Population Dynamics of *Oreochromis mossambicus* and *O. niloticus* (Cichlidae) in Two Reservoirs in Sri Lanka

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Abstract

Population dynamics of two cichlid species, *Oreochromis mossambicus* and *O. niloticus* in two reservoirs in Sri Lanka were studied using length-based methods. Asymptotic total length (L_∞) and growth constant (K per year) of *O. mossambicus* (L_∞ = 43.7 cm and K = 0.52 in Kaudulla; L_∞ = 45.0 cm and K = 0.45 in Minneriya) and *O. niloticus* (L_∞ = 54.5 cm in both reservoirs; K = 0.35 and 0.43 in Kaudulla and Minneriya, respectively) were used to estimate mortality and exploitation rates (E). The growth performance of *O. mossambicus* in both reservoirs was better than that of *O. mossambicus* populations in various geographical areas. This may be due to introgressive hybridization between *O. mossambicus* and *O. niloticus* or a very favorable environment for *O. mossambicus* in Sri Lankan reservoirs which provide a variety of nutritious food sources. Length-structured Virtual Population Analysis indicates that fishing mortality rates are approximately constant throughout the recruited stocks, suggesting that the effects of gill-net selectivity on the catch samples are small.

Relative yield-per-recruit analyses incorporating probabilities of capture indicate that *O. mossambicus* and *O. niloticus* yields in Minneriya could be increased by increasing size at first capture. In Kaudulla, any increase in E of *O. mossambicus* stock would adversely affect the *O. niloticus* stock. Also, increase in size at first capture of *O. niloticus* to optimize yield would leave the *O. mossambicus* stock underexploited.

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Introduction

The inland fishery of Southeast Asia, where reservoirs alone cover $5,563 \cdot 10^6$ ha, accounts for nearly 57% of the world's total inland fish production (De Silva 1988a). In Sri Lanka, the reservoir fishery is almost entirely dependent on introduced cichlid species (Fernando and Indrasena 1969; De Silva 1983; Fernando 1984). Scientific management of the reservoir fishery in Sri Lanka, as elsewhere in Asia, is crucial because it is a cheap protein source for rural communities.

Since a wide array of length-based stock assessment methodologies is now available (Pauly and Morgan 1987; Sparre et al. 1989), it is possible to select appropriate techniques to assess exploited fish stocks in reservoirs. Although some attempts have been made to assess the fisheries of some reservoirs in Sri Lanka (Amarasinghe 1987; Amarasinghe et al. 1989), information is inadequate (De Silva 1988b) to get a general idea about the country's reservoir fishery and to define effective management strategies.

This paper attempts to study the population dynamics of *Oreochromis mossambicus* (Peters) and *O. niloticus* (Linn.) stocks in two reservoirs in Sri Lanka using length-based methods.

Description of Reservoirs

The two reservoirs, Kaudulla and Minneriya, situated in the dry zone of Sri Lanka, receive less than 200 cm annual rainfall (Fig. 1) and are primarily irrigational reservoirs. Kaudulla is a terminal reservoir of the irrigation system; Minneriya is an upstream reservoir. The major inflow of Kaudulla is one of the outflows of Minneriya. Kaudulla has decaying submerged tree stumps which perhaps prevent the intensive exploitation of fish stocks; in Minneriya, tree stumps are absent.

Some morphometric and edaphic characteristics of the two reservoirs are given in Table 1. The fisheries of both reservoirs rely on nonmechanized outrigger canoes as crafts and on gillnets as major gear. Fishers usually use fleets of gillnets of mesh sizes ranging from 7.5 to 14.0 cm. The hanging ratio (Hamley 1975) of these gillnets is 0.5. Beach seining, which is illegal, is also practiced. A few fishers in Kaudulla also use cast nets. Further details of the fisheries of these two reservoirs are given in Amarasinghe (1988) and De Silva (1988b).
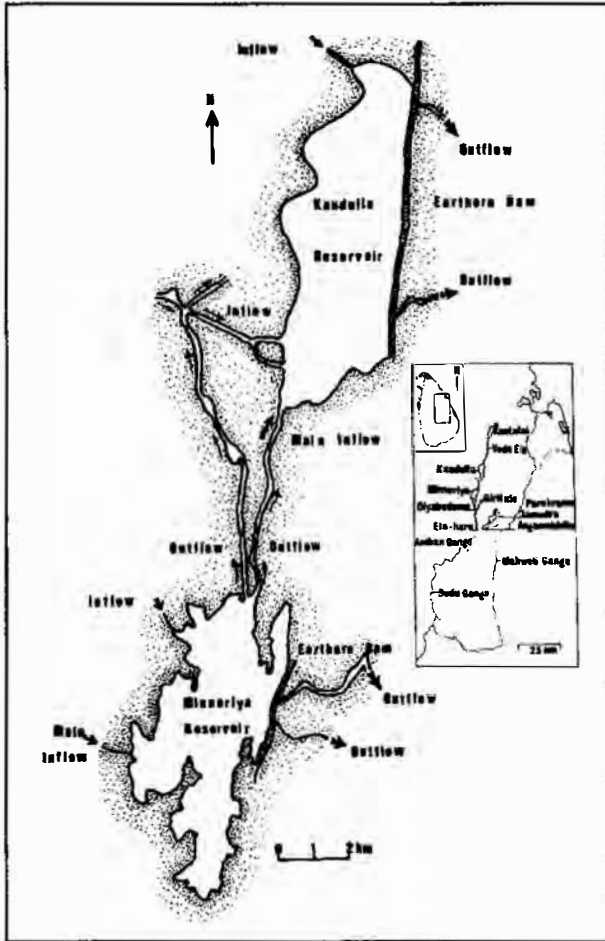
Fig. 1. Maps of Kaudulla and Minneriya reservoirs. Inset shows the locations of the two reservoirs in Sri Lanka.

Materials and Methods

Length-frequency data of *O. mossambicus* and *O. niloticus* in the gillnet catches of two reservoirs were collected monthly from randomly selected crafts in the fisheries from May 1986 to February 1989. Sampling was carried out 3-4 days each month in each reservoir. Where possible, length-frequency data of the two cichlid species caught by other fishing gears were also collected. Since other types of gear are used only sporadically, samples could not be obtained regularly. In both reservoirs, some fishers beat the water

	Kaudulla	Minneriya	Source
Table 1. Some morphometric and edaphic characteristics of two Sri Lankan reservoirs.			
Area at full supply level (ha)	2,712.6	2,550.6	Anon. (1975)
Full supply level (m above mean sea level)	73.2	93.7	Anon. (1975)
Mean depth (m)	9.1	11.7	Anon. (1975)
Catchment area (km^2)	90.95	239.83	Anon. (1975)
pH	7.9	8.2	De Silva (1988a)
Conductivity (μS)	279.0 (200-380 range)	276.0 (155-620 range)	De Silva (1988a)
Alkalinity (meq l^{-1})	2.47	2.76	De Silva (1988a)
Chlorophyll-a ($\mu g\, l^{-1}$)	58.5	12.5	De Silva (1988a)

with wooden poles or weighted ropes from their crafts to drive fish into gillnets. Further details of this modified gillnet fishing method ("water beating") are given by Amarasinghe and Pitcher (1986). The fishes caught in normal gillnetting and water beating could not be measured separately since length measurements had to be performed as quickly as possible before disposal of the landings to fish vendors. As such, length-frequency data of gillnet catches in this study include those from normal gillnetting and water beating. Measurements (total length) were made to the nearest 0.5 cm below the actual length. Very small samples (< 40) were disregarded in the analysis of length-frequency data which were based on 1.5 and 2.0 cm length-classes for *O. mossambicus* and *O. niloticus*, respectively.

