

On the life history of a cyprinid fish, *Labeo cylindricus*

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Synopsis

Aspects of the life history of *Labeo cylindricus* in Lake Chicamba, a man made hydroelectric dam in central Mozambique were investigated. *L. cylindricus* was found to be a potadrometic, synchronous spawner concentrating in river mouths prior to migrating up flowing rivers in January to spawn. Length-at-(50%)-maturity was attained at a fork length (FL) of 96 mm for males and 98 mm for females, both within their first year of life. The adult sex ratio was found to be female dominated at 1 male : 1.63 females. Scales were used to age the species, with two growth checks deposited annually. Growth was rapid and was best described by the von Bertalanffy growth model as $L_t = 224.2(1 - e^{-0.66(t+0.03)})$ mm FL. A maximum age of 4 years was observed for *L. cylindricus* with the largest male and female measuring 210 mm FL and 235 mm FL, respectively. The rate of natural mortality was estimated to be extremely high at 1.93 year⁻¹ using length-converted catch curve analysis and is possibly a response to heavy predation by the introduced piscivore *Micropterus salmoides*.

Introduction

Fishes of the genus *Labeo* are widely distributed throughout Africa and consist of at least 80 species which comprise 16.4% of the African cyprinid ichthyofauna (Reid 1985). Most labeo species are also commercially important throughout the African continent, having contributed significantly to various fisheries. Their roe (sensu caviar) is often harvested as an additional bycatch (Skelton et al. 1991). Despite their obvious importance, the few studies that have investigated aspects of their life history have been conducted on the larger commercial species (Lowe 1952, Mulder 1973, Balon et al. 1974, Potgieter 1974, Baird 1976, Tomasson et al. 1984, van Zyl et al. 1995).

Data that are available on labeo life histories suggest that they could be vulnerable to overfishing. These life history characteristics include their annual mass aggregations at river mouths and the subsequent migrations up these rivers to spawn, which tends to be dependent

on rainfall and other proximate environmental conditions (Bowmaker 1973, Bayley¹, Jackson & Coetzee 1982). In addition, their eggs, embryos and larvae are particularly vulnerable to flash floods and associated siltation which can significantly reduce survival and fishery recruitment (Skelton et al. 1991). As a result they exhibit fluctuating inter-annual recruitment patterns (Tomasson et al. 1984).

The redeye labeo, *Labeo cylindricus* Peters, 1852 is a common, widely distributed species inhabiting East African rivers in the south through the Zambezian system and east coastal drainages to the Phongolo system in Northern Natal, South Africa. It has also been reported from the Zambian Zaire and the Lulalaba system in the Zaire basin. It is a relatively small species

¹ Bayley, P.B. 1982. The biology of *Labeo horie* Heckel in Lake Turkana. pp. 803–827. In: A.J. Hopson (ed.) Lake Turkana, A Report on the Findings of the Lake Turkana Project 1972–1975, Institute of Aquaculture, University of Stirling, Stirling.

attaining a maximum length and mass of 25 cm standard length and 0.9 kg, respectively (Skelton 1993). There is limited quantitative information available on the life history of this species. What is known, is that it is a shoaling species, inhabiting rocky habitats of small and large rivers and in lakes and dams. It feeds by grazing algae and 'aufwuchs' from the surface of rocks, tree trunks and other firm surfaces (Gaigher 1973). To contribute to the knowledge on the life history of this species, this communication investigates various biological aspects including reproductive seasonality, length- and age-at-(50%)-maturity, age and growth using scales, estimation of mortality rates and a description of potadromesis associated with spawning within Lake Chicamba, a man-made impoundment situated in central Mozambique.

Materials and methods

Study area

Lake Chicamba (19°08'S, 33°08'E), is situated in central Mozambique at an altitude of 625 m above mean sea level (Figure 1). Rainfall in the region follows two distinct seasons, a rainy season from November

to March and a dry winter season from May to August (Figure 2). The lake therefore undergoes a flooding in summer commencing in late December through April and a gradual drawdown from May to December as water is released from the dam for the generation of electricity (Figure 2). The substratum is typically silty with stands of drowned trees extending down to the former river channels. The drawdown phase of the lake exposes large areas of silty soils, which are rapidly covered by dense grassland vegetation during the beginning of the rainy season or are used for subsistence agriculture by the rural community living on the lakeshore. Subsequently, during flooding a large biomass of terrestrial vegetation is inundated. Mean secchi depths were 150 cm, with a range from 10 cm in river inlets at the height of river discharge to 400 cm in the main lake during winter. In summer, the mean water temperature was 27.6°C (25.2–32.7°C) while in winter its mean was 22°C (18.5–25.5°C). The mean annual water temperature was 25.8°C (Figure 3).

