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The biology of *Tilapia rendalli* and *Oreochromis mossambicus* (Pisces: Cichlidae) in a subtropical lake in Mozambique

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This study of age and growth, reproduction and juvenile recruitment of *Tilapia rendalli* and *Oreochromis mossambicus* was undertaken in Lake Chicamba, a large, clear subtropical lake in central Mozambique. Sectioned otoliths were used to estimate age. Marginal zone analysis showed that annulus formation occurred during winter, in July and August. Maximum age estimates for *T. rendalli* and *O. mossambicus* were 16 and 10 years, respectively. Growth was described by the 3 parameter von Bertalanffy model as $L_t = 238.74\ (1\text{-}e^{-0.636(t + 0.905)})$ mm TL for *T. rendalli* and $L_t = 266.06\ (1\text{-}e^{-0.7904(t + 0.269)})$ mm TL for *O. mossambicus*. The length-at-50% maturity (Lm_{50}) of male *T. rendalli* was 218 mm total length (TL) and 205 mm TL in females. In *O. mossambicus* the Lm_{50} for males was 251 mm TL and for females 223 mm TL. Both species spawned throughout summer. Lake level was found to have no effect on spawning periodicity although recruitment was flood dependent.

Lake Chicamba is a man-made hydroelectric dam situated in the subtropical region of Manica Province in Mozambique (Figure 1). Large-scale migrations by the rural population into 'safe areas' during Mozambique's civil war in the 1980s and early 1990s (Streck 1994) caused a large increase in participation in the fishery from 67 fishers in 1980 (Robelus & Vissers 1984) to over 550 in 1996 (Weyl, unpublished data). Undoubtedly the lake has played a major role in food security during the war years and continues to do so today for the rural population in the area. However, the need for effective fisheries management is critical to ensure the sustainability of the stocks and the livelihood of the fishers. The red breast tilapia, *Tilapia rendalli*, and the Mozambique tilapia, *Oreochromis mossambicus*, make up over 53% of the total subsistence catch in the Lake Chicamba fishery (Weyl, unpublished data).

The life history of fishes in different water bodies is highly variable with respect to growth rate, size at sexual maturity and reproductive periodicity (Lowe-McConnell 1958; Garrod 1959; Le Roux, 1961; Hecht 1980a). It has been proposed that fishes tend towards either an altricial or precocial life history style, depending upon environmental conditions (Balon 1979 & 1981; Noakes & Balon 1982). The precocial life history style that includes traits such as delayed maturity and a large size is more prevalent in large, deep, stable habitats such as reservoirs and lakes. On the other hand, fish in unstable or harsh environments, which undergo unpredictable and near cataclysmic physio-chemical changes, tend towards the altricial life history style of early maturation at a small body size (Noakes & Balon 1982). Therefore, the proper assessment and management of a fishery requires an understanding of locality-specific growth and reproductive life history parameters of the species.

The accurate determination of age in fishes is a fundamental requirement for calculating the population age structure and population growth rate (Beamish & McFarlane 1987), upon which reliable stock assessments can be based. Both otoliths and scales have been used with varying degrees of success in ageing studies (Summerfelt & Hall 1987; Weatherly & Gill 1987), but scales have been found to underestimate longevity and thus overestimate growth rate (Hecht 1980a,b; Boxrucker 1986; Hammers & Miranda 1991; Booth, Merron & Buxton 1995). Sectioned otoliths are currently considered the most suitable hard tissue for age and growth determination in tropical and subtropical areas (Hecht 1980a,b; Beamish & McFarlane 1987; Hammers & Miranda 1991; Booth *et al.* 1995).

The determination of the age and growth and reproductive biology of these two cichlids in Lake Chicamba is a vital first step towards the development of a sustainable participatory management strategy for the Lake Chicamba fishery.

Materials and methods

Study area

Lake Chicamba (19°08'S, 33°08'E), is situated in Mozambique at an altitude of 625 m above mean sea level (Figure 1). At maximum capacity the lake covers a surface area of 116 km² and has a maximum and mean depth of 61 m and 16 m respectively. The lake experiences large seasonal fluctuations in water levels (Figure 2). 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). In summer, from late December to April, the lake undergoes a flooding stage, which is followed by a gradual drawdown phase 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. No aquatic macrophytes exist in the lake, which may be a consequence of fluctuations in lake level. 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 vegetation is inundated. Mean Secchi depth was 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 at 0.3 m depth was 27.6 °C with a range from 25.2°C to 32.7°C (Figure 3). In winter, mean water temperature was 22°C with a range from 18.5°C to 25.5°C (Figure 3). The annual average water temperature

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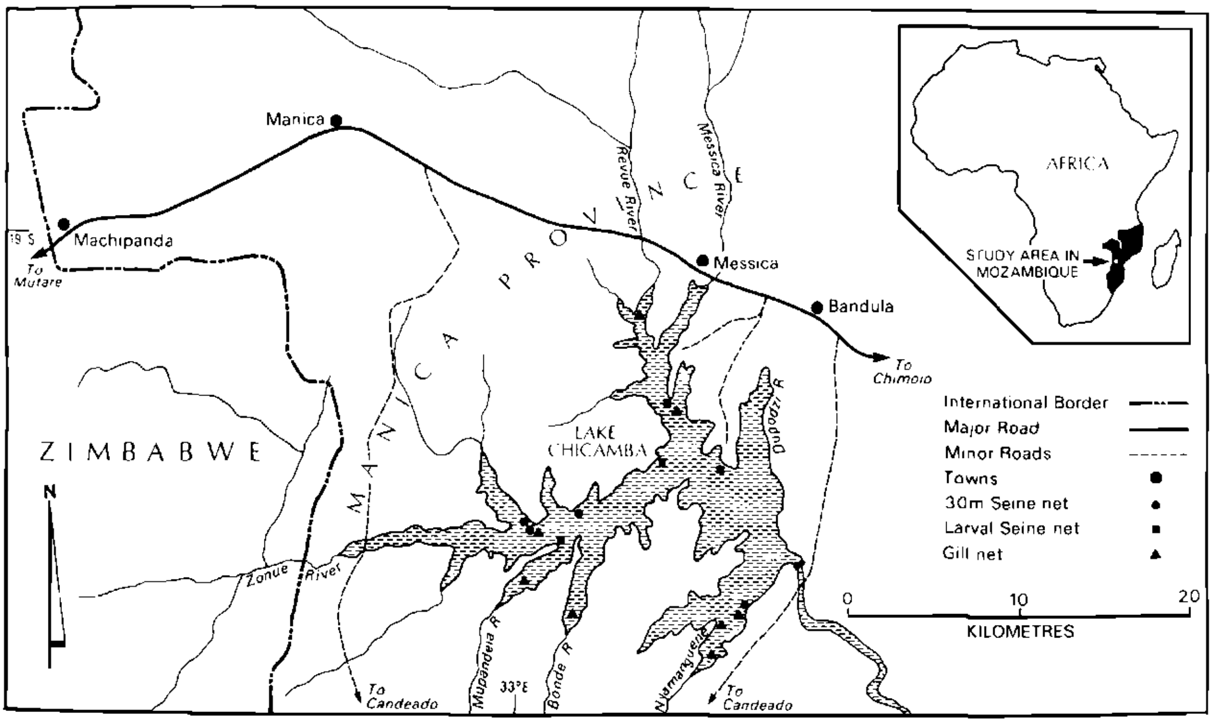