Introgressive hybridization between *O. mossambicus* and *O. niloticus* is said to take place in natural habitats and culture systems (Macaranas et al. 1986; Pullin and Capili 1988; De Silva and Ranasinghe 1989). Some specimens of *O. mossambicus* and *O. niloticus* have mixed characteristics probably due to phenotypic color variations resulting from cross-hybridization. As such, to obtain length measurements, fish were identified as *O. mossambicus* or *O. niloticus* based on the characters given by Trewavas (1983). The

fishes with mixed features were also considered either as *O. mossambicus* or *O. niloticus* depending on their prominent characteristics.

Total landings of *O. mossambicus* and *O. niloticus* in both reservoirs were estimated by simultaneous catch and effort surveys. Samples of two cichlid species in gillnet catches and beach seine catches were obtained and the sex ratio in each size class was determined separately for the two fishing methods.

Length-frequency data of *O. mossambicus* and *O. niloticus* in the gillnet catches were analyzed using the Compleat ELEFAN version 1.1 software package (Gayanilo and Pauly 1989; Gayanilo et al. 1989) in which further improvements have been incorporated (Gayanilo and Pauly 1990). The complete stepwise procedure of estimation of growth parameters is rarely stated in published work on the use of ELEFAN. Therefore, we include here the steps we followed in the analysis. The steps are:

1. estimating an initial value of asymptotic length (L_∞) and Z/K (Z = total mortality and K = growth constant) using the Wetherall method (Pauly 1986a; Wetherall 1986);
2. obtaining preliminary estimates of growth parameters by ELEFAN I, using the initial estimates of L_∞ estimated by the Wetherall method;
3. estimating probabilities of capture by detailed analysis of the left ascending part of the catch curve, and by constructing a selection curve using Z and natural mortality (M; see below) values estimated from the preliminary estimates of L_∞ and K;
4. correcting the original length-frequency data using probabilities of capture (Pauly 1986b); and
5. obtaining improved estimates of L_∞ and K from the corrected length-frequency data.

As the monthly length-frequency distributions of *O. mossambicus* and *O. niloticus* in Kaudulla appeared to follow similar yearly patterns of recruitment and growth, i.e., peak size classes were similar for corresponding months of each year (Figs. 6-7), the length-frequency data of corresponding months in different years were pooled and a series of length-frequency samples from January to December was obtained. Using these, a "mean" (artificial) year for each species was constructed to estimate growth parameters according to the stepwise procedure described earlier.

42

However, in Minneriya, water level dramatically decreased in July-October 1987 and fishing intensity, especially beach seining, increased (Fig. 2). This resulted in the removal of large specimens of *O. mossambicus* and *O. niloticus*, thus reducing the mean size of remaining fish. Mean landing size of *O. mossambicus* and *O. niloticus* started to increase from June 1988 onwards. Hence in the analysis, special emphasis was given to the growth of fish represented by the samples from June 1988 to February 1989.

Z values of *O. mossambicus* and *O. niloticus* were calculated using length-converted catch curves and from the mean length of
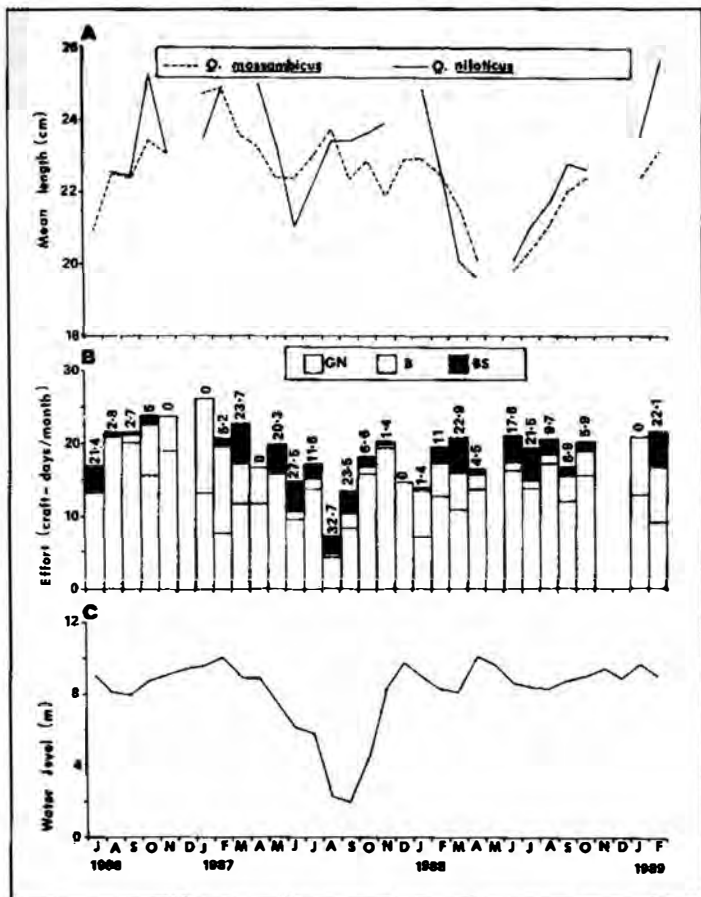
Fig. 2. A. Mean lengths of *O. mossambicus* and *O. niloticus*, B. Fishing effort from different fishing methods (GN - gillnetting; B - water beating; Bs - beach seining; arabic numerals - % crafts in beach seining), and C. Mean monthly water level in Minneriya.

fish above full retention length (Beverton and Holt 1956). M was estimated for each species using the following empirical equation (Pauly 1980):

$$\log_{10}M = -0.006 - 0.279 \log_{10}L_\infty + 0.6543 \log_{10}K + 0.4634 \log_{10}T$$

where L_∞ is expressed as total length in cm, K is on an annual basis and T (mean annual temperature) is in degrees Celsius. Fishing mortality (F) estimates were obtained by subracting M from Z, and exploitation rates (E) were calculated by the relationship E=F/Z.

Length-structured Virtual Population Analysis (VPA), a modification of Jones' cohort analysis (Jones 1981), implemented as VPA II in the Compleat ELEFAN package, was used to estimate F in each size class of fish. Estimated total landings of *O. mossambicus* and *O. niloticus* in the two reservoirs were used in this analysis.

Probabilities of capture were estimated from the catch curve as described above and incorporated in computing relative yield-per-recruit (Y/R) for each species in each reservoir (Pauly and Soriano 1986). The Y/R analysis was performed for five different sizes of 50% retention (L_c) and selection patterns.

Results

The overall length-frequency distributions of *O. mossambicus* and *O. niloticus* in gillnet and beach seine catches are shown in Fig. 3. This suggests that the effect of gillnet selectivity on the catch sample is small, beyond the size of approximately 20 cm in Minneriya (Figs. 3C and 3D). However in Kaudulla, where beach seines can be operated only in limited areas due to the presence of tree stumps, frequency distribution of large fishes (above 30 cm total length) in the beach seine catches is exceptionally high. Usually the frequency distribution of fishes in the fully recruited phase of a catch sample explains a negative exponential curve unless it is affected by selection. Length-wise sex ratios in beach seine and gillnet catches (Fig. 4) indicate that in Kaudulla, males dominate large size groups of beach seine catches.