Reproductive biology

Samples of *L. cylindricus* were collected monthly from 5 riverine and 4 lacustrine sites between December 1995 and December 1996 (Figure 1). The riverine sites

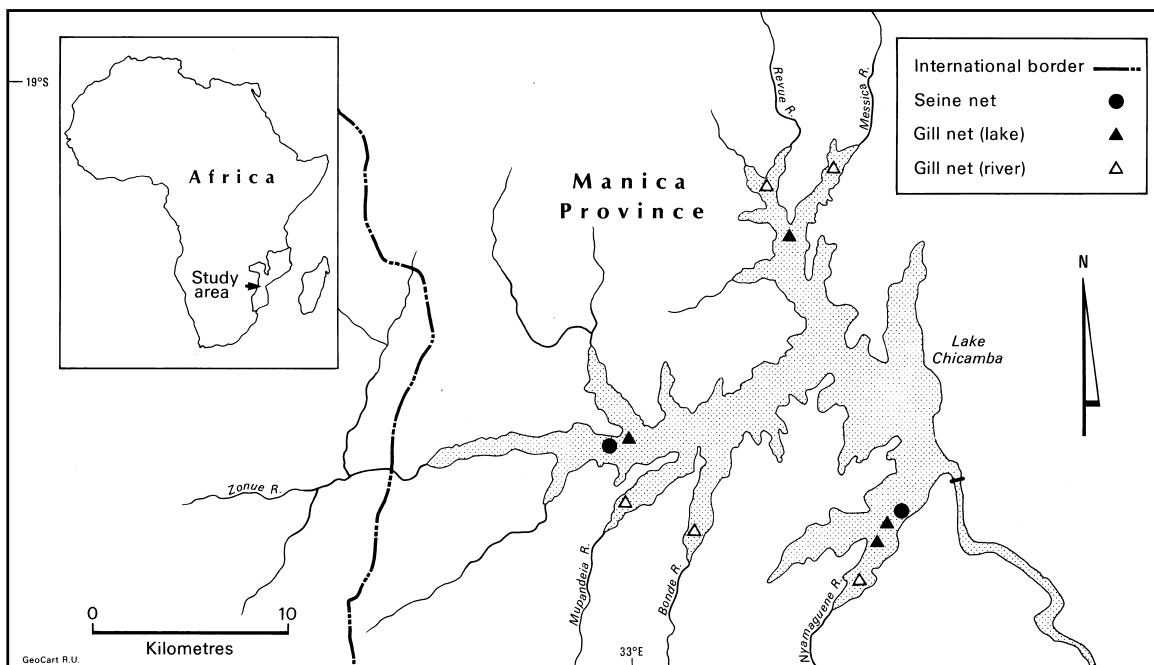


Figure 1. Map of Lake Chicamba, Mozambique, showing the gill and seine net sampling sites.

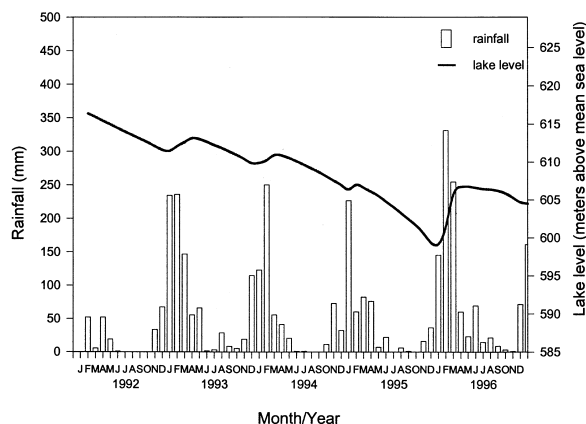


Figure 2. Monthly rainfall (mm) and lake level in metres above mean sea level (m amsl) for Lake Chicamba, Mozambique from the period January 1992 to December 1996.

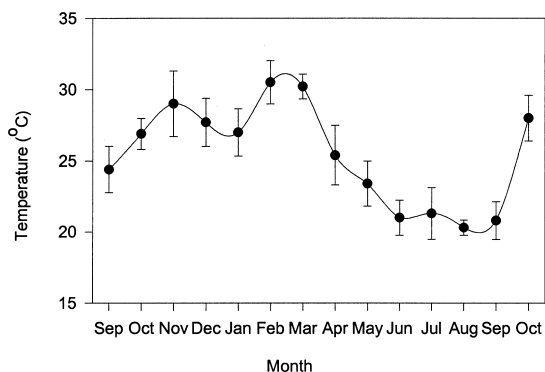


Figure 3. Mean monthly water temperature ($^{\circ}\text{C}$) \pm standard deviation for Lake Chicamba, Mozambique from the period September 1995 to October 1996.

were selected on the criteria that the rivers were perennial and accessible, whereas the lacustrine sites were selected randomly. Gill net fleets comprising of six 30 m^2 panels with stretched mesh sizes of 25, 50, 70, 90, 110 and 130 mm, were set monthly at these sampling sites. Further samples were obtained using 30 m seine nets mesh sizes of 10 mm and 25 mm at two lacustrine sites (Figure 1). All fish were measured to the nearest millimeter fork length (FL) and standard length (SL) and weighed whole. The fish were then dissected and sexed. The gonads were removed, weighed and categorized according to the developmental stages described in Table 1. The eviscerated mass of the fish was then recorded.

Length-at-(50%)-sexual maturity was calculated by fitting a logistic ogive to the proportion of reproductively active fish (ripe or spent) during the spawning

Table 1. Macroscopical criteria used to stage gonadal recrudescence in *Labeo cylindricus*.