Figure 1 Map of Lake Chicamba, Mozambique, showing gill net and seine net sampling sites.

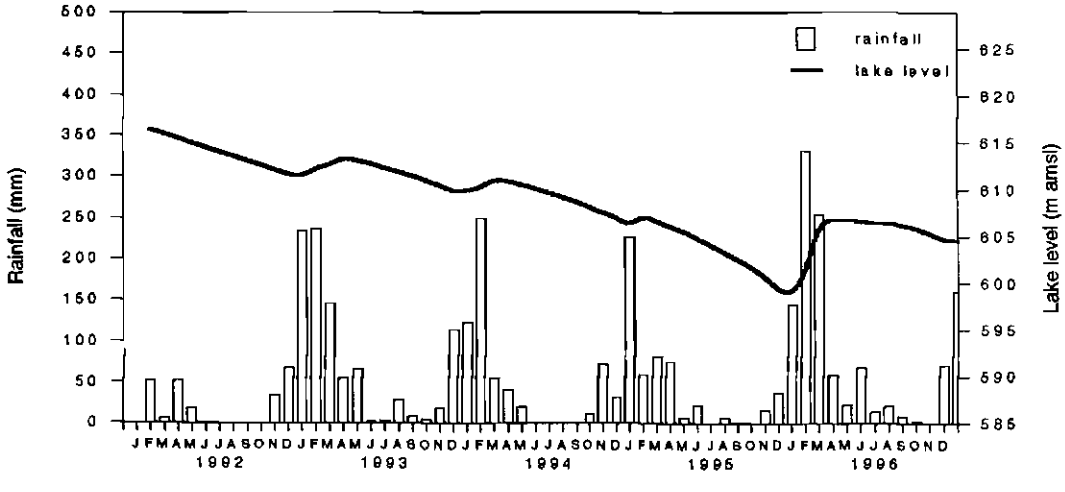

Figure 2 Monthly rainfall (mm) and lake level in metres above mean sea level (m amsl) for the period January 1992 to December 1996 in Lake Chicamba, Mozambique.

was 25.8°C.

Samples of *T. rendalli* and *O. mossambicus* were collected monthly from selected sampling sites in the lake between October 1995 and September 1996 (Figure 1). Fish were collected from the dam using 30 m seine nets with mesh sizes of 10 mm and 25 mm and gill net fleets consisting of six 10 × 3 m (30 m^2) panels with stretched mesh sizes of 25 mm, 50 mm, 70 mm, 90 mm, 110 mm and 130 mm. Gill nets were set in 3 m depth to touch the substratum between 16h00 and 17h00 and collected no later than 08h00 the next morning.

All fish were measured to the nearest millimetre total length (TL) and weighed whole. The fish were then dissected and sexed. The gonads were removed, weighed and categorised according to the developmental stages described in Table 1. The eviscerated mass of the fish was then recorded.

Otolith examination

Samples of *T. rendalli* and *O. mossambicus* samples for age and growth determination were selected according to the length frequency of each size class in the experimental catch. Sagittal otoliths were removed from 199 *O. mossambicus* (83–364 mm TL) and 300 *T. rendalli* (70–310 mm TL), sampled between October 1995 and September 1996. Otoliths were cleaned and stored dry in cross-referenced manilla envelopes. Otolith length (along the longitudinal axis) and width (along the transverse axis) were recorded to the nearest 0.05 mm using vernier callipers. Fish TL and standard lengths (SL) were recorded to the nearest millimetre. To enhance the

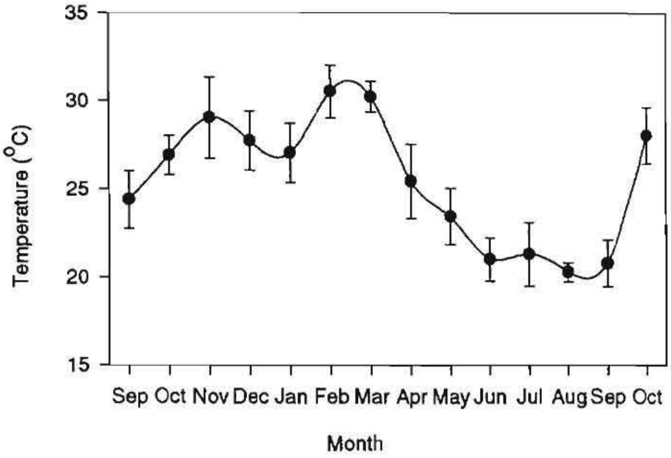

Figure 3 Mean monthly water temperature (°C) ± standard deviation at 0.3 m depth in Lake Chicamba, Mozambique.