For *O. mossambicus* and *O. niloticus* in Kaudulla and Minneriya, modified Wetherall plots (Pauly 1986a) are given in Fig.
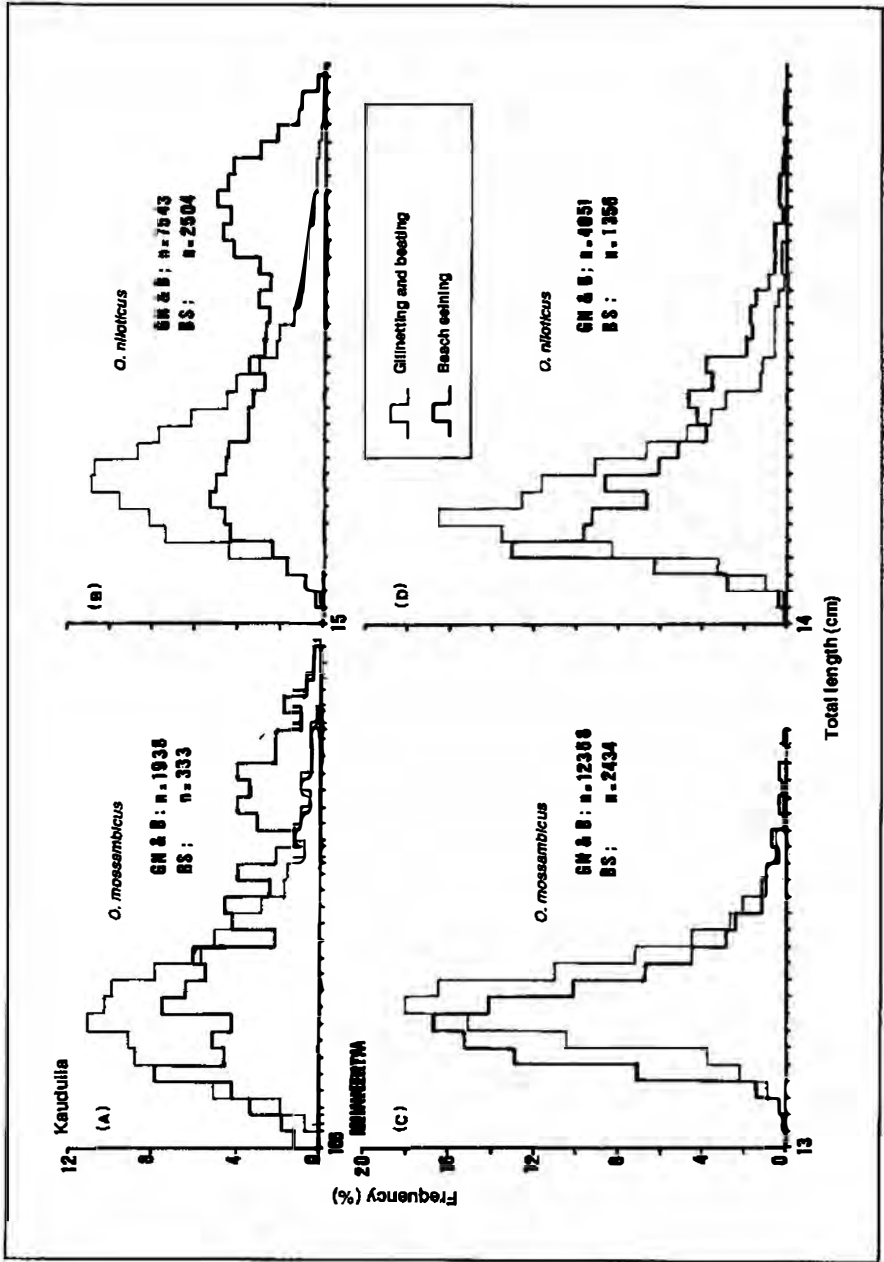
Fig. 3. The overall length-frequency distributions of *O. mossambicus* and *O. niloticus* in the gillnet catches and beach seine catches in Kaudulla and Minneriya (GN & B - gillnetting and water beating; BS - beach seining; n - number of fish measured).

5; growth parameters (from Wetherall method and ELEFAN technique), mortality rates and L_c are given in Table 2; growth performance indices (ϕ') in Table 3; and growth curves superimposed on length-frequency distributions of catch samples from different fishing methods in Figs. 6-9. They indicate that the growth parameters of *O. mossambicus* and *O. niloticus* estimated from the length-frequency data of gillnet catches in two reservoirs fit well with length-frequency data from other fishing methods.
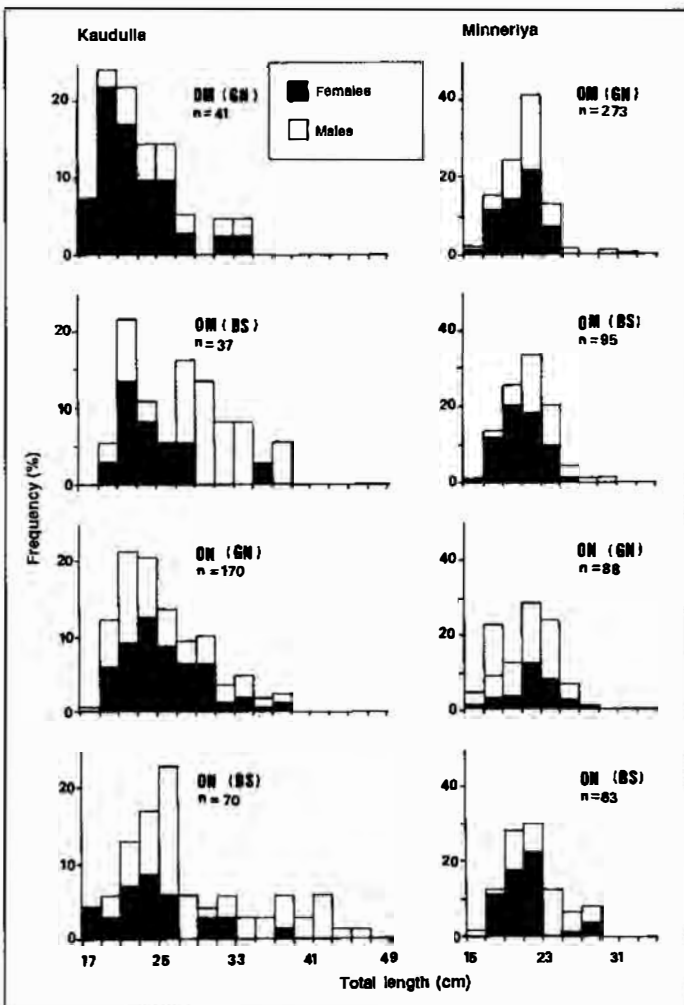

Fig. 4. Length-frequency distributions of male and female *O. mossambicus* (OM) and *O. niloticus* (ON) in gillnet (GN) and beach seine (BS) catches in Kaudulla and Minneriya.
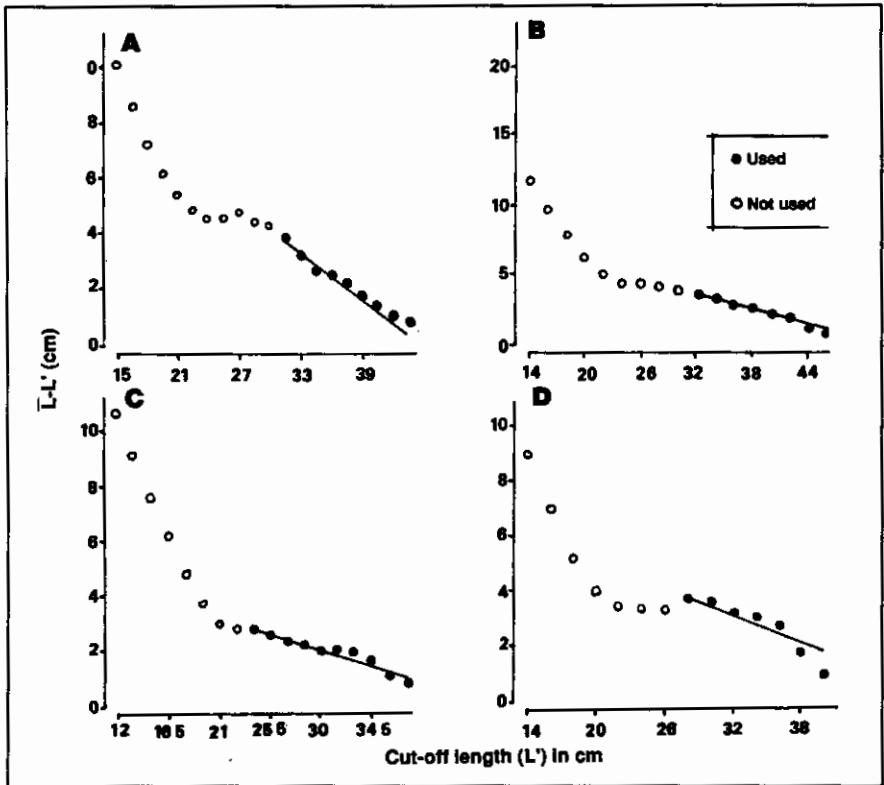
Fig. 5. The modified Wetherall plots for *O. mossambicus* and *O. niloticus* in Kaudulla and Minneriya. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.