Stage	Macroscopic appearance
Juvenile	Not possible to visibly distinguish sex. Gonad as appears a translucent gelatinous strip.
Resting	Sex distinguishable. Ovary small band of orange-red tissue. Testis discernible as a thin white band.
Developing	Ovary increases in size, is flattened dorso-ventrally and is orange-red in colour. Oocytes visible. Testis increases in size and is white in colour. Sperm is not extrudable from the testis.
Ripe	Ovary turgid with oocytes and fills the entire abdominal cavity. Oocytes are olive-green to brown in colour and loosely attached to ovigerous lamellae. Testis creamy white, showing constrictions. Sperm can be extruded from the testis.
Spent	Ovary flaccid and sac like with few vitellogenic oocytes visible. Testis reduced in size and dirty grey in colour.

season in centimeter size classes. The two parameter logistic ogive is described by the equation

$$P(L) = \frac{1}{1 + e^{-(L - Lm_{50})/\delta}}, \quad (1)$$

where $P(L)$ is the percentage of mature fish at length L , Lm_{50} the length-at-(50%)-maturity and δ the width of the ogive. A gonadosomatic index was calculated by expressing gonad mass as a percentage of eviscerated body mass. Sex ratio was determined from fish larger than the size-at-(50%)-maturity collected during the spawning season. Sex ratio was tested for unity using a chi-square test.

Spawning migration

To facilitate an understanding on the possibility of a spawning migration in this species, the monthly abundance of *L. cylindricus* was determined from gill net catch-per-unit-effort (CPUE). CPUE was standardised at number of fish fleet $^{-1}$ net night $^{-1}$. To determine when juvenile fish recruit into the lake and to determine the modal progression of length over time, *L. cylindricus* were sampled using seine nets.

Age and growth

Scales from fish samples were removed from the region between the lateral line and just behind the pectoral fin and stored dry in manilla envelopes. Later, the scales from fish ranging in length from 38–235 mm FL were soaked in water containing domestic dishwashing detergent for at least an hour, before rubbing gently between the fingers to remove any dried mucous and skin. Scale samples were read with transmitted light using a microfiche reader. Both authors read each scale on two occasions. If the two age estimates did not agree a third was taken. An age estimate was accepted if two estimates were the same, however, if the three age estimates differed the scale was rejected as unreadable.

The periodicity of growth check formation on the scales was investigated using marginal increment analysis. The distance from the anterior scale margin to the last growth check was measured in a sample of scales collected monthly and plotted as a function of time.

Length-at-age was described by the 3 parameter, specialised von Bertalanffy growth model of the form

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \quad (2)$$

where t_0 the age-at-‘zero’-length; L_t is the length at age t ; L_∞ is the predicted asymptotic length and K is the Brody growth co-efficient (Ricker 1975). The models were fitted using a non-linear minimisation routine to obtain parameter estimates. The model was fitted by minimising the sum of the squared absolute differences between the observed and predicted lengths-at-age. Variance estimates were calculated by using (conditioned) parametric bootstrap resampling with 1000 bootstrap iterations (Efron 1982). Standard errors and 95% confidence intervals were constructed from the sorted bootstrap parameter estimates using the percentile method described by Buckland (1984).

Mortality

To obtain estimates for the instantaneous rate of total annual mortality (Z), length frequency data collected from experimental 30 m seine nets with mesh sizes of 10 mm and 25 mm from December 1995 to February 1996 were analysed by means of a linearised length-converted catch curve (Pauly 1983, 1984a,b). This method uses the von Bertalanffy growth parameters to plot of $\ln(F/dt)$ against t , where F is the frequency of individuals in each length class, t is the relative age of

the fish. The value dt is the time taken for the fish to grow through a particular length class and allows for decreased growth with increased age. The negative of the slope of the resultant linear regression line through the descending data points gives a first approximation of Z .

Due to the inherent difficulty in the accurate calculation of natural mortality (M) the mean M from four estimates was accepted for the *L. cylindricus* stock. Estimates for M were derived from the four empirical models described by Pauly (1980), Rihkter & Efanov (1977), Gunderson & Dygert (1988) and Hoenig (1983). Although the Hoenig (1983) equation was developed to estimate total mortality (Z), the model was derived from empirical data obtained from unexploited or lightly fished stocks. In addition, the widest possible range of *L. cylindricus* age classes were sampled and little fishing pressure exists on the *Labeo* stock in the lake. Therefore, the derived value would more closely approximate M than Z . Having obtained Z and M , fishing mortality was derived by subtraction ($F = Z - M$).

Results

Reproductive biology

Of 176 mature *L. cylindricus* sampled in December and January, 38% were male and 62% female. The sex ratio was female dominated at 1 male : 1.63 females, differing significantly from unity ($\chi^2 = 12.18$, $df = 12$, $p = 0.08$). The largest male and female sampled measured 210 mm FL and 235 mm FL respectively. Length-at-(50%) maturity was estimated at 96 mm FL for males and 98 mm FL for females (Figure 4).

Gonadal recrudescence followed a distinct seasonal pattern. Over 85% of the ovaries were in a ‘resting’ condition during the winter months from June to August. In October over 92% of the samples had ‘developing’ ovaries. By November, over 57% of the female fish were in ripe condition and in December and January all mature female fish were ‘ripe’. By February, spawning activity had ceased with 88% of *L. cylindricus* ovaries sampled in a ‘spent’ condition (Figure 5). This trend was mirrored by the rapid rise in the gonadosomatic index from a winter low of 0.6% in June and July, a steady rise from October and peaking in December and January at 27.1% and 35.2% respectively.

