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Maturity, age and growth of *Oreochromis karongae* (Teleostei: Cichlidae) in Lakes Malawi and Malombe, Malawi

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Size-at-50% maturity, age and growth, of *Oreochromis (Nyasalapia) karongae* ('chambo') in Lakes Malawi and Malombe were studied. *Oreochromis karongae*, a major component of the chambo species flock, attained 50% maturity at 225 mm TL in Lake Malawi and at 203 mm in Lake Malombe. The estimated age-at-50% maturity was 2.19 and 1.49 years in Lakes Malawi and Malombe, respectively. Estimated growth parameters for populations at Karonga, Nkhotakota, Salima and Mangochi in Lake Malawi, and for that in Lake Malombe were L_∞ = 328, 319, 308, 388, and 314 mm TL, respectively; and *K*-values were 0.31, 0.29, 0.34, 0.20 and 0.35, respectively. Similar size-at-50% maturity and growth patterns (age, L_∞ and *K*-values) were found for *O. karongae* populations in Lake Malawi, but differences were observed for Lake Malombe populations, suggesting that the current chambo fisheries management regulations, based on findings from the southern part of Lake Malawi, may be applicable to the central and southern parts of that lake, but may not be applicable to Lake Malombe.

Keywords: artisanal fishers, chambo fishery, closed season, fishing effort, management, populations

Introduction

The collapse of the chambo (*Oreochromis* 'Nyasalapia') fishery in southern Lake Malawi and Lake Malombe (Figure 1) as a result of unsustainable fishing effort (FAO 1993) is an issue of national concern for Malawi (Banda *et al.* 2005). Chambo are the most valuable commercially harvested fish species in Malawi (Turner 2003, Banda *et al.* 2005). In an attempt to manage the fishery, various fisheries management strategies were developed, based on research results from the shallow and productive southeast arm (SEA) of Lake Malawi and from Lake Malombe (Lowe-McConnell 1952, Trewavas 1983, FAO 1993).

The biology of chambo in these areas was reviewed by Lewis (1985) and FAO (1993). Of the three species comprising the *Oreochromis* 'Nyasalapia' flock, *Oreochromis karongae* (Trewavas, 1941) is the most widely distributed (Turner 1995) and is commonly harvested by artisanal fisheries (FAO 1993). In the SEA and Lake Malombe, *O. karongae* matured at 250 mm TL, with an average of 275 mm TL in the SEA and at 160–170 mm TL in Lake Malombe (Lewis 1985). The peak spawning period was from August to October in the SEA and from July to October in Lake Malombe (Lewis 1985).

To protect juveniles from exploitation, a closed season was implemented from October to December in Lake Malombe and from November to January in Lake Malawi.

However, Lake Malawi is a large ecosystem (30 800 km^2, Hutchinson 1957) and possible variations in life-history characteristics within one species require investigation in the development of a holistic management strategy. The aim of this study was to test the hypothesis that growth rates and maturity of *O. karongae* are dependent on geographic locality within the Lake Malawi system.

Materials and Methods

Study sites

Oreochromis karongae were collected from five localities along the lake axis: Lake Malombe, and Mangochi, Salima, Nkhotakota and Karonga in Lake Malawi (Figure 1). These areas differ in physiogeography, limnology and trophic gradient (FAO 1993). Lake Malombe is a highly productive shallow (mean depth = 7 m) 390 km^2 lake formed by a widening of the Shire River 15 km from its outflow from