Table 2. Growth parameters, mortality rates, exploitation rates (E) and sizes at first capture (L_c) of *O. mossambicus* and *O. niloticus* in Kaudulla and Minneriya. Z1 = total mortality from length-converted catch curve; Z2 = total mortality from Beverton and Holt (1956) method; M = natural mortality; F = fishing mortality.

Reservoir/ species	Wetherall method		ELEFAN I method							L_c (cm)
	L_∞ (cm)	Z/K	L_∞ (cm)	K	Z1	Z2	M	F	E	
Kaudulla										
O. mossambicus	44.8	2.59	43.7	0.52	1.399	1.707	1.005	0.394	0.282	18.8
O. niloticus	54.9	5.24	54.5	0.34	1.823	1.955	0.753	1.070	0.587	20.9
Minneriya										
O. mossambicus	46.0	6.99	45.0	0.45	3.031	3.193	0.955	2.076	0.685	19.6
O. niloticus	52.0	5.21	54.5	0.43	3.494	3.578	0.876	2.618	0.749	19.4

Table 3. Growth performance indices (ϕ') of two cichlid species in different localities. $\phi' = \log_{10} K + 2 \log_{10} L_\infty$ (Moreau et al. 1986). ϕ' values were calculated using standard lengths (approximately 0.8 x total length) for comparison with values estimated by other authors. Where available, ranges are given in parentheses.
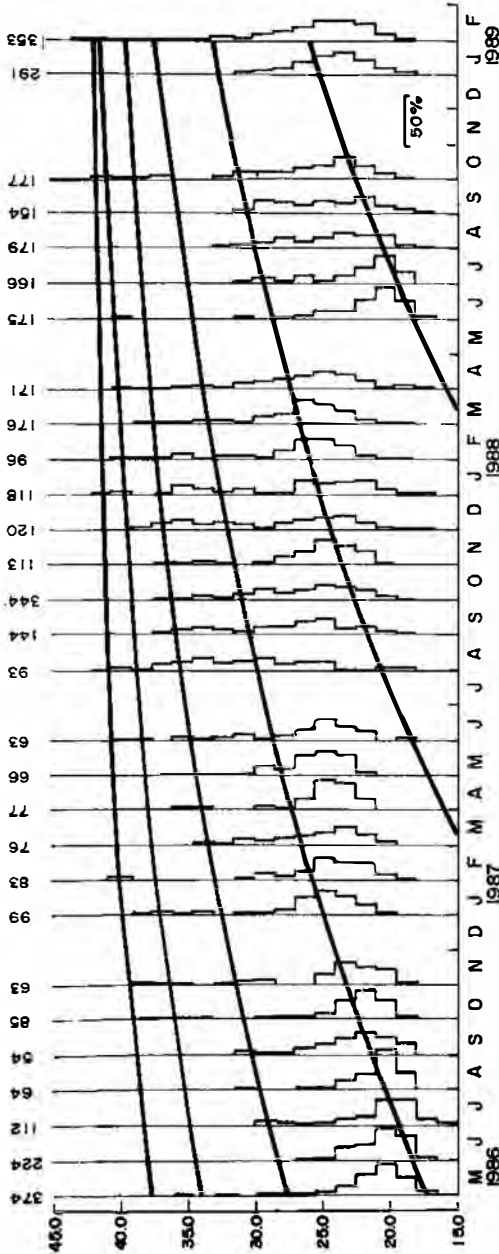
Reservoir/species	ϕ'	Source
African lakes		
O. mossambicus	2.48	Moreau et al.
	(2.05 - 2.8)	(1986)
O. niloticus	2.85	Moreau et al.
	(2.41 - 3.11)	(1986)
Sri Lankan reservoirs		
O. mossambicus	2.48	De Silva and
	(2.29 - 2.7)	Senaratne (1988)
Parakrama Samudra, a Sri Lankan reservoir		
O. mossambicus	2.37	Amarasinghe
(3 populations)		et al. (1989)
Seletar reservoir, Singapore		
O. mossambicus		
Male	2.38 - 2.45	Khoo and Moreau
		(1990)
Female	2.31 - 2.47	Khoo and Moreau
		(1990)
Kaudulla		
O. mossambicus	2.8	Present study
O. niloticus	2.81	Present study
Minneriya		
O. mossambicus	2.77	Present study
O. niloticus	2.91	Present study

Average F values of different size classes as obtained from VPA II are shown in Fig. 10. This indicates that F values are approximately constant throughout the recruited phase of fish stocks in both reservoirs. Length-converted catch curves and selection curves are given in Figs. 11 and 12, respectively.

Y/R values as functions of exploitation rates for different sizes at first capture (L_c) are shown in Fig. 13. They indicate that by increasing L_c, higher *O. niloticus* yields in both reservoirs and higher *O. mossambicus* yields in Minneriya could be obtained at the present level of E. In Kaudulla, optimum *O. mossambicus* yield could be obtained by increasing L_c approximately at the exploitation rate of 0.5.

Discussion

Reservoirs generally differ from other water bodies in a number of features. Reservoirs lack the stability of various fish communities following impoundment, have impediments to fishing, a high turnover rate and irregular allochthonous input, among others. As a result, the application of conventional methods for stock assessment in reservoirs is problematic (Pauly 1984). The reservoirs Kaudulla and Minneriya are very old and effects of gillnet selection on catch samples have been shown to be small. Therefore, it is appropriate to assess the exploited stocks of *O. mossambicus* and *O. niloticus* using methodologies structured around steady-state assumptions and assessment procedures applicable to stocks with probability of capture of unity throughout the exploited phase.