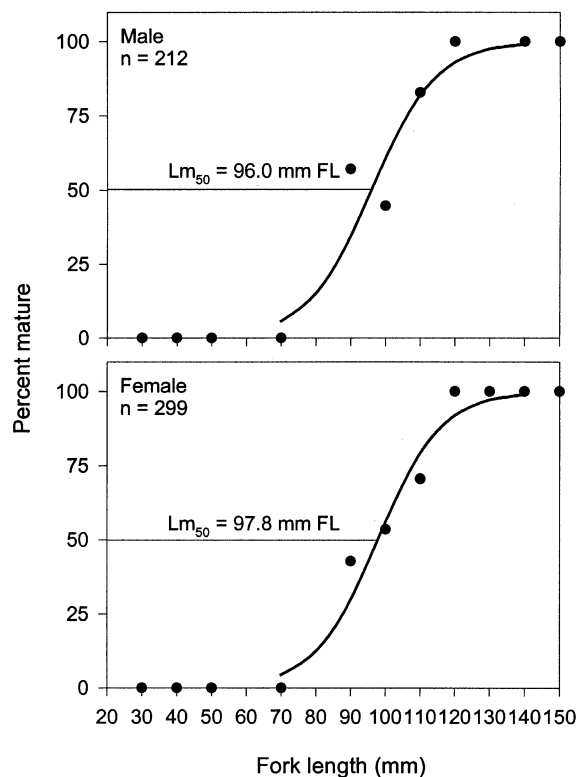


Figure 4. Logistic ogives fitted to the percentage of sexually mature male and female *Labeo cylindricus* from Lake Chicamba, Mozambique (L_{m50} = length-at-(50%)-maturity).

Abundance

CPUE in the in-flowing rivers peaked in January with 34.6 fish fleet⁻¹ night⁻¹ (Figure 6). CPUE in other months ranged from 0 to 8.0 fish fleet⁻¹ night⁻¹. The CPUE from main lake sites ranged from 0 to 6 fish fleet⁻¹ night⁻¹. The length frequency of *L. cylindricus* in seine net catches is illustrated in Figure 7.

Age and growth

The marginal increment analysis, presented in Figure 8, illustrates that two growth checks are formed on the scales annually, one in April and one in October (Figure 7). Despite the absence of scale samples collected during March, these growth checks were further validated by the use of modal progression analysis. When seine net catches of fish were graphed monthly, it was noted that fish averaged 100 mm at the end of the first year of life. This cohort, by April, averaged 120 mm in length and

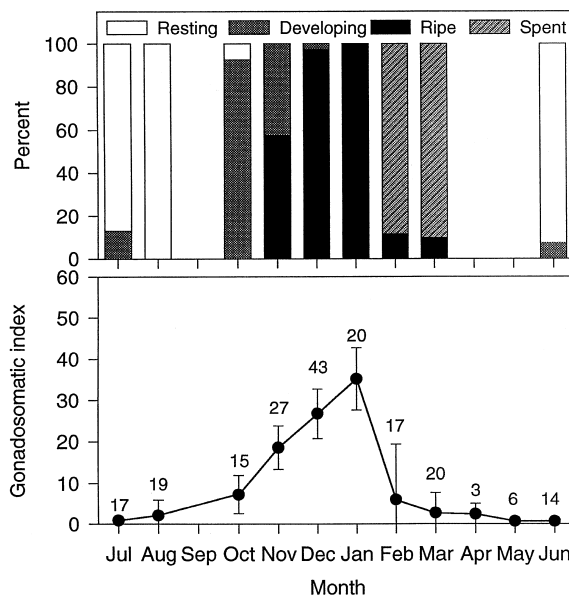


Figure 5. Female monthly maturity stages and gonadosomatic indices (GSI) (\pm standard deviation) for *Labeo cylindricus* from Lake Chicamba, Mozambique.

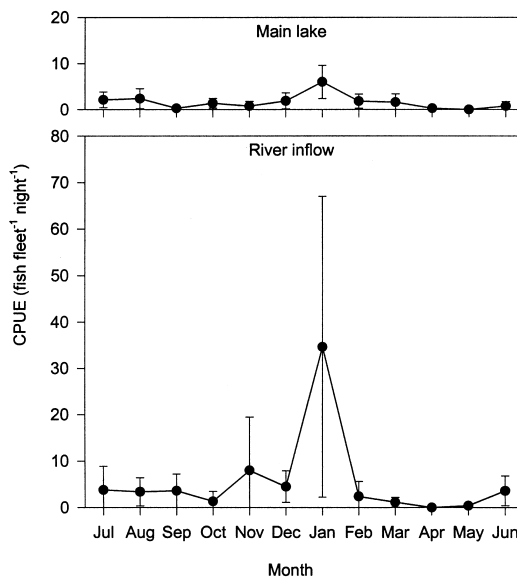


Figure 6. Monthly mean catch per unit effort (CPUE) \pm standard deviation of *Labeo cylindricus* in gill net fleets set in river inflow and main lake sampling sites on Lake Chicamba, Mozambique.