Table 1 The descriptive criteria used to stage male and female *Tilapia rendalli* and *Oreochromis mossambicus* gonad development (adapted from Arthington & Milton 1986)

Stage of gonad development	Description
Juvenile	Gonads not fully formed but present as two transparent threads of tissue. Sex not distinguishable macroscopically.
Resting	Ovary white or slightly yellowish. Oocytes macroscopically distinguishable. Testis distinguishable as small white bands.
Developing	Ovary enlarged, oocytes readily visible and yellow. Testis broadened, distended and cream in colour.
Ripe	Oocytes of maximum size (2.5–3.4 mm along the long axis), readily extruded from female under abdominal pressure. Testis swollen to maximum size.
Spent	Ovary partly empty and flaccid with irregular oocyte size. Testis flaccid.

visibility of the otolith rings, the otoliths were burnt over a low intensity ethanol flame until they turned pale brown. Care was taken not to char the otoliths, as this tends to obscure the internal structure and margin of the otolith (Booth & Merron 1996). The otoliths were mounted medial side down in clear polyester casting resin and sectioned transversely through the nucleus using a double-bladed diamond-edged saw and mounted on slides with DPX mountant.

The number of opaque zones was read on two occasions with a dissecting microscope under transmitted light. If the two readings were the same then the age estimate was accepted. If the two readings did not agree a third reading was taken and the age estimate was accepted if two of the three readings were the same. If three readings differed by two years then the mean of the three estimates was taken. If the readings differed by more than two years, the otolith was rejected.

The outer margin of 141 *T. rendalli* and 185 *O. mossambicus* otoliths sampled at monthly intervals was examined. In otoliths, growth is reflected as alternating opaque and translucent zones (Figure 4 A & B). The composition of the outer margin was noted and expressed as a percentage of the monthly sample (Figure 5 A & B).

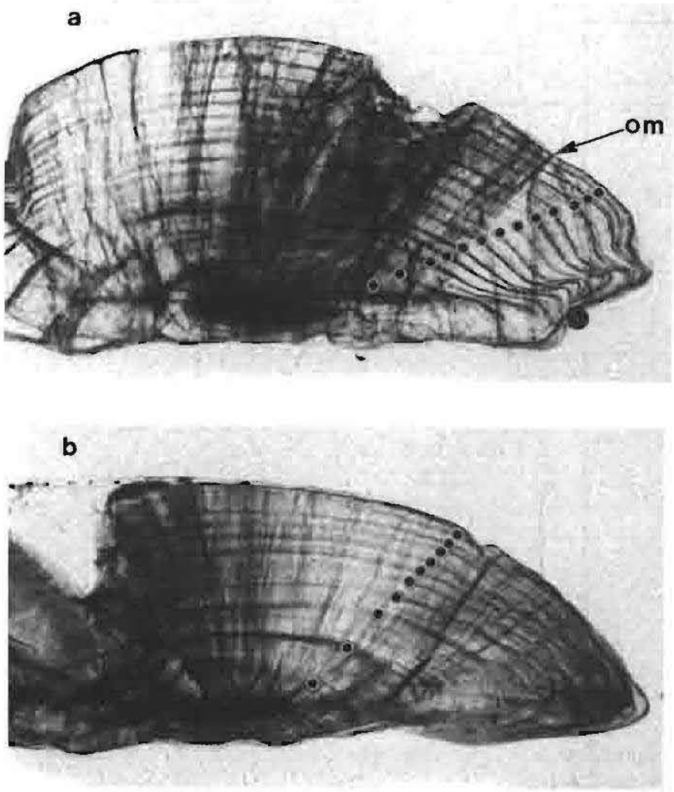

Figure 4 Photomicrographs of sagittal otoliths from a 231 mm total length, 14-year-old *Tilapia rendalli* (a) and 320 mm total length, 10-year-old *Oreochromis mossambicus* (b) from Lake Chicamba, Mozambique. Dots indicate opaque zones. Note the opaque margin (om) on the *T. rendalli* otolith.

Growth parameter calculation

Recommendations by Punt & Hughes (1992) for determining and fitting appropriate growth models were followed. The non-parametric one-sample runs test for randomness and the Bartlett's test for homoscedascity (Hughes 1986) were applied. Variance estimates were calculated using the (conditioned) parametric bootstrap resampling method (Efron 1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). PC-YIELD 2.2 (Punt & Hughes 1992) was used to execute the above procedure. This software uses a non-linear minimisation routine (simplex method) to obtain parameter estimates for the selected growth model. The selected model was the 3 parameter specialised von Bertalanffy growth model of the form

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

where t_0 is the age at 'zero' length; L_∞ is the predicted asymptotic length and K is the Brody growth co-efficient (Ricker 1975; Punt & Hughes 1992).

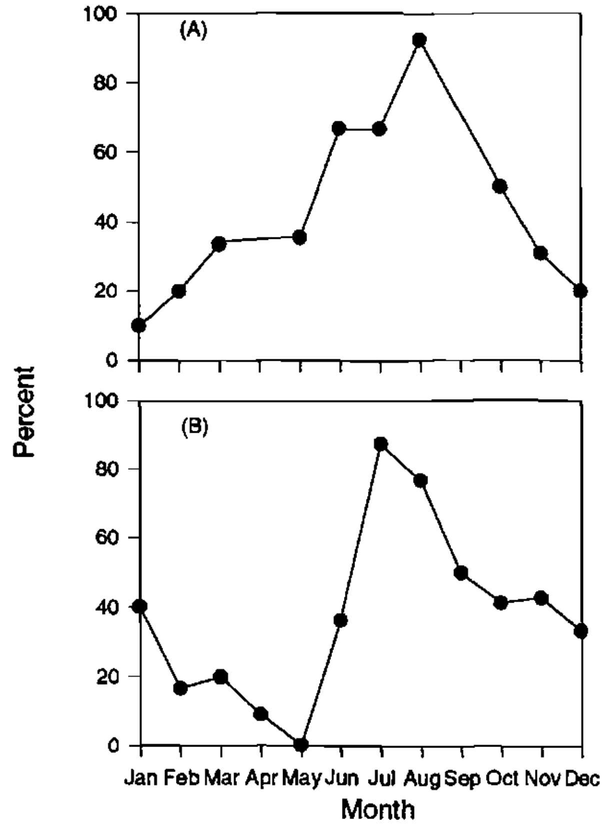

Figure 5 The monthly percentage of *Tilapia rendalli* (A) and *Oreochromis mossambicus* (B) otolith samples with an opaque margin. Samples were obtained monthly from Lake Chicamba, Mozambique.