Basson et al. (1988) stated that ELEFAN and similar methods in concept for estimating growth parameters from length-frequency data are most effective when one of the parameters of the growth equation, usually L_∞, is

Fig.6. Growth curves of *O. mossambicus* in Kaudulla, superimposed on the length-frequency distributions of the samples from gillnet catches. Number of fish measured in each month is also indicated here.
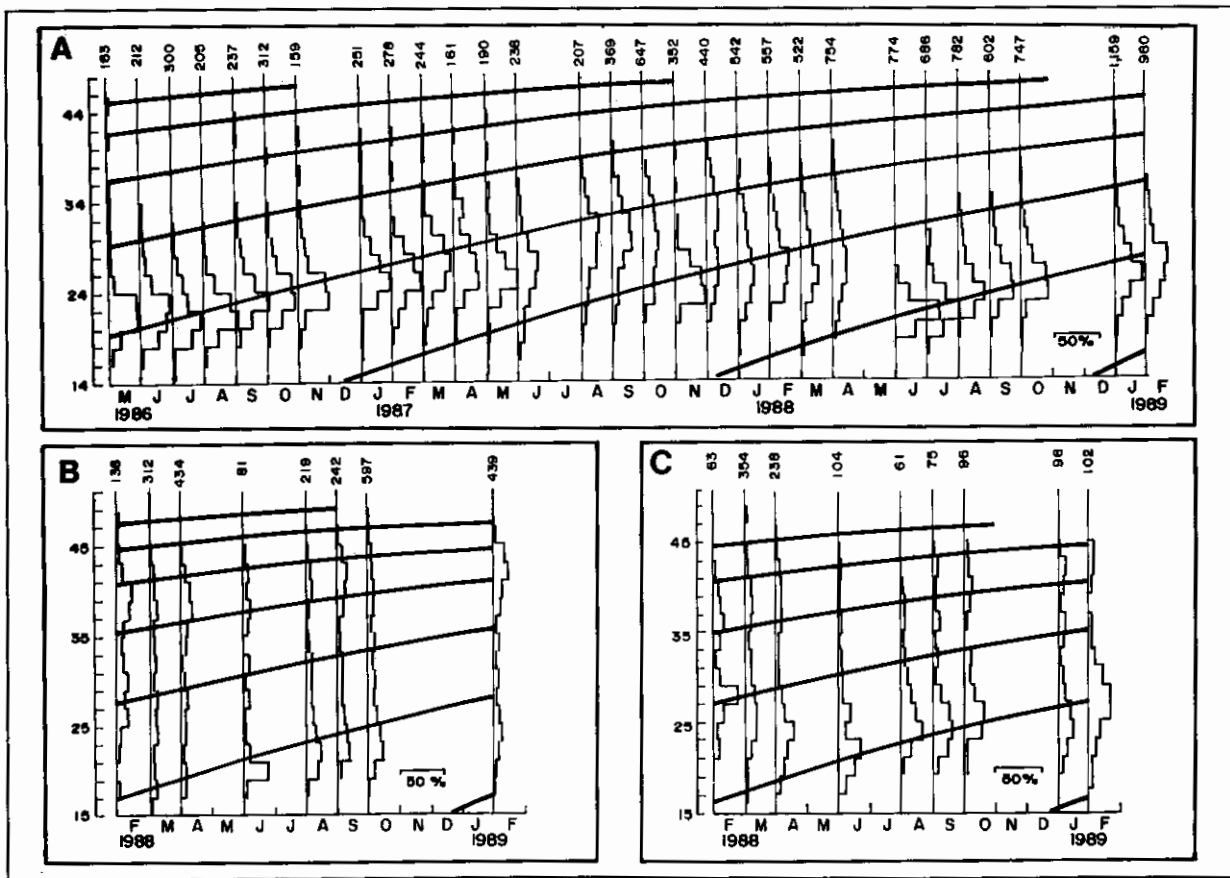
Fig. 7. Growth curves of *O. niloticus* in Kaudulla, superimposed on the length-frequency distributions of the samples from A. gillnet catches, B. beach seine catches, and C. cast net catches. Number of fish measured each month is also indicated.
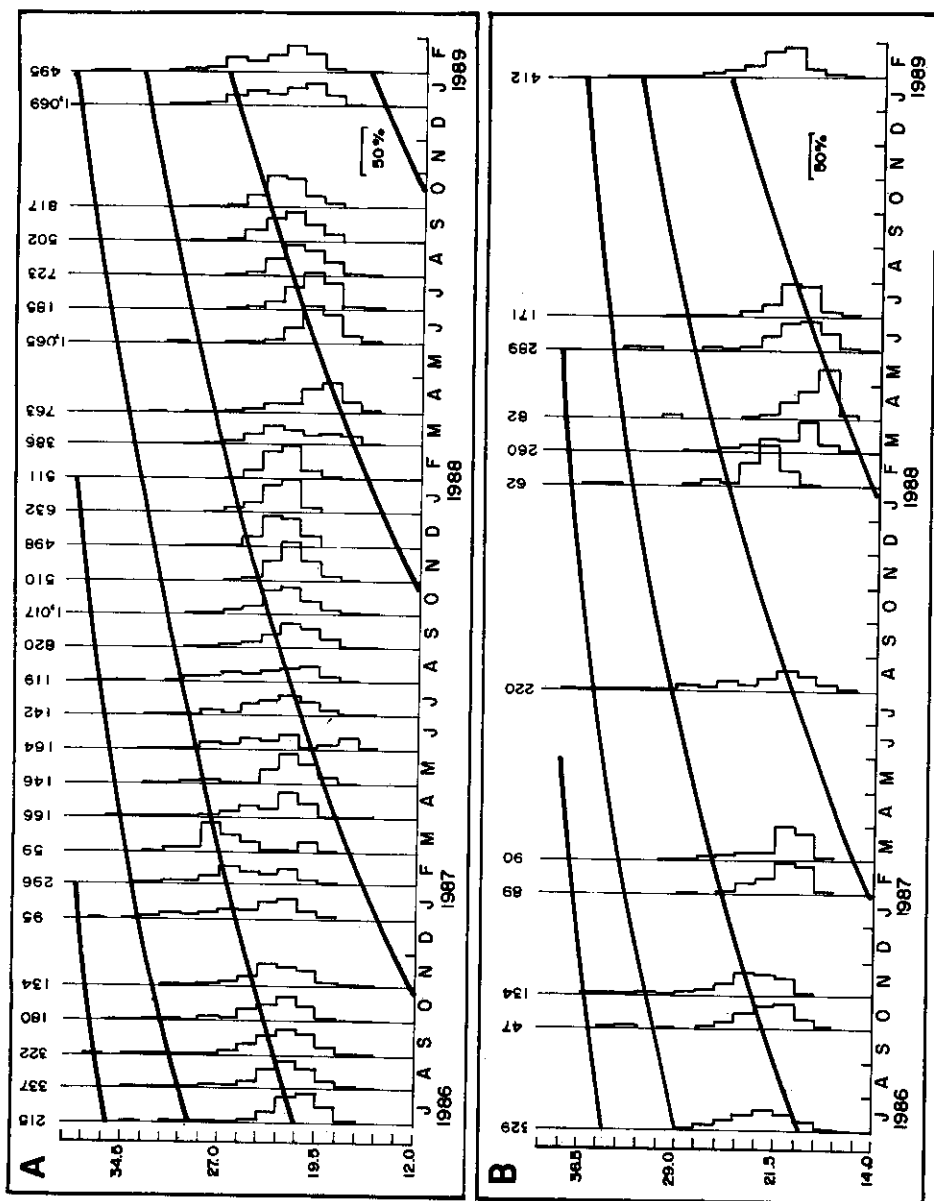
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Fig. 8. Growth curves of *O. mossambicus* in Minneriya, superimposed on length-frequency distributions of samples from A. gillnet catches and B. beach seine catches. Number of fish measured each month is also indicated.
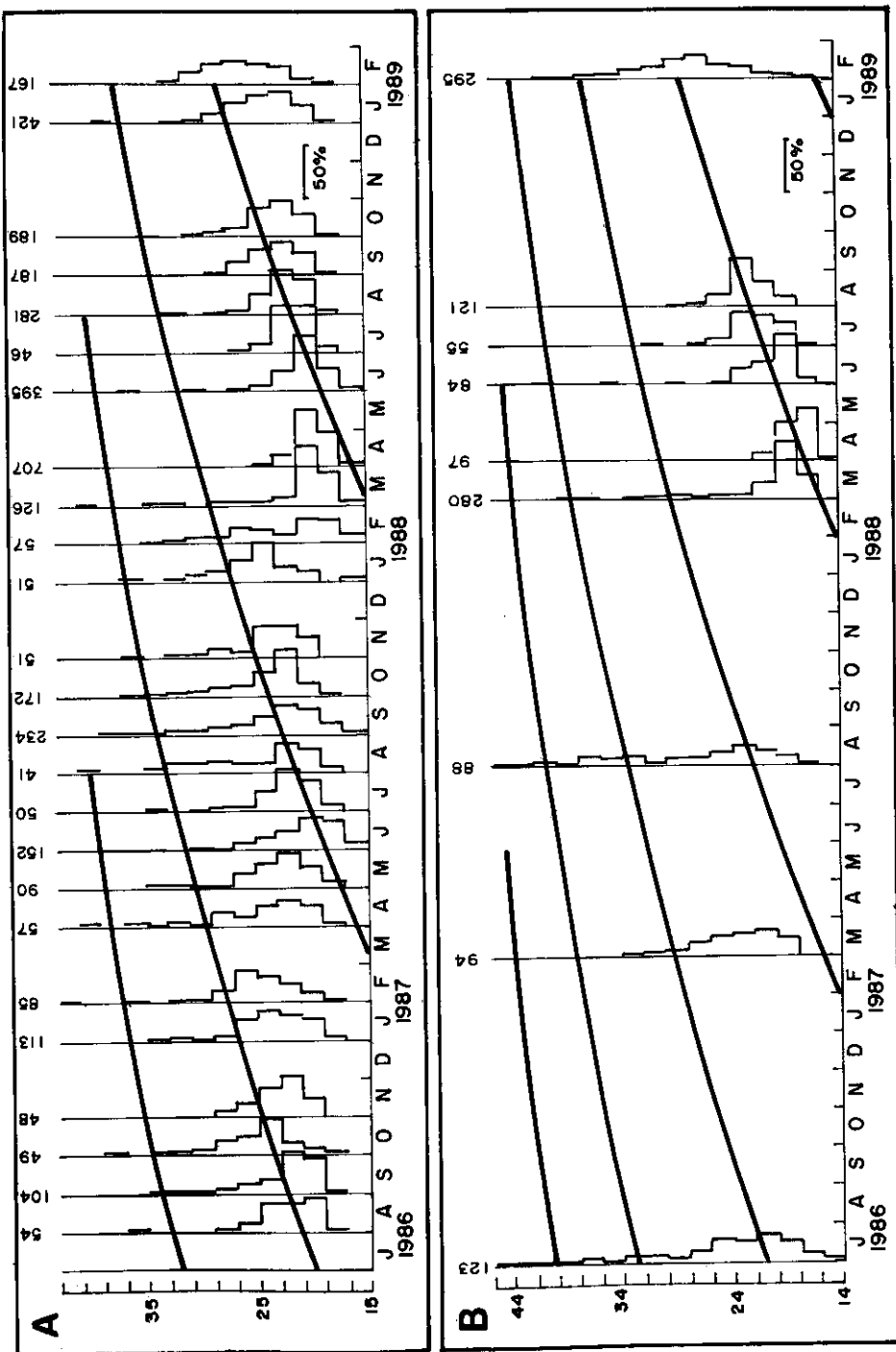
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Fig. 9. Growth curves of *O. niloticus* in Minneriya, superimposed on the length-frequency distributions of samples from A. gillnet catches, and B. beach seine catches. Number of fish measured each month is also indicated.
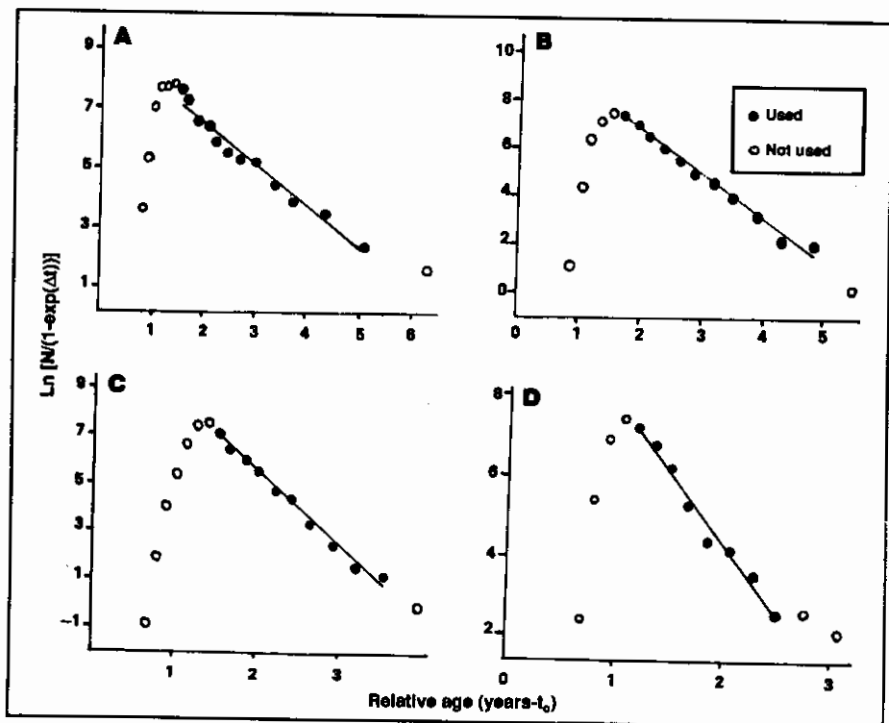
Fig. 10. Length-converted catch curves for *O. mossambicus* and *O. niloticus* in Kaudulla and Minneriya. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.
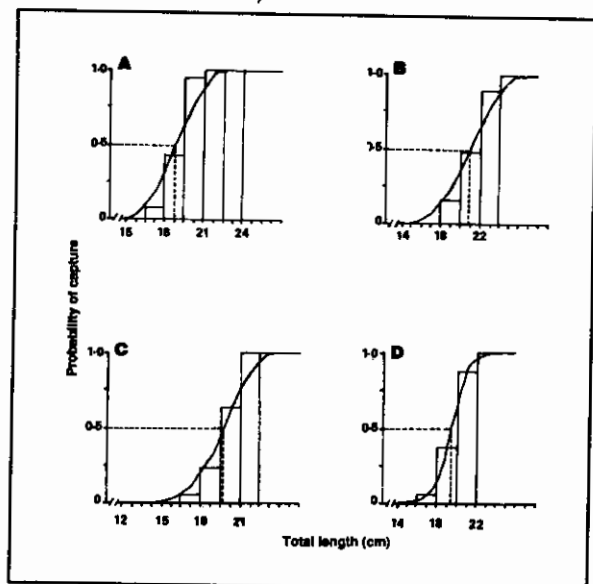