clearly showed two checks on the scales. Of the 236 scales analysed, 60 (25.4%) were rejected as unreadable with the remainder of the age estimates used for the estimation of growth parameters. Length-at-age

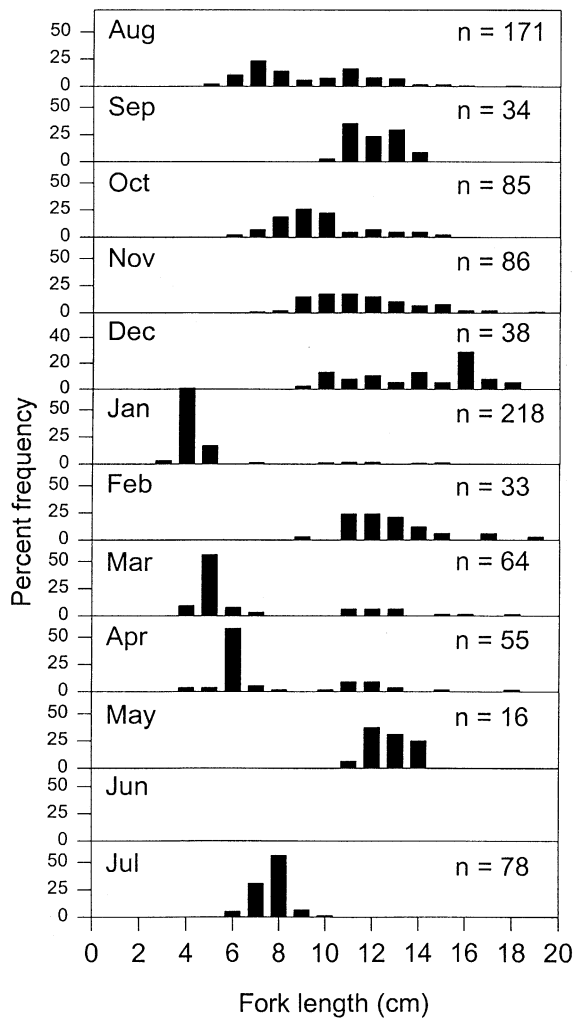


Figure 7. Monthly length frequency of *Labeo cylindricus* in seine net samples collected from Lake Chicamba, Mozambique between December 1995 and December 1996.

was adequately described by the von Bertalanffy growth model with its parameters being chosen as they are commonly used in empirical estimates of natural mortality (Pauly 1980), per-recruit modelling (Ricker 1975) and ease of comparison between growth studies conducted on other species. The observed and predicted lengths-at-age, von Bertalanffy growth parameters, their associated estimates of variation and confidence intervals are summarised in Tables 2, 3 and Figure 9.

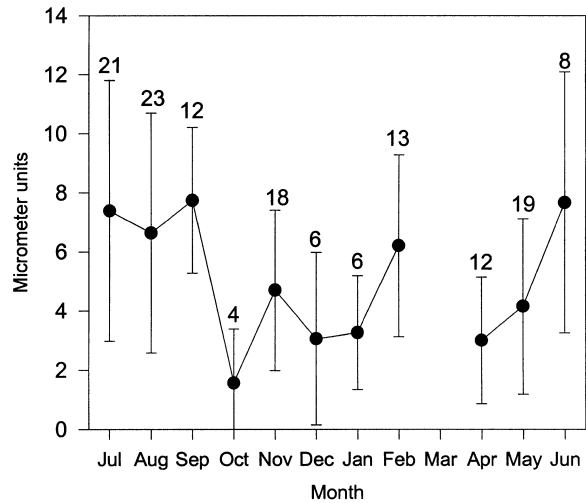


Figure 8. Temporal changes in the scale marginal increment, measured from the last visible growth check to the anterior scale margin, for *Labeo cylindricus* sampled from Lake Chicamba, Mozambique between December 1995 and December 1996.

Table 2. Observed and predicted mean lengths-at-age (\pm standard deviation) for combined sex *Labeo cylindricus*, determined using scales. Samples were collected from Lake Chicamba, Mozambique during the period December 1995 to December 1996.

Age (years)	Observed mean \pm sd	n	Length range	Predicted mean
0.5	59.0 \pm 19.0	3	38–75	66.5
1.0	98.6 \pm 7.3	14	90–120	111.1
1.5	136.3 \pm 29.2	81	90–200	143.1
2.0	177.6 \pm 13.7	28	152–214	166.1
2.5	176.6 \pm 14.9	41	192–193	182.5
3.0	192.5 \pm 0.7	2	165–201	194.4
3.5	202.2 \pm 4.9	5	198–210	202.8
4.0	235.0	1	—	208.9

Mortality

Estimates of the instantaneous rate of total mortality from length converted catch curves (Figure 10) and natural mortality using empirical models are summarised in Table 4. From the length-converted catch curve, total mortality (Z) was estimated at 1.93 year⁻¹ and from a mean of the empirical models of natural mortality, natural mortality (M) was estimated at 0.91 year⁻¹. Fishing mortality (F) was calculated by subtraction at 1.02 year⁻¹.

Table 3. Point estimates, associated standard errors and 95% confidence intervals for combined sex data ($n = 175$) fitted using the specialised three parameter von Bertalanffy growth model for *Labeo cylindricus*. Samples were collected from Lake Chicamba, Mozambique between December 1995 and December 1996.