Maturity and spawning periodicity

Mean length at sexual maturity was determined from 328 male and 401 female *T. rendalli* and 125 male and 442 female *O. mossambicus* collected during the peak reproductive season between October and December. The proportion (P) of sexually mature individuals by length (L) was fitted to the logistic curve:

$$P = 1/(1 + \exp[-r(L - Lm_{50})])$$

where r is the slope of the curve and Lm_{50} is the mean length at sexual maturity. Since the highest proportion of mature *O. mossambicus* females was 76.9% the logistic curve for this plot (Figure 4D) was fitted to data which were multiplied by a correction factor of 1.3. This correction factor was applied since fitting the logistic curve directly to data from populations where not all mature individuals are in reproductive condition at the same time leads to an overestimation of Lm_{50} (King 1995).

Temporal patterns in reproductive activity were assessed on the basis of gonadosomatic index and development stages of the gonads of 201 female *T. rendalli* and 228 female *O. mossambicus* sampled at monthly intervals. All fish in the sample were above the mean size at sexual maturity. Gonadosomatic index (GSI) was expressed as:

$$GSI = \left[\frac{Gonad\ mass\ (g)}{Eviscerated\ mass\ (g)}\right] \times 100$$

Eviscerated mass was used to minimise bias from variable gut fullness.

Juvenile cichlid abundance

Juvenile cichlid abundance in the shallow littoral (depth < 0.5 m) was determined using a 1 m × 2 m seine net with a mesh size of 1 mm. Monthly samples were taken from five sites on the lake (Figure 1) with five hauls being performed at each site. Each haul covered an area of 10 m^2 and in sites with drowned forests hauls were performed between the trees. To validate the estimates of cichlid abundance in the shallow littoral, a 30 m long × 3 m deep seine net with a mesh size of 10 mm was used to determine juvenile cichlid abundance in lake areas less than 2 m deep. Ten seine net hauls were conducted in three sampling areas (Figure 1) per month. Each haul covered an area of approximately 140 m^2. In both cases only cichlids of less than 50 mm TL were used for subsequent analysis.

Statistical analysis

The proportions of ripe females, GSI values and juvenile cichlid densities were grouped into three categories according to season. These were flooding summer (January–April), winter (May–September) and drawdown summer (October–December). The seasonal distribution of ripe females was analysed using a 2 × 3 contingency table. Seasonal variations in GSI values and cichlid densities were compared using the non-parametric Kruskal-Wallis One Way Analysis of Variance (ANOVA) on ranks. To isolate the group or groups that differed from the others an All Pairwise Multiple Comparison Procedure (Dunn's Method) was performed. A significance level of $p < 0.05$ was used in all tests.

Results

Age and growth

Morphometric relationships between total length and weight, otolith length along the longitudinal axis, otolith diameter along the transverse axis and standard length are summarised in Table 2. The results presented in Figure 5 show that one

Table 2 Morphometric relationships of *Tilapia rendalli* and *Oreochromis mossambicus* sampled in Lake Chicamba, Mozambique. Wt = weight, TL = total length, SL = standard length, OL = otolith length along the longitudinal axis, OD = otolith diameter along the transverse axis

	Relationship	r^2	p	n
T. rendalli				
Wt (g)	$= 0.000012\ TL\ (mm)^{3.136}$	99.1	< 0.001	821
TL (mm)	$= 23.28\ OL\ (mm)^{1.184}$	98.0	< 0.001	100
TL (mm)	$= 36.57\ OD\ (mm)^{1.217}$	96.0	< 0.001	100
SL (mm)	$= -2.290 + 0.797\ TL\ (mm)$	95.3	< 0.001	366
O. mossambicus				
Wt (g)	$= 0.000021\ TL\ (mm)^{2.984}$	99.1	< 0.001	602
TL (mm)	$= 18.84\ OL\ (mm)^{1.224}$	96.6	< 0.001	61
TL (mm)	$= 31.41\ OD\ (mm)^{1.270}$	95.0	< 0.001	61
SL (mm)	$= -1.722 + 0.802\ TL\ (mm)$	98.2	< 0.001	250

Table 3 Age-length key for *Tilapia rendalli* collected from Lake Chicamba, Mozambique. Age was estimated by reading sectioned saggital otoliths

	Age																
Length	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1–70	1																
71–80	14																
81–90	14																
91–100	21	1															
101–110	29																
111–120	22	2															
121–130	11																
131–140	4	1		1													
141–150	1	2				1											
151–160	5	8															
161–170	4	2															
171–180		2		1		1											
181–190		3	1	1	1	1											
191–200	1	2		5	4	1	1										
201–210	1		4	4	3	1											
211–220	1	1	5	5	2	5	1	1	1	2		1					
221–230		1	2	4	2	6	5	1	2	1		4	2				1
231–240			3	4	2	5	1	3	1		1				1	1	
241–250				1	3		6	1	1	1	2		1				
251–260			1	1	1	2	1	3						1			
261–270				1		2	2	2			1						
271–280						1						1					
281–290						1				1			1				
291–300																	
301–310								1									
n	130	25	16	28	18	27	17	12	5	5	4	5	5	1	1	1	1

hyaline and opaque zone are deposited in the otoliths of both species each year. These were considered as annuli and could be used to estimate the age of the two species.

Of the 300 *T. rendalli* and 199 *O. mossambicus* otoliths examined, 9 (3%) and 14 (7%), respectively, were rejected as unreadable. *T. rendalli* otoliths were assigned a maximum age of 16 years (Table 3) and *O. mossambicus* otoliths were assigned a maximum age of 10 years (Table 4). The observed length-age keys for *T. rendalli* and *O. mossambicus* are presented in Tables 3 and 4 respectively. The von Bertalanffy growth parameters for *T. rendalli* and *O. mossambicus* in Lake Chicamba are summarised in Table 5 and the growth rates and fitted von Bertalanffy growth models for the two species are illustrated in Figure 6.

Reproductive biology

Male *T. rendalli* attained Lm_{50} at 218 mm TL and females at 205 mm TL (Figure 7A & B). *O. mossambicus* males and females attained Lm_{50} at 251 mm and 223 mm TL, respectively (Figure 4C & D).

The monthly proportion of female *T. rendalli* and *O. mossambicus* in each maturity stage is illustrated in Figure 8.