Fig. 11. The selection curves of the two cichlid species in Kaudulla and Minneriya. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.
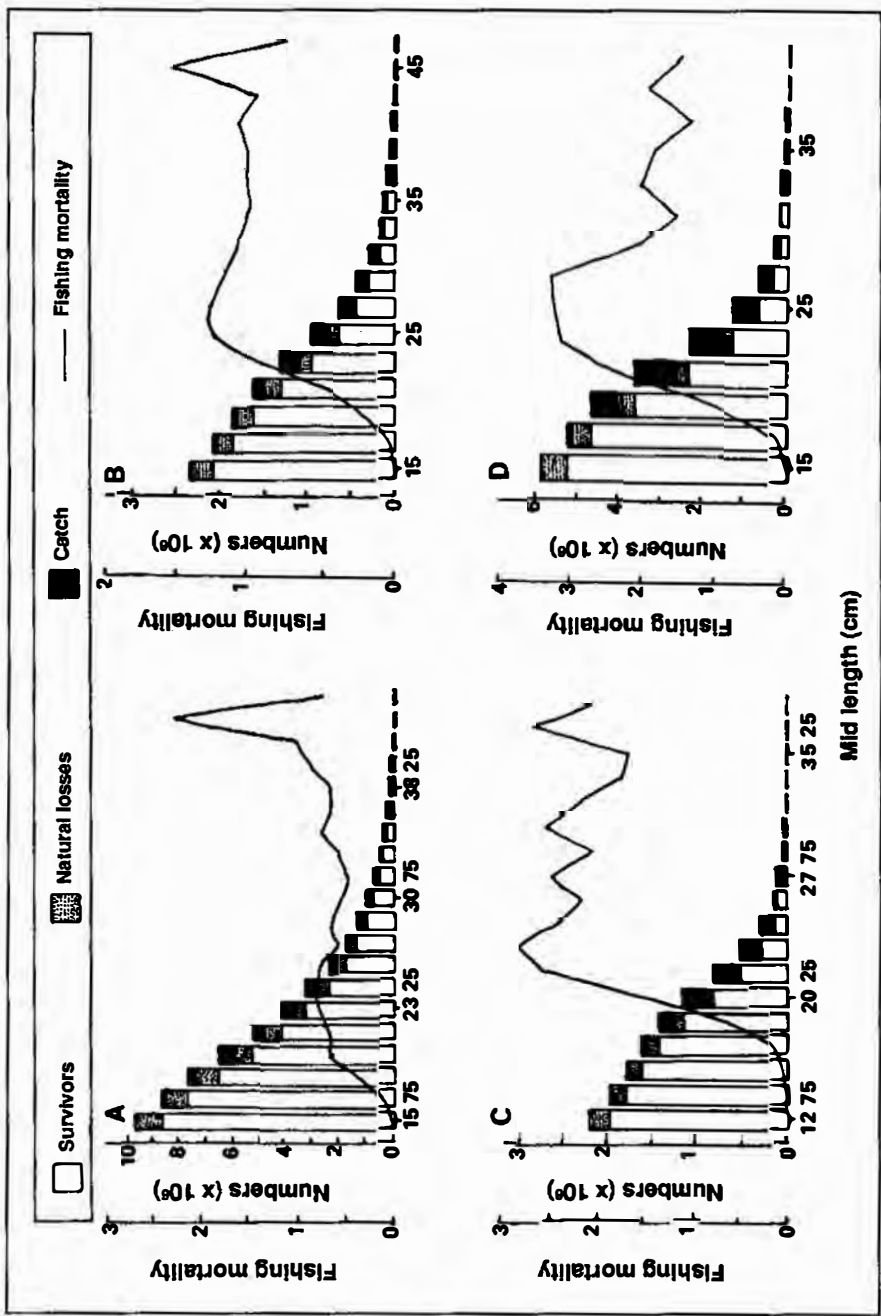
Fig. 12. Results of VPA II. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.
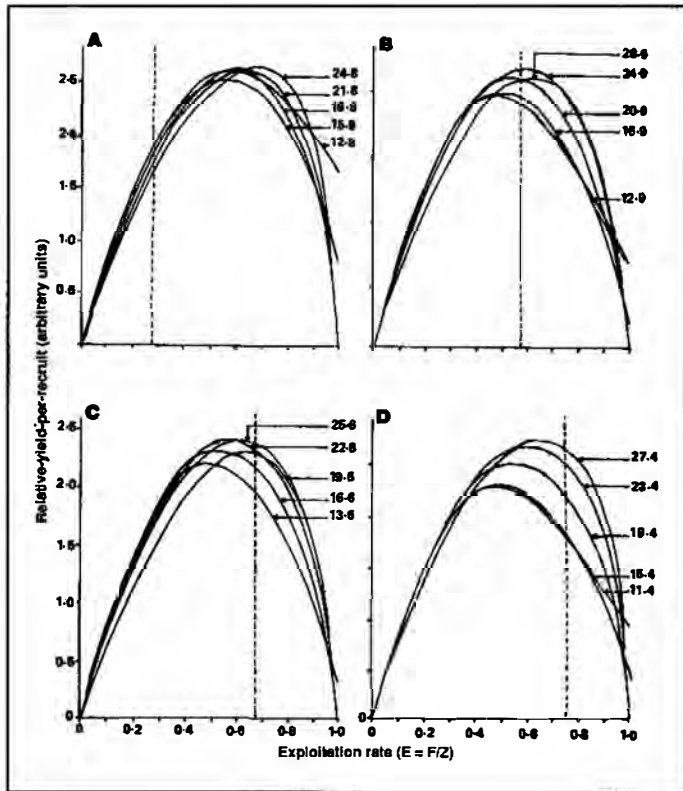
Fig. 13. Relative yield-per-recruit values as functions of exploitation rates. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.