	Point estimate	SE	95% CI
L_{∞}	224.2 mm FL	11.37	[208.09, 251.91]
K	0.66 year ⁻¹	0.09	[0.47, 0.83]
t_0	-0.03	0.10	[-0.28, 0.11]

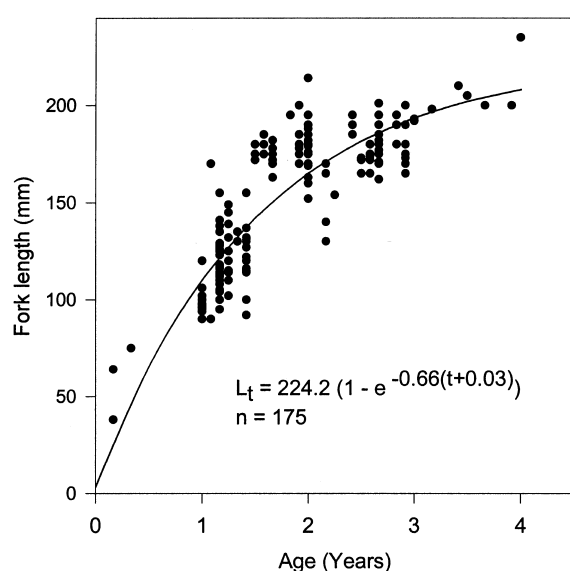


Figure 9. Observed individual mean lengths-at-age of *Labeo cylindricus* using scales sampled from Lake Chicamba, Mozambique between December 1995 and December 1996. The growth curve was fitted to combined sex data using the von Bertalanffy growth model with an absolute error structure.

Discussion

A single short annual spawning season preceded by an upstream migration out of the main lake or river to spawn appears to be the norm rather than the exception in fishes inhabiting latitudes with marked seasonal rainfall patterns (Lowe-McConnell 1979, Jackson 1989). Amongst the labeines, mass upstream migrations are well documented (Bowmaker 1973, Tomasson et al. 1984, Skelton 1993). The congregation at river mouths 6 weeks before flooding and the subsequent upstream migration for spawning by *L. altivelis* has been documented in Lake Kariba (Bowmaker 1973). In addition,

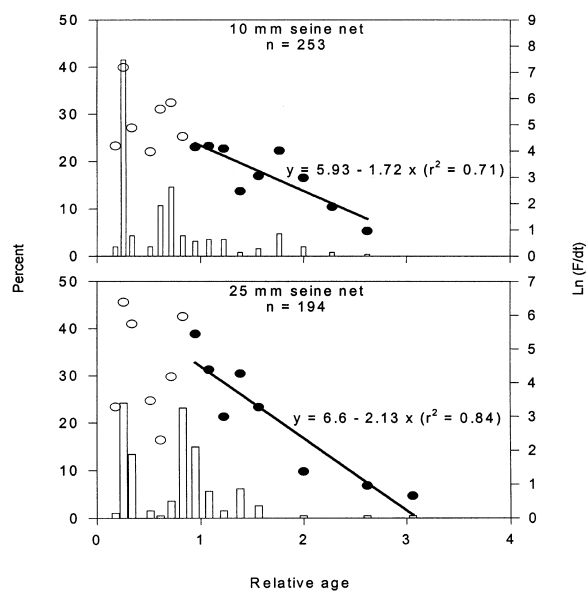


Figure 10. Linearised-length-converted-catch curves applied to age-frequency data collected from *Labeo cylindricus* sampled in 10 mm and 25 mm mesh size seine net in Lake Chicamba, Mozambique.

Table 4. Instantaneous total (Z) and natural (M) mortalities rates estimated for *Labeo cylindricus* sampled from Lake Chicamba, Mozambique between December 1995 and December 1996. Instantaneous total mortality was estimated from linearised catch curves using age frequencies from various mesh seine net catches while the natural mortality estimates were derived from various empirical models.

Z	M	Method
	0.52	Pauly(1980).
	1.37	Rihkter & Evanov (1977).
	0.62	Gunderson & Dygert (1988).
	1.15	Hoening (1983).
1.72		Catch curve (10 mm)
2.31		Catch curve (25 mm)

three other species of *Labeo* including *L. cylindricus* were found to be potamodromous, migrating upstream to spawn (Bowmaker 1973).

In Lake Chicamba, gonadal recrudescence first became evident in October with the increasing water temperatures after the winter months probably being the primary stimulant. The gonads matured rapidly and by January all female fish were ripe with a high gonadosomatic index. Although ripe fish were recorded in November, marking the initiation of the rainy season

(cf. Figures 2, 5), the high river discharge rates and concomitant flooding of the lakes shoreline occurred in January, by which time all the *L. cylindricus* sampled were in a 'ripe' condition. Peaks in gill net CPUE in the river inlets indicated that like *L. altivelis* in Lake Kariba (Bowmaker 1973), Lake Chicamba's stock of *L. cylindricus* aggregated at the river mouths prior to spawning. By February, the majority of female *L. cylindricus* had spawned and were in a 'spent' condition with no 'ripe' fish being recorded in the samples after March. Both the macroscopic and histological examination of the ovaries revealed that all oocytes (excluding the perinuclear oocytes) in the ovary were of a similar size and were in the final stages of vitellogenesis. During the winter period there was only evidence of atresia in vitellogenic oocytes, common in synchronous iteroparous spawning fish (Wallace & Selman 1981, Booth & Weyl 1999). These data together with a short spawning period and the relatively large size of the ovaries provided further evidence of a synchronous spawning pattern with all oocytes being ovulated and deposited during the annual migration up the rivers. The remaining perinuclear oocytes would develop and mature during the following summer providing another batch of vitellogenic oocytes. These would then in turn be replaced by mitotic division of the oogonia embedded in the ovigerous lamellae.