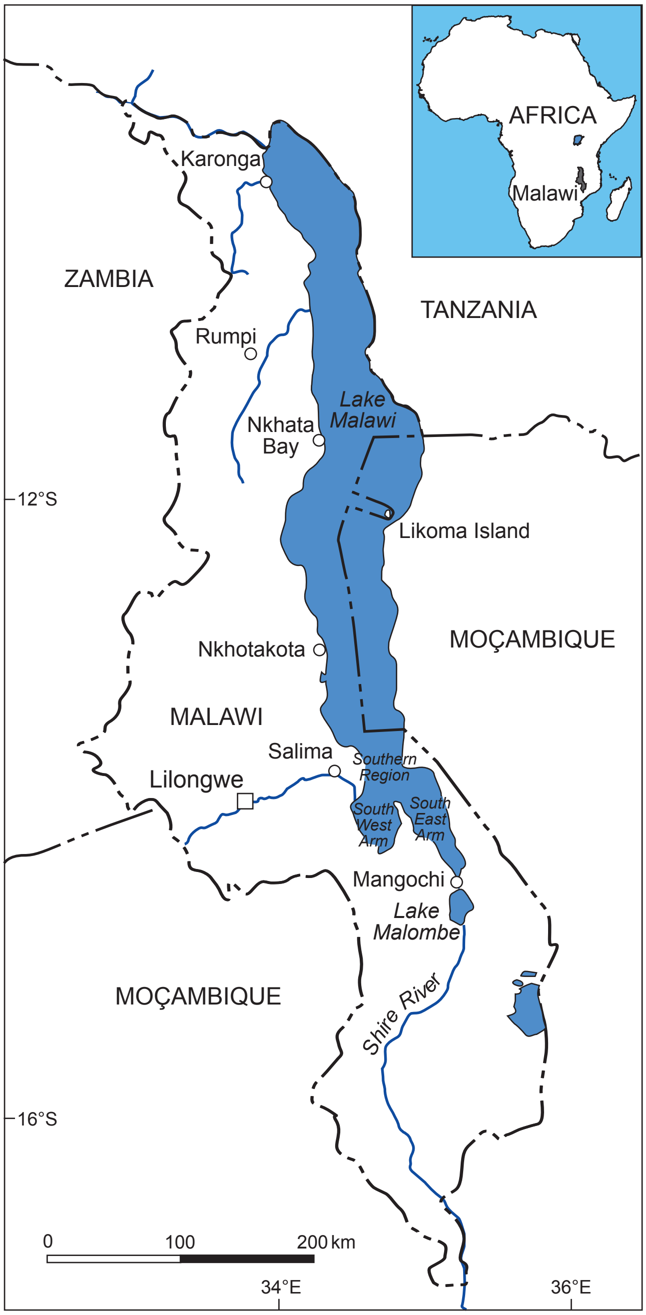

Figure 1: Lakes Malawi and Malombe, joined by the Shire River, showing all fish sample collection sites — Karonga, Nkhotakota, Salima, Mangochi (South East Arm) and Lake Malombe

Lake Malawi (FAO 1993). Lake Malawi is an oligotrophic rift valley lake, 630 km long, and has a maximum depth of 700 m (Hutchinson 1957). The sampling sites represent the main areas of the lake. Mangochi and Salima are located in the southern end of the lake, which is shallower (max depth <250 m) and more productive because of the winter mixing that drives the thermocline to the bottom, causing the entire column to mix resulting in the upwelling of nutrient-rich water (Eccles 1962, FAO 1993). Nkhotakota, a shallow area situated at the mid-region of the lake, is bordered by deep water and is considered less productive than the southern part of the lake (Eccles 1962). Karonga, situated in the northern part of the lake, is the deepest and least productive area (Eccles 1974).

Field sampling

A total of 1 329 *O. karongae* ranging from 67–395 mm TL were collected over a one-year period from July 2001–December 2002 from four sites within Lake Malawi, namely Karonga (*n* = 363), Nkhotakota (*n* = 216), Salima (*n* = 370) and Mangochi (*n* = 192), and from Lake Malombe (*n* = 188). All samples were procured from local fishermen at the beaches, except for one occasion when fish were bought fresh at the nearest fresh fish market. Fish were identified using procedures outlined by Turner and Mwanyama (1992). Fish were sampled systematically to obtain representatives of all sizes. Samples were collected once every two months from each site. During collection the samples were put in labeled polythene bags and preserved fresh on ice blocks to prevent spoilage of the gonads.

Laboratory sample analysis

Fish were thawed in cold water and each fish was subsequently weighed to the nearest 1 g using a multi-function electronic weighing balance (A&D Limited, series HR-300). Total length (TL) was measured to the nearest mm. Each fish was then dissected, its sex determined by internal examination, and the gonads were removed. Individual gonads were then macroscopically staged using the key in Table 1.

Determination of length at 50% maturity

Mean length at 50% maturity was determined by fitting a logistic curve to the proportion of reproductively active (ripe and spent) fish sampled during the spawning season in 10 mm size-classes (Kaunda and Hecht 2002, King and Etim 2003):

$$\psi = 1/\left[1 + e^{-(L - Lm_{50})/\delta}\right]$$

where: Lm_{50} = total length-at-50% sexual maturity;
δ = width of the logistic curve.

The proportion of mature fish for each stage of maturity was expressed as a percentage of the total number of fish in that category by plotting a cumulative frequency graph. All fish lengths corresponding to 50% cumulative frequency were then taken as the sizes at which 50% of the fish were mature (King and Etim 2003).