Table 4 Age-length key for *Oreochromis mossambicus* collected from Lake Chicamba. Age was estimated by reading sectioned saggital otoliths

	Age										
Length	0	1	2	3	4	5	6	7	8	9	10
1–70	2										
71–80	18										
81–90	21	1									
91–100	17										
101–110	19	3									
111–120	23	1									
121–130	20	2									
131–140	8	8	2	1							
141–150	2	1	1	1							
151–160	2	1	1								
161–170	2	1			1						
171–180	3	1	1								
181–190	1	3	2	1							
191–200		1		1		2					
201–210		2	1	1	2						
211–220			2	1	1	4	1				
221–230		1	1	5	1	2					
231–240		2	4	9	5	2	1	1			
241–250			3	7	3	3	2				
251–260				6	8	3	3				
261–270			1	3	4	6		1			
271–280				1	1			1			
281–290			1	2	3	1	1				
291–300				2	2	1	1		1		
301–310			1	4	3						1
311–320				2	3	1				1	
321–330			1					1			
331–340											
341–350											
351–360											
361–370							1				
n	138	28	22	47	37	25	10	4	1	1	1

Table 5 Von Bertalanffy growth parameters, standard error (STE) and 95% confidence intervals for *Tilapia rendalli* and *Oreochromis mossambicus* sampled from Lake Chicamba, Mozambique

Parameter	Estimate	STE	95% confidence
T. rendalli			
K	0.636 year^{-1}	0.06	[0.539, 0.76]
L_∞	238.74 mm TL	3.16	[232.21, 245.18]
t_0	–0.905	0.079	[–1.059, –0.762]
O. mossambicus			
K	0.790 year^{-1}	0.23	[253.67, 285.11]
L_∞	266.06 mm TL	8.01	[0.470, 1.361]
t_0	–0.269	0.340	[–1.048, 0.245]

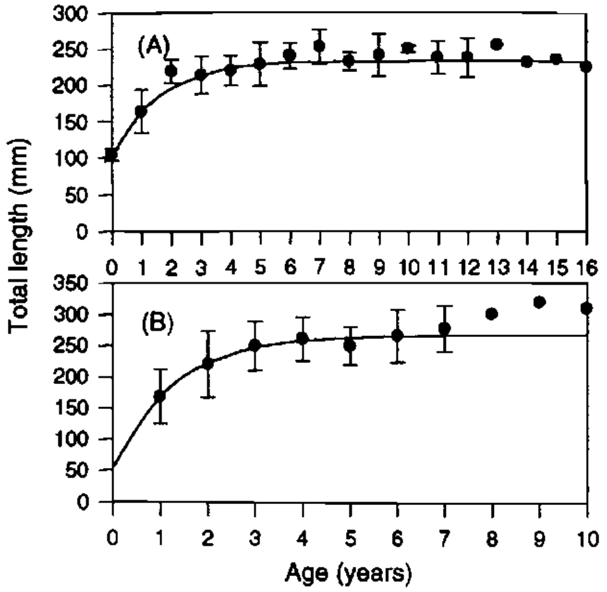

Figure 6 Observed mean lengths-at-age ± standard deviation of *Tilapia rendalli* (A) and *Oreochromis mossambicus* (B) sampled from Lake Chicamba, Mozambique. The curve was fitted using the specialised von Bertalanffy growth model.

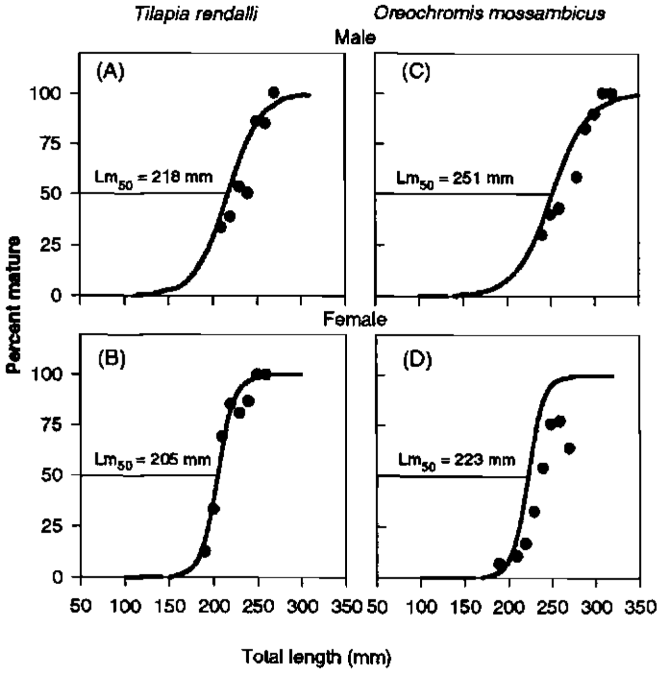

Figure 7 Logistic ogives fitted to the percentage of sexually mature *Tilapia rendalli* males (A), *T. rendalli* females (B), *Oreochromis mossambicus* males (C) and females (D) from Lake Chicamba, Mozambique. Lm_{50} = total length at 50% maturity.

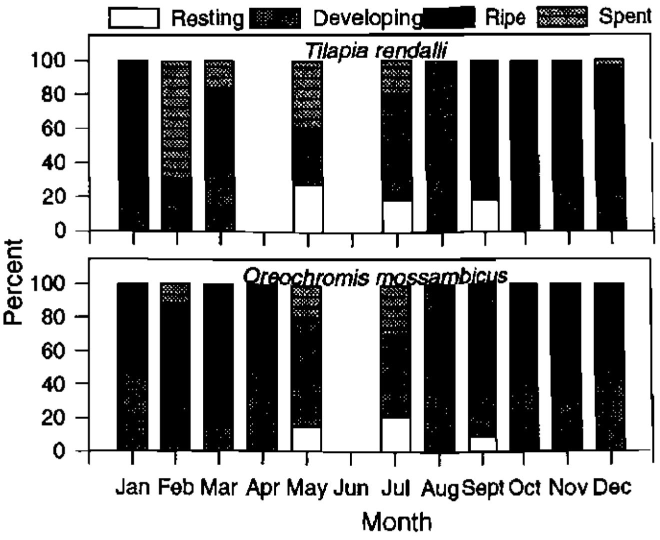

Figure 8 Monthly maturity stages of female *Tilapia rendalli* (n = 201) and *Oreochromis mossambicus* (n = 228) sampled from Lake Chicamba, Mozambique.