known or approximated to a narrow range. In the present study, the growth parameters were estimated using the L_∞ values estimated from the Wetherall method as root values. The apparent poor fit of growth curves superimposed on length-frequency distributions (Figs. 6-9) may be due to effects of gear selection and/or seasonality in recruitment.

Although in the multimesh gillnet fishery, effects of gillnet selection on the catch samples are small, length-frequency data in smaller size classes are affected by gear selection. In the present study, the original length-frequency data were corrected for gear selection using probabilities of capture. This method of estimating growth parameters, as suggested by Pauly (1986b), gives more precise values because smaller fishes are given more emphasis. Usually a more accurate fitting of the von Bertalanffy growth

formula is possible for smaller size classes. In the smaller size classes of the original length-frequency data (Figs. 6-9) which have been considered for obtaining growth curves after correcting for gear selection, peaks are not conspicuous. This may be one reason for the apparent poor fit of growth curves superimposed on the length-frequency distributions.

The seasonal recruitment patterns of *O. mossambicus* and *O. niloticus* (Fig. 14), obtained by projecting each length-frequency sample backward on the time axis using growth parameters (Gayanilo et al. 1989), indicate that two peak recruitment seasons occur annually for each cichlid species in each reservoir. In another Sri Lankan reservoir, monthly gonadosomatic indices of *O. mossambicus* showed two major peaks suggesting two recruitment seasons (De Silva and Chandrasoma 1980). As indicated in Figs. 6-9, two growth curves superimposed on each length-frequency distribution perhaps correspond to these two peak recruitment seasons for each species. This suggests that obtaining reasonable estimates of growth parameters from length-frequency data is possible through the ELEFAN method after checking whether assumptions behind the method are met, as stated by Pauly (1986c). Subsequent analyses were based on these estimated growth parameters.

The approaches to estimating M of fish stocks based on the observations that M often correlates with life history parameters such as the empirical equation by Pauly (1980) have some disadvantages. The estimated M values using these methods are no better than the methods used to estimate the values of M which have been used to derive the regression equation (Vetter 1988). However, since Pauly (1980) has used 175 independent estimates of M for an extremely wide range of sizes, taxa and habitats, including the cichlids in tropical freshwaters, his equation could be employed for obtaining a reasonable approximation of M of the two cichlid species in Kaudulla and Minneriya.