Age and growth determination

Both opercula bones (Figure 2) were removed from selected fish, soaked in boiling water for 30 seconds to remove tissue, dried and stored in labeled envelopes. In the laboratory they were examined under reflected light on a black background using a dissecting microscope at ×5 magnification using glycerol fluid dissolved in ethanol (1:1 ratio) as a refracting medium. Growth zones on each

Table 1: Key to gross morphological description of gonad maturation stages in *Oreochromis karongae*. (after Maluwa 2000)

Maturity stage	Stage/ Symbol	Gonad appearance (ovary)	Gonad appearance (testes)
Immature	I/Im	Ovary thread-like, transparent and close to abdominal wall	Testes very thin, threadlike, flesh colored, colourless to transparent
Inactive	II/In	Ovary cream-coloured, translucent, elongates wider than testis; no oocytes visible	Translucent, wider than above, generally longer than ovaries in (In) females
Active	III/A	Ovary not yet swollen, oocytes visible, yellowish with red hue	Dull, white/yellowish, thickened and elongate, covering about 75% of visceral cavity
Ripe	IV/R	Yellow, green, orange eggs characteristic of the species, large uniform size; ovary occupies all visceral cavity space	Cream white, distended fully over the length of visceral cavity, milt evident if testes are cut Males show intensified breeding colours and nesting behaviour
Ripe Running	V/RR	Ovary extremely swollen and eggs run under hand pressure or separate if ovary is opened.	White/silvery testes, which are fully extended, milt runs freely under pressure, breeding evident
Spent	VI/S	Flaccid, shrunken ovary, reddish with blood capillaries and small eggs discernible	Fresh/red colour and shrunken testes with blood capillaries evident

Figure 2: Right opercular bone of a two-year-old male *Oreochromis karongae*, 246 mm TL, showing rings (arrowed)

operculum were read twice by a single reader, with an interval of two weeks between readings to minimize bias (Weatherley and Gill 1987). The two readings were then averaged. Precision of aging between the two readings was estimated by calculating the percent agreement between the two readings, the coefficient of variation (CV) (Kimura and Lyons 1991) and the average percent error (APE) (Beamish and Fournier 1981).

Growth parameters for *O. karongae* (combined sexes) were estimated by fitting the von Bertalanffy growth model $L_t = L_\infty[1 - \exp(-K(t_1 - t_0))]$ (Sparre and Venema 1998) after plotting individual fish lengths against estimated ages from opercula (Figure 4). The growth curves were compared using regression analysis (Kimura 1980). A pair-wise comparison of mean length-at-age for all sites was also carried out. Phi Prime- (ϕ') values (growth performance index) were computed using the equation $\phi' = \log_{10}K + 2\log_{10}L_\infty$ (Marshall 1990) (Table 4).

Validation of annuli or growth checks

Growth zones on the opercula were independently validated using marginal zone analysis, by plotting the proportion of opercula with alternating opaque (dark) zones against age (measured in months) (Kaunda and Hecht 2002, Bwanika *et al.* 2007). Fish ageing is highly subjective (Weatherley and Gill 1987) and therefore the term ‘annulus’ is used with caution, as these may not necessarily be ‘annual’ rings but ‘seasonal’ growth checks in response to environmental changes such as temperature and food availability.

Results

Annuli or growth checks

An opaque zone was deposited on the opercula of *O. karongae* twice per year, at around March and in September (Figure 5). This deposition corresponds to periods of slow fish growth (Jepsen *et al.* 1999), which is assumed for tropical fish (Beckman and Wilson 1995). A similar observation was made by Lowe-McConnell (1952), who attributed the deposition of opaque zones on opercula of *O. karongae* in Lake Malawi in September and March to breeding seasonality. *Oreochromis karongae* breeds from September to December (Lowe-McConnell 1952, Turner and Mwanyama 1992). In the north section of the SEA of Lake Malawi *O. karongae* continues to breed until March (Lowe-McConnell 1952), which could be the reason for the smaller peak in March. September and March are also months of lower primary production in Lakes Malawi and Malombe (FAO 1993) and, coupled with breeding, fish growth would then be reduced (Yosef and Casselman 1995, Jepsen *et al.* 1999). Banda (1992), who indirectly validated the age data on *O. karongae* from the SEA of Lake Malawi by corroboration with length-frequency analysis, also assumed that growth zones on opercula of *O. karongae* were formed bi-annually. Working on other tilapia species, Admassu and Casselman (2000) also reported two zones formed annually. The present study therefore assumed that growth checks on *O. karongae* opercula were laid down bi-annually. Although this assumption was made in this study, it is likely that growth increment formation rate in *O. karongae* is constant throughout the lake, and its breeding pattern also appears to be protracted.