During April 1996 less than 20 mature female *T. rendalli* and during June 1996 less than 20 mature female *T. rendalli* and *O. mossambicus* were sampled. Therefore, these data have been excluded from Figure 8. From October to January, over 60% of female *T. rendalli* were in the 'ripe' condition (Figure 8). The proportion of ripe female redbreast tilapia decreased sharply in February to 15%, with the majority of females (69%) being in the 'spent' condition (Figure 8). During July 1996 and August 1996 no 'ripe' females were recorded (Figure 8). By September 1996, the proportion of ripe females increased to 38% (Figure 8). The proportion of ripe females was significantly dependent on season (χ^2 = 62.08, *df* = 2), however there was no difference in the proportion of ripe females between drawdown summer and flooding summer (χ^2 = 0.267, *df* = 1).

Over 50% of *O. mossambicus* were in the ripe condition between October and March (Figure 8). By April 1996 this proportion had dropped to 45% and in May, July and August no ripe female *O. mossambicus* were sampled (Figure 8). The proportion of ripe females was significantly dependent on season (χ^2 = 49.63, *df* = 2). However, there was no significant difference between drawdown and flooding summer (χ^2 = 0.200, *df* = 1).

In both species the mean GSI values in summer (October to March) were significantly higher than in winter (May to August) GSI ($p < 0.05$; Figure 9). GSI values during the drawdown and flooding summer did not differ significantly from each other.

Juvenile cichlid densities

In the shallow littoral (< 0.5 m) juvenile cichlid densities were highest in January (8.4 fish/m^2) and April (8.9 fish/m^2) and lowest in September (0.1 fish/m^2) and October (0.3 fish/m^2; Figure 10). During the other months juvenile cichlid densities ranged from 2.2 fish/m^2 to 5.8 fish/m^2 (Figure 10). Juvenile cichlid densities in the lake margins were significantly higher during the summer flooding phase of the dam than during the winter and summer drawdown phases ($p < 0.05$; Figure 7). At depths of up to 2 m similar results were obtained. Cichlid densities during the flooding summer (2.4 ± 2.1 fish/m^2) were significantly higher than during the summer drawdown phase (0.9 ± 1.3 fish/m^2; $p < 0.05$). In addition, drawdown summer cichlid density did not differ significantly from winter cichlid density (0.5 ± 0.4 fish/m^2).

Discussion

Growth rings on hard structures such as scales, otoliths and

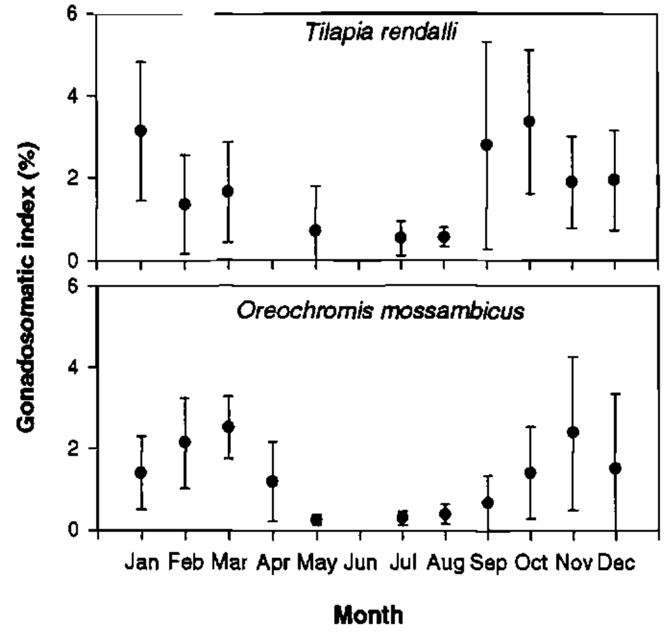

Figure 9 Monthly gonadosomatic indices ± standard deviation for female *Tilapia rendalli* (n = 201) and *Oreochromis mossambicus* (n = 208) sampled from Lake Chicamba, Mozambique.

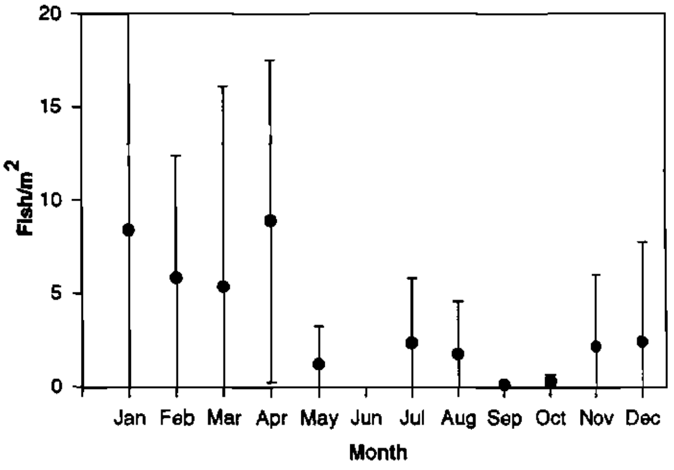

Figure 10 Monthly juvenile cichlid densities expressed as fish per m^2 in the shallow littoral areas of Lake Chicamba, Mozambique.

spines, are formed as a response to one or more environmental variables that reduce metabolic rate and result in a slowing of the growth rate (Gauldie & Nelson 1990). In tropical and subtropical waters, the period during which rings are formed in the hard parts of cichlids varies considerably. Annulus formation in cichlids from the Kafue floodplain (*Oreochromis andersonii* and *Tilapia rendalli*) and the Okavango delta (*O. andersonii* and *O. macrochir*) occurred during summer (Dudley 1974; Kapetsky 1974; Booth *et al.* 1995; Booth & Merron 1996). In these and other tropical and subtropical areas ring formation has been attributed to a decrease in somatic metabolic rate resulting from reproductive activities such as courtship, nesting behaviour, movement to and from nesting areas and temporal variation in feeding (Garrod 1959; Bruton & Allanson 1974; Pannella 1974; Hecht 1980a) rather than to a climatic winter. However, ring formation in hard tissues during winter has been recorded in several localities. Ring formation in *O. mossambicus* scales in a number of Transvaal impoundments occurred in August marking the end of winter (Le Roux 1961). This winter 'check' was confirmed in otoliths of *O. mossambicus* sampled from the Luphephe/Nwanedzi impoundment in South Africa (Hecht 1980a). However, the deposition of a second opaque band coinciding with peak reproductive activity was also noted in this population (Hecht 1980a).