The occurrence of juvenile *L. cylindricus* in seine net samples collected in January was indicative of spawning activity prior to the mass aggregation of mature fish recorded over this time period. Bowmaker (1973) suggests that the triggering mechanism for upstream migration results from the combination of many physical and chemical factors associated with flooding. It is therefore plausible that individuals inhabiting the riverine environment may be subject to these stimuli earlier in the rainy season than individuals inhabiting the lacustrine environment. Therefore, small-scale spawning migrations of riverine individuals early in the rainy season and concomitant recruitment of early spawned juveniles into the lake may in part explain the occurrence of juveniles in mid-January when the main lake stock migrates. *L. cylindricus* therefore has an extended spawning season which may commence as early as November and runs through to the end of January.

Growth check formation in hard tissues such as scales, otoliths, vertebrae and operculae has been documented as a response to one or more environmental variables that reduce metabolic rate and result in a slowing of the growth rate (Summerfelt & Hall 1987,

Weatherly & Gill 1987, Gauldie & Nelson 1990). In tropical and subtropical areas check formation has often been linked to a physiological 'winter', such as temporal variation in feeding (Bruton & Allanson 1974) or reproductive periodicity (Garrod 1959, Bruton & Allanson 1974, Pannella 1974, Hecht 1980, Booth et al. 1995, Booth & Merron 1996) rather than to a climatic winter. In contrast, Hecht (1980) in a study of the growth of *Oreochromis mossambicus* using sectioned sagittae, recorded the deposition of two checks per year, one during February/March coinciding with the end of peak reproductive activity and the other during July/August, over the winter period. Le Roux (1961) also found that ring formation in *O. mossambicus* scales in a number of Transvaal impoundments occurs in August marking the end of winter. Similarly, Weyl & Hecht (1998) reported that in the otoliths of both *Tilapia rendalli* and *O. mossambicus* from Lake Chicamba, growth checks were deposited in winter.

In *L. cylindricus* there is a high investment in reproduction. In addition, all ripe fish dissected between December and January were observed to have empty digestive tracts, which indicated a cessation in feeding prior to and during the spawning period. These two factors could be responsible for sufficient physiological stress that may account for the growth check observed subsequent to spawning. A second growth check occurred during the winter, in response to the low water temperatures. The presence of two growth checks in the scales of *L. cylindricus* was further validated directly by the presence of two checks in known age-1 fish.

Growth check validation and the discrete spawning period of *L. cylindricus* allowed for the accurate estimation of lengths-at-age and in the modelling of growth in this species. From the modelled lengths-at-age, it appears that *L. cylindricus* is a fast growing short-lived species, with a maximum age of 4 years having been recorded. Both male and female fish matured within their first year of life having similar lengths- and ages-at-maturity.

Fish species that spawn in temporary environments such as floodplains are typically subject to high juvenile mortalities as a consequence of habitat desiccation and predation when the juveniles migrate off the floodplain. Natural mortality estimates based on empirical models were considerably lower than the total mortality in Lake Chicamba. Since no directed fishery exists at present, the high mortality rates can therefore not be attributed to high fishing mortality. It was for this reason

that the empirical estimates of natural mortality were rejected and the length-converted catch curve estimate of total mortality accepted as the first approximation of natural mortality for the species. In Lake Chicamba the main food source 'aufwuchs' grows on inundated timber and rocky outcrops, which have been shown to be the preferred habitats for the introduced piscivore, the largemouth bass, *Micropterus salmoides* (Weyl unpublished data). High rates of predation may therefore in part explain the high adult mortality rate in the lake. However, data on other populations of *L. cylindricus* are unavailable for comparison.

Growth in the *L. cylindricus* was rapid with 43% of the maximum theoretical size attained before sexual maturity within the first year of life. In contrast sexual maturation occurred at 25% of the maximum observed age. This fast growth in the Lake Chicamba population of *L. cylindricus* could allow for the attainment of fish large enough to migrate up the rivers during the annual spawning migration, as well as to maximise individual reproductive capacity. In addition, highly seasonal growth due to the cessation of feeding and high energetic requirements for gonadal recrudescence during the summer period and the decreased metabolic rate over the winter period could ensure high fecundity without much additional somatic growth. The high natural mortality in this species, with the population being reduced at least half in size annually, could also provide a selective pressure for this growth pattern. In this scenario, if fish reproduced at a relatively large size (large enough to provide a reasonably high fecundity) and early in life, it would enable fish to reproduce at least once during their lifetime. In contrast, in large migratory species with a low adult mortality rate, maturity is often attained relatively late in life yet at a size large enough to enable successful migration and to maximise fecundity (Griffiths & Hecht 1995).