Length at 50% maturity

Oreochromis karongae from Lake Malombe matured earlier (at 1.5 years) and at smaller sizes (203 mm TL) than in Lake Malawi (Table 2, Figure 3). A strong relationship ($p \leq 0.05$) existed between the percent maturity of the gonads and total length of the fish at all the five sample sites. In general, more small individual fish were collected in Lake Malombe than in Lake Malawi.

Age and growth

Of the 1 329 opercula collected, 13% were rejected as unreadable due to cloudiness and very closely-spaced growth zones, especially in fish larger than 250 mm. A brown-yellowish fatty substance and porous appearance in most large opercula compounded the difficulty of reading them. This observation has been supported by several studies (Weatherley and Gill 1987, Lowe-McConnell 1952) which point out that age assessment from calcified structures in tropical fish is difficult and strongly subjective. Nevertheless, careful reading of the opercula bones revealed that most had two opaque bands. Coefficients of variation (Table 3) were low, suggesting that minimal errors occurred in the age estimation process. The ages of most sampled fish were between 2 and 4 years. Very few individuals of 1, 5 or 6 years were observed from any of the sites. A regression analysis of the slopes in Figure 4 showed significant differences ($p \leq 0.05$) in the observed L_∞ and K-values (Table 4). Pair-wise comparisons of mean length-at-age (Table 5) showed significant differences ($p \leq 0.05$) among the populations of *O. karongae.* The hypothesis that age, growth rate and size at 50% maturity of *O. karongae* differs along the lakeshore areas of Lakes Malawi and Malombe was therefore accepted.

Discussion

While fish populations living in favourable environmental conditions would normally have a greater size at 50% maturity (Lowe-McConnell 1982), our results demonstrate that, despite the relatively high primary productivity of Lake Malombe compared to Lake Malawi (FAO 1993, Turner 1995), *O. karongae* in Lake Malombe mature at a smaller size and younger age than those in Lake Malawi. Although early maturity in fish could be a response to environmental conditions (Bruton and Allanson 1974, Khallaf *et al.* 2003), in Lake Malombe their early maturity could be a direct result of the high fishing pressure that has caused the collapse of the chambo fishery in the lake (FAO 1993, Weyl *et al.* 2004b). The juvenile chambo in Lake Malombe are heavily exploited by *nkacha* nets (small-scale purse seines with illegally small mesh sizes) resulting in severe recruitment pressure and gross over-fishing (Weyl *et al.* 2004b). With chambo nearly eliminated, more than 60% by weight of the fishery in Lake Malombe is now dominated by a small haplochromine cichlid species known locally as *kambuzi* (Weyl *et al*. 2004b). Size at 50% maturity is highly variable and has been shown to be influenced by over-fishing, among other parameters (Belk 1995, Duponchelle and Panfili 1997). In an unnaturally-harsh environment, such as Lake Malombe, where fish mortality is very high due to excessive and uncontrolled fishing (FAO 1993), altricial life history traits (Noakes and Balon 1982) could well be evident in tilapias. The relatively smaller mean size (TL) of the *O. karongae* observed in Lake Malombe compared to Lake Malawi (Table 2 and Figure 3) could indicate that the mortality of large adult fish in the former lake is high. Direct effects of fishing on the life history of fish, such as age and size-at-maturity have been reported by Law (2000), such that in a fishery where larger (older) fish are removed, early maturity dominates. Trippel (1995) supports the concept that over-fishing could cause phenotypic evolution in fish stocks. Maturity responses, such as a lowering in age-at-maturity, may depict an important stock response to reductions in population size (Trippel 1995), which could be the case in Lake Malombe. Although differences in the size and area of Lakes Malawi and Malombe may also explain the differences in sizes and age-at-maturity of their *O. karongae* populations (Legendre and Ecoutin 1996, Duponchelle and Panfili 1997), in that Lake Malawi is a much larger ecosystem than Lake Malombe, heavy fishing appears to explain

Table 2: Estimated size and age-at-maturity of male and female *Oreochromis karongae* from five sites in Lakes Malawi and Malombe. L_{50} = length (mm) at which 50% of the fish are matured, R^2 = is the correlation coefficient (%), *This graph did not fit satisfactorily, because of the scarcity of small individuals, although its R^2 was acceptable

Site	Females			Males		
	Length at maturity (mm)		Est. age (yr)	Length at maturity (mm)		Est. age (yr)
	L_{50}	R^2		L_{50}	R^2	
Karonga	219	0.79	1.7	225	0.83	1.89
Nkhotakota	220*	0.84	2.34	244	0.73	3.26
Salima	223	0.76	2.39	222	0.85	2.02
Mangochi	225	0.81	2.15	222	0.92	2.06
Lake Malombe	206	0.82	1.57	199	0.89	1.39