It has been recorded that male *Oreochromis* spp. may hold a territory where they build nests for several days, then move to feeding grounds (Lowe-McConnell 1982; Bowen 1984). The terraces used for nest-building by male *O. mossambicus* are visited by adult females for a brief courtship (Bruton and Bolt 1975). *O. mossambicus* has also been recorded to be confined to certain depths depending upon maturity, sex and water temperature (Caulton and
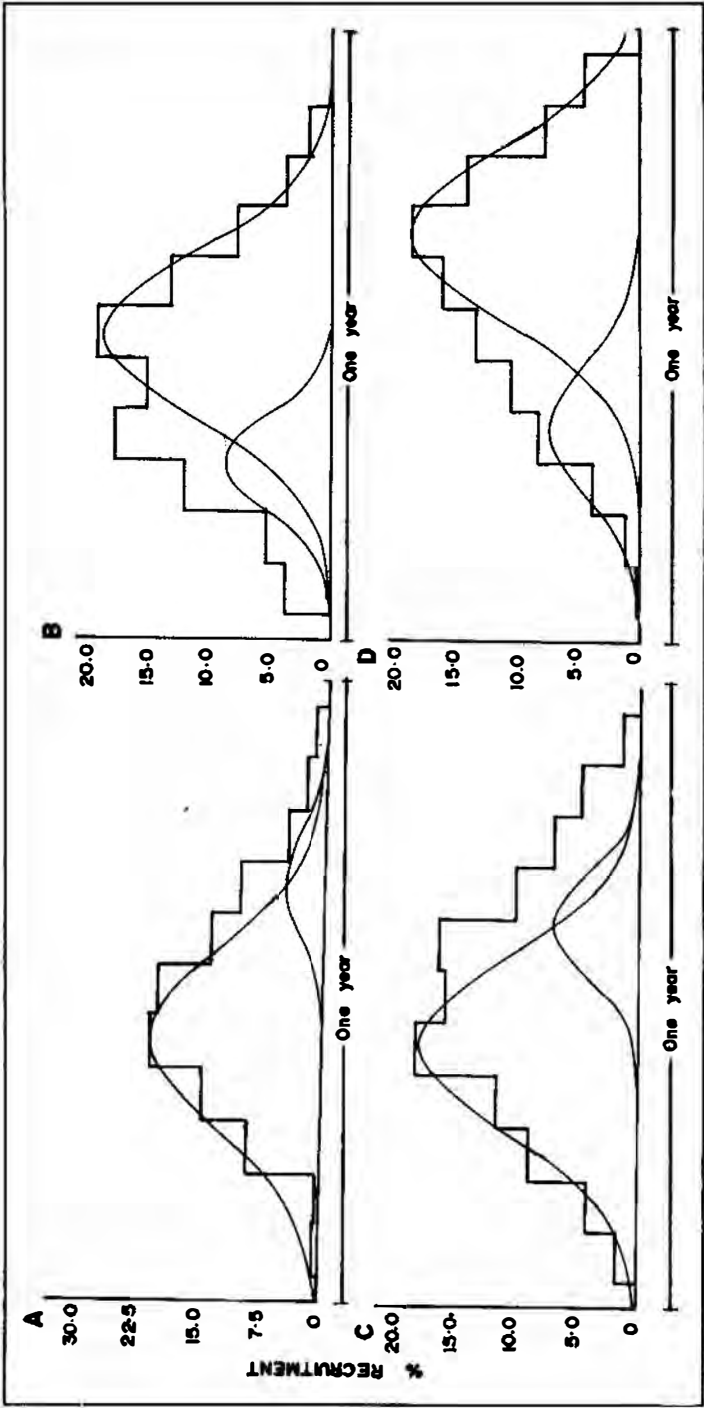
Fig. 14. Seasonal recruitment patterns of the two cichlid species in Kaudulla and Minneriya. A - *O. mossambicus* in Kaudulla; B - *O. niloticus* in Kaudulla; C - *O. mossambicus* in Minneriya; D - *O. niloticus* in Minneriya.

Hill 1973, 1975). Similar trends for *O. niloticus* have also been recorded (Bishai 1961). As such, the high proportions of large fish of two cichlid species in the beach seine catches in Kaudulla were perhaps due to "behavioral selection."

The ϕ' values calculated for the reservoir populations of the two cichlid species are within the range of ϕ' recorded in literature (Table 3). However, ϕ' of *O. mossambicus* in both reservoirs is in the upper limit of the recorded range for the species, close to ϕ' value of *O. niloticus* (Table 3). The reason for this is not immediately apparent. Possible reasons are, among others, gene introgression in *O. mossambicus* and *O. niloticus* (De Silva and Ranasinghe 1989), the favorable environment for *O. mossambicus* in Sri Lankan reservoirs which provides a variety of highly nutritious food sources (De Silva et al. 1984; De Silva 1985a), and a combination of these and/or some other unknown factors. This is an important line for future reservoir fishery research in Sri Lanka.

The estimated values of L_{∞} of *O. mossambicus* in Kaudulla and Minneriya in the present study are higher than those studied by De Silva and Senaratne (1988) for a series of Sri Lankan reservoir populations which ranged from 26.7 to 32.7 cm in total length. Their estimates have perhaps been influenced by the small sample sizes obtained from gillnet catches. In the present study, however, randomly chosen large samples which covered wide ranges of recruited phase have been used and the effect of gillnet selection on catch samples from multi-mesh gillnet fisheries have been very small.

Y/R analyses incorporating selection parameters, as performed in the present study, are more realistic than those based on the assumption of knife-edge recruitment, especially for short-lived species. From the Y'/R analysis, it is evident that both *O. mossambicus* and *O. niloticus* in Minneriya are heavily exploited, whereas in Kaudulla, *O. niloticus* is exploited close to the optimum level and *O. mossambicus* is underexploited. Decline in mean landing size of *O. mossambicus* in Minneriya from 23.5 cm in 1975-82 (De Silva 1985b) to 22.1 cm in gillnet catches and 21.3 cm in beach seine catches (present study) also indicates that *O. mossambicus* is overexploited. The differences in exploitation rates between the two reservoirs may be due to the fact that submerged tree stumps in Kaudulla, unlike in Minneriya, provide refuge for fish and prevent intensive exploitation. When the optimization of

fish yields in the artisanal fishery of Minneriya is viewed from the sociological context, reducing the exploitation rate by withdrawing fishing crafts is impractical. As such, to obtain high fish yields in Minneriya, the most appropriate management strategy would be to increase the size of first capture.

In Kaudulla, *O. mossambicus* yield could be optimized by increasing L_c at a higher level of E (approximately 0.5). However, since *O. niloticus*, which accounts for over 70% of total landings in Kaudulla, is exploited close to optimum, any increase in E for *O. mossambicus* is likely to affect adversely *O. niloticus* stock in the reservoir. On the other hand, although *O. niloticus* yield could be increased by increasing L_c at the present level of E, increase in L_c of *O. mossambicus*, which is exploited by the same fishing gear, would lead to decreased *O. mossambicus* yield. Nevertheless, since *O. mossambicus* presently accounts for less than 23% of total landings in Kaudulla, management of the fishery of *O. niloticus* is considered more important because the livelihood of fishing families depends on the fishery of this species. Therefore increasing L_c of *O. niloticus* to about 25 cm at the present level of E (see Fig. 13) is a useful management strategy in Kaudulla. It could also be expected that compensation would be made for the decline in *O. mossambicus* yield in such a management strategy, by the increase of yield of *O. niloticus*.

Most Asian reservoir fisheries depend on one or a few closely related species of similar sizes, having comparable selection curves, mostly carps and cichlids. Because of limitations of topography, the gear is mostly gillnet. As such, the situation dealt with in the present study is not unique to Sri Lankan reservoirs. The present study, therefore, will be useful in introducing management strategies under comparable situations and could provide insights into the meaningful application of length-based methods for stock assessment to specific situations such as multi-mesh gillnet fisheries in reservoirs.

Acknowledgements

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