing pressure might further lead to push the population towards the extreme of 'r-selected' life strategy so that continuation of the fishery at the present exploitation levels is advisable. In Udawalawe, Y'/R analyses predicted further increase of E for O. niloticus and L. dussumieri too (Table 6). As these two populations are also characterized by high Z values, reflecting high turnover rates (Allen 1971), they are capable of withstanding heavy fishing pressures. In Udawalawe reservoir, percentage contributions of O. mossambicus, O. niloticus and L. dussumieri to the total landings were 28%, 25.8% and 28% respectively (Athukorala and Amarasinghe, in press). As all three species are caught in the same fishing gear, E for O. niloticus and L. dussumieri should be increased to a level which might not lead to over-exploitation of O. mossambicus stock. Hence, for optimization of fishing strategies in this reservoir, in addition to biological aspects associated with the resilience of the fish stocks to the changing fishing pressure, consumer preference for different species and other sociological aspects should be taken into account. In the dry zone of Sri Lanka, exotic cichlids, most notably O. niloticus, are preferred by rural communities compared to exotic and indigenous cyprinids (Fernando 1984; De Silva 1988; Amarasinghe, pers. obs.). Stunting of O. niloticus is also not evident in Sri Lankan reservoirs. As such, optimization of Y'/R of O. *niloticus* in Udawalawe by increasing E slightly above the present level is advocated. As $E_{0,1}$ allows some provisions to increase exploitation without exceeding the optimal level, overexploitation of O. mossambicus and L. dussumieri stocks is unlikely when the Y'/R of O. niloticus is optimized.

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