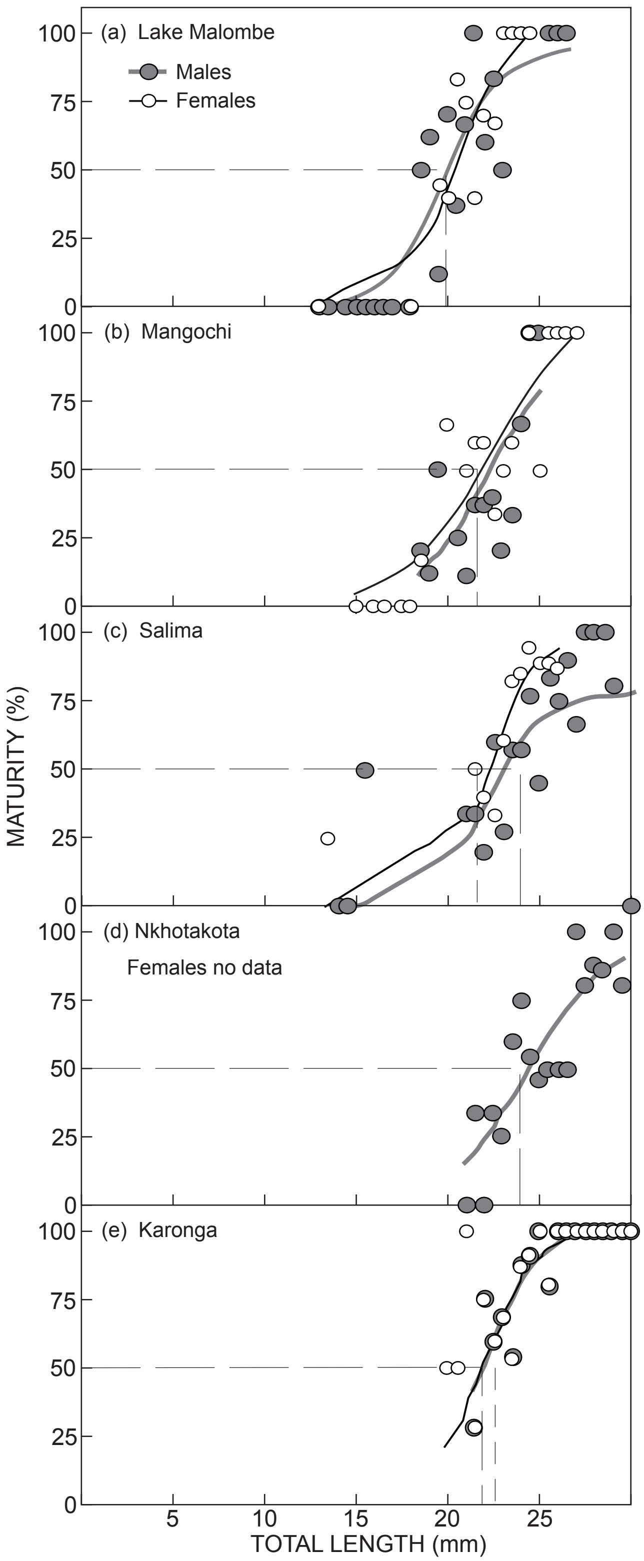

Figure 3: Size at 50% maturity (mm TL) of *Oreochromis karongae* at (a) Lake Malombe (L_{50} = 199 mm, 206 mm; *n* = 88, 100) (b) Mangochi (L_{50} = 222 mm, 225 mm; *n* =109, 83) (c) Salima (L_{50} = 222 mm, 223 mm; *n* = 218, 152) (d) Nkhotakota (L_{50} = 244 mm; *n* = 122 males only) The graph for female fish did not fit satisfactorally because of the scarcity of small individuals, and (e) Karonga (L_{50} = 225 mm, 219 mm; *n* = 208, 155) for males and females, respectively

Table 3: Summary of comparison of age estimates, using opercula, of *Oreochromis karongae* from all the five sites using opercula

Site	Average Percent Error (APE %)	Coefficient of Variation (CV %)	Index of precision (*D*)
Karonga	14.5	10.3	7.3
Nkhotakota	8.2	5.8	4.1
Salima	11.1	7.9	5.6
Mangochi	11.2	7.9	5.6
Lake Malombe	10.8	7.7	5.4

the differences in the life histories of their *O. karongae* best. Fishing mortality in the northern part of Lake Malawi is not as intensive as it is in the SEA of