It has been proposed that fishes may tend towards an altricial or precocial life history style, depending upon abiotic and biotic conditions (Balon 1979, Adams 1980, Balon 1981, Noakes & Balon 1982, Bruton 1989). A precocial life history style, including traits such as delayed maturity, small annual reproductive output, slow growth and high longevity, is favoured in large, deep, stable habitats such as reservoirs and lakes. Fish from unstable or harsh environments, which undergo unpredictable and near cataclysmic physiochemical changes, tend towards an altricial life history style which is characterised by early maturation, large reproductive output, fast growth and a short lifespan.

Furthermore, Roff (1984) noted that there was a statistically significant correlation between several life-history characteristics such as reproductive output, growth and survival. He hypothesised that there would be a trade-off between these life-history characteristics, for example, if reproductive costs were high, then there would be a resultant decrease in age-at-maturity and an increase in growth rate.

When the ratios of size- and age-at-maturity relative to maximum size and age are compared to other *Labeo* species in the sub-region (Table 5) it becomes evident that a similar trend exists in species from the Incomati/Limpopo system (Potgieter 1974) and Lake Kariba (Balon et al. 1974). In these systems the *Labeo* species typically exhibited a relatively small size and age-at-maturity relative to maximum size and age. The opposite trend is exhibited in the large *Labeo* species *L. umbratus* and *L. capensis* from the Orange-Vaal River system and *L. mesops* from Lake Malawi, all of which display a delayed maturity and a high size- and age-at-maturity relative to maximum size. Furthermore, the length and age-at-maturity of *L. cylindricus* in the Incomati/Limpopo system was similar to that found in Lake Chicamba.

L. cylindricus clearly exhibits the altricial (generalist/r-selected) life history characteristics associated with environmental instability despite the relatively stable environment provided by the lake for adult fish. The altricial life history characteristics of *L. cylindricus* probably evolved in the relatively unstable riverine environment prior to the lakes construction and appear to have been retained by the species. This suggests that *L. cylindricus* in Lake Chicamba have retained the inherent reproductive characteristics of a riverine population. Periodic flooding of the inflowing rivers during the warmer summer period, therefore, appears to be one of the most important variables in determining spawning success of *L. cylindricus* in Lake Chicamba. This is of concern as it has been documented that potamodromous cyprinids have failed to colonise the lacustrine environment provided by the large African lakes with *Labeo* species often declining to insignificant levels in the main lake basins (Begg 1974, Jackson & Rogers 1976).

The combination of a high instantaneous rate of total mortality, obligatory potamodromy, synchronous spawning and short life-span make this fish highly susceptible to the failure of the annual hydrological cycle. These life history characteristics would also make this fish particularly vulnerable to any increase in

Table 5. Size-at maturity (L_{mat}) and age-at-maturity (T_{mat}) relative to maximum size (L_{max}) and maximum age (T_{max}) for seven *Labeo* species from Lake Chicamba¹ (present study), the Incomati/Limpopo² system (Potgieter 1974), Lake Kariba³ (Balon et al. 1974), Vaal River⁴ (Mulder 1973), Caledon River⁵ (Baird 1976) and Lake Malawi⁶ (Lowe 1952). M = male, F = female, FL = fork length, SL = standard length, TL = total length.

Species	Sex	Locality	Length	L_{mat}	L_{max}	$L_{\text{mat}}/L_{\text{max}}$	T_{mat}	T_{max}	$T_{\text{mat}}/T_{\text{max}}$
<i>L. cylindricus</i>	M	Lake Chicamba ¹	FL	96	210	0.46	1	4	0.25
	F	Lake Chicamba ¹	FL	98	235	0.42	1	4	0.25
<i>L. ruddi</i>	M	Incomati/Limpopo ²	FL	100	211	0.47	1.22	4	0.31
	F	Incomati/Limpopo ²	FL	100	248	0.40	1.22	5	0.24
<i>L. rosae</i>	M	Incomati/Limpopo ²	FL	150	254	0.59	1.42	5	0.28
	F	Incomati/Limpopo ²	FL	150	272	0.55	1.29	5	0.26
<i>L. altivelis</i>	M	Lake Kariba ³	SL	129	400	0.32	2	9	0.22
	F	Lake Kariba ³	SL	192	400	0.48	3	9	0.33
<i>L. umbratus</i>	M	Vaal river ⁴	FL	220	455	0.48	2.03	6	0.34
	F	Vaal river ⁴	FL	300	473	0.63	2.91	6	0.48
<i>L. capensis</i>	M	Vaal river ⁴	FL	260	407	0.64	4.15	8	0.52
	F	Vaal river ⁴	FL	310	416	0.75	5.48	9	0.61
<i>L. mesops</i>	M	Caledon river ⁵	FL	200	369	0.54	3.29	8	0.41
	F	Caledon river ⁵	FL	230	381	0.60	4.06	8	0.51
<i>L. mesops</i>	M	Lake Malawi ⁶	TL	250	340	0.74	2.50	4	0.62
	F	Lake Malawi ⁶	TL	300	340	0.88	3.28	4	0.82

exploitation levels. Any increase in the mortality rate, such as through the development of a directed fishery, would seriously compromise the survival of the species and would need to be incorporated into the development of a rational sustainable management plan of this species in the future.

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