The formation of a single opaque band (transmitted light) in the otoliths of *T. rendalli* and *O. mossambicus* in Lake Chicamba during July and August (Figure 4A & B) corresponds with the end of winter, when water temperatures are at their lowest and the lake is in its drawdown phase (Figure 2 & 3). Since reproductive activity of these two species in Lake Chicamba is confined to the summer period from October to April, the formation of otolith rings is not a consequence of reproductive activity in this locality. Although it was not possible to determine accurately what factors were responsible for ring formation in the otoliths of the two cichlids in Lake Chicamba, it is likely that low winter temperatures and decreased food availability during the drawdown phase contribute to the formation of the rings.

The initial growth rate of both species was rapid, with asymptotic length being reached within three years (Figure 6). Since both species mature at lengths corresponding to ages of 2+ years (Table 6), the attainment of asymptotic length occurs soon after sexual maturation and reflects a shift from somatic growth to reproductive energy requirements. This growth pattern is typical of many cichlid populations (Bruton & Allanson 1974; Hecht 1980a; van der Waal 1985) and allows the juvenile fishes to attain quickly a size large enough to avoid predation and simultaneously to reach sexual maturity to enable reproduction in unstable environments.

The high variability in growth rate and the length-at-50% maturity in cichlids are evident when the data from this study are compared to those from other populations (Table 6). These variations have been linked to reservoir size (De Silva 1986), habitat stability (Noakes & Balon 1982) and food availability (Balon & Coche 1974). James & Bruton (1992) recorded lengths at maturity ranging from 110 mm SL to 265 mm SL for male *O. mossambicus* in water bodies in the Eastern Cape. The large variation in the length at maturity has been attributed to the response of the fish to environmental variability (James & Bruton 1992). Greater lengths at maturity have been recorded in stable environments (De Silva 1986; James & Bruton 1992) and smaller lengths at maturity have been found in harsher habitats, such as smaller dams in which food is limiting and high temperature fluctuations are common (James & Bruton 1992).

The growth rate of *O. mossambicus* and *T. rendalli* in Lake Chicamba is relatively fast when compared to other populations in the southern African region (Table 6). The growth rate of *O. mossambicus* in Lake Chicamba was faster than in Lake Sibaya (Bruton & Allanson 1974) but was similar to the population from the Luphephe/Nwanedzi impoundment described by Hecht (1980a) for the first three years. However, slower growth and smaller maximum size of *O. mossambicus* in Lake Sibaya can be attributed to early maturity and precocious breeding in this abiotically harsh environment (Bruton

Table 6 Length-at-50% maturity (*Lm*₅₀), calculated length-at-age and the von Bertalanffy growth parameters for *Oreochromis mossambicus* and *Tilapia rendalli* in southern African water bodies based on published data. All data have been standardised to standard length (SL). (m = male, f = female, t = both sexes)

			Length (mm SL)-at-age (years)						Growth parameters		
Locality	Sex	Lm_{50}	0	1	2	3	4	5	t_0	L_∞	K
O. mossambicus											
Chicamba[1]	m	171									
	f	161									
	t			134	176	198	207	198	–0.269	212	0.790
Luphephe[2]	t	nd		110	168	206	225	234	–0.299	273	0.425
Sibaya[3]	m	120		85	124	148	177	187	–0.360	217	0.358
	f	100		83	113	134	147	166	–1.054	217	0.240
Mill farm dam[4]	m	265	185	224	256	282	304	322	–3.154	406	0.193
	f	263	132	200	246	278	300	315	–1.272	348	0.376
Bradshaw's Mill dam[4]	m	168	51	122	173	211	239	260	–0.578	317	0.306
	f	186	50	166	212	230	238	240	–0.248	242	0.924
T.rendalli											
Chicamba[1]	m	171									
	f	161									
	t		82	132	158	172	180	184	–0.905	188	0.636
Liambezi[5]	m	109	108	119	129	181	203	216	–1.953	240	0.479
	f	109		117	173	190	198	207	–0.935	366	0.128
Kariba[6]	m	184									
	f	168									
	t			72	115	151	183	211	–0.419	387	0.145

[1]Present study — Lake Chicamba, Mozambique; [2]Hecht 1980a — Luphephe/Nwanedzi impoundment, South Africa; [3]Bruton & Allanson (1974) — Lake Sibaya, South Africa; [4]James (1989) — Eastern Cape, South Africa; [5]van der Waal (1985) — Lake Liambezi, Botswana; [6]Kolding *et al.* (1992) — Lake Kariba, Zimbabwe.

1979). When the Lake Chicamba population was compared to temperate populations in the Eastern Cape of South Africa (James 1989), it was slower growing than the Mill farm dam population where feeding conditions were highly favourable, but grew faster than the Bradshaw's mill dam population where feeding conditions were less favourable (James 1989).

The growth rate of *T. rendalli* in Lake Chicamba was similar to that in Lake Liambezi (van der Waal 1985) and Lake Kariba (Kolding, Tirasin & Karenge 1992) for the first three years, whereafter the growth in Lake Chicamba was slower (Table 6). However, the Lake Liambezi *T. rendalli* population was aged using scales which have been shown to be poor indicators of age after asymptotic length has been attained (Hecht 1980a; Booth *et al.* 1995). Since the oldest *T. rendalli* sampled in Lake Chicamba was 16 years and the oldest fish in Lake Liambezi was 7 years old, it is possible that the larger lengths-at-age in this locality are an effect of age underestimation.

T. rendalli and *O. mossambicus* from Lake Chicamba are relatively large when they reach Lm_{50} (Table 6). The large size at maturity is similar to the lengths at maturity recorded for *T. rendalli* in Lake Kariba (Kolding *et al.* 1992) and *O. mossambicus* in Sri Lankan reservoirs (De Silva 1986). Lake Kariba and the Sri Lankan reservoirs tend towards environmental stability. In contrast, the abiotically harsh environment of Lake Sibaya has led to early maturation and precocious breeding in *O. mossambicus*, despite the large area of the lake (Bruton 1979). Similarly, *T. rendalli* in the shallow Lake Liambezi also mature at a relatively smaller size although the temperature regime and surface area (Seaman, Scott, Walmsley, van der Waal & Toerien 1978) are similar to Lake Chicamba. The relatively large length-at-50% maturity of *T. rendalli* and *O. mossambicus* in Lake Chicamba is indicative of a precocial life history style associated with environmental favourability (Noakes & Balon 1982; James & Bruton 1992).

Spawning periodicity in cichlids is often independent of flooding but has been linked to other factors such as water temperature and day length (Fryer & Iles 1972; Bruton & Allanson 1974; van der Waal 1985; James & Bruton 1992; Lowe-McConnell 1991; Merron & Bruton 1993). This is illustrated in the Phongolo floodplain where *O. mossambicus* dominates after a period of flood failure (Merron & Bruton 1993). Similarly, in Lake Liambezi the spawning of *T. rendalli* was not dependent on flooding (van der Waal 1985). In Lake Chicamba, the reproductive activity of both cichlids was confined to the summer period from September to May (Figure 8 & 9), when mean water temperatures were in excess of 24°C (Figure 3). Since the gonadosomatic indices and the proportion of ripe individuals in both species did not differ significantly throughout summer, it was concluded that gonad development and spawning were independent of flooding in this locality.

Since tilapias have evolved under riverine conditions (Fryer & Iles 1972; Greenwood 1974), where fluctuating water levels and flooding are common, the tilapias may retain the ability to successfully utilise flooded habitats in lacustrine conditions. The higher density of juvenile cichlids, both in the shallow littoral zone and up to a depth of 2 m, during the flooding phase of the lake from January to April, than during the drawdown phase from September to December (Figure 10), suggests that the recruitment of juvenile cichlids into the lakes' littoral area was dependent on flooding.

Welcomme (1979) showed that the higher the magnitude of the flood and the longer its duration on the floodplain, the greater the overall production of fish. In non-cichlid species such as *Perca flavescens*, *Morone chrysops* and centrarchids, reproductive success was found to be enhanced when flooded vegetation was available during the spawning and nursery period (Martin, Mengel, Novotny & Walburg 1981). In addition, the breeding success and recruitment of *Oreochromis andersonii* and *O. macrochir* in the Kafue floodplain was much better during years with high flood levels (Dudley 1972). De Silva (1985) suggested that fluctuations in lake level could influence reproductive output of *O. mossambicus* in Sri Lankan lakes to such an extent that the commercial catches were affected three years later.

T. rendalli falls within the reproductive guild of guarders whilst *O. mossambicus* is a mouthbrooder (Balon 1975). Since both species build nests in shallow water (Bruton & Boltt 1975; Bruton & Kok 1980) the large drawdowns in

Lake Chicamba may impede nest building and guarding activity in these two cichlids. However, other factors such as increased food availability and cover associated with flooding may also contribute to increased recruitment of cichlids during this time.

T. rendalli is generally regarded as a macrophytic browser but, like many other cichlids, it feeds opportunistically on a variety of food sources including aquatic insect larvae and zooplankton (Munro 1967; Wagner & Rowe-Rowe 1972; Caulton 1976). Young *O. mossambicus* have been reported to feed mainly on diatoms in the detrital floc, periphyton and zooplankton (Le Roux 1956; Bruton & Boltt 1975; Whitfield & Blaber 1978; De Moor, Wilkinson & Herbst 1986). During the flooding phase on Lake Chicamba, vegetation with a mean dry biomass of 820 g/m^2 is submerged (Weyl, unpublished data). During the flooding phase from January 1996 to April 1996 the lake level rose by 7.92 m (Figure 2), inundating an area of 17.2 km^2 and a total dry plant biomass of approximately 14 100 tons. Thus, flooding provides an immediate though temporary food supply of submerged vegetation for *T. rendalli*, and the decaying vegetation provides a nutrient source for increased primary productivity that leads to an increase in the availability of planktonic diatoms and periphyton for *O. mossambicus*. This increase in the availability and quality of food leads to improved growth, which may ultimately enhance survival through avoidance of predation and increased competitiveness. In the Kafue floodplain up to 75% of the expected first year growth in *Oreochromis andersonii* and *Oreochromis macrochir* took place within six weeks of the peak flood (Dudley 1974, 1979).

The effect of submerged vegetation on prey evasion has been widely documented (Strange, Berry & Schreck 1975; Gotceitas & Colgan 1989; Savino & Stein 1982; Godinho & Ferreira 1994; Werner, Gilliam, Hall & Mittelbach 1983). In Lake Kariba, juvenile *T. rendalli* inhabit densely vegetated nursery areas in the littoral zone to avoid intense predation by *Hydrocynus vittatus* (Donnelly 1969). In largemouth bass *Micropterus salmoides* piscivory is mediated by the abundance of aquatic vegetation (Bettoli, Maceina & Betsill 1992). Heman, Campbell & Redmond (1969) showed that the density of *Lepomis macrochirus* fry was reduced after a reservoir drawdown. This reduction was attributed to increased predation by bass as vegetation cover was eliminated by falling lake levels. In Lake Chicamba predation on juvenile cichlids by the alien *Micropterus salmoides* (Weyl & Hecht in press) during periods of reduced vegetation cover may partly explain the reduced recruitment of juvenile cichlids during the drawdown phase.

Although it was not possible to attribute the reduction of recruitment in juvenile cichlids during periods of drawdown to any one factor, the increase in food availability and cover during flooding, coupled with the possibility of increased spawning success, are likely to contribute towards the increase of recruitment during this period.

This study has shown that *O. mossambicus* and *T. rendalli* in Lake Chicamba display precocial life history traits such as a long lifespan and a large size at maturity. In addition, spawning in *T. rendalli* and *O. mossambicus* was independent of flooding, but recruitment of juveniles of both species was highly dependent on the flooding of the vegetated lake margins. The failure of an annual drawdown phase, during which the depleted vegetation can recover, followed by a flooding phase may therefore lead to recruitment reduction in Lake Chicamba. Future management of the *T. rendalli* and *O. mossambicus* stocks in Lake Chicamba must take into account not only the rapid growth rate of these cichlids but also the relatively large size-at-50% maturity and the dependence of recruitment on flooding and drawdown events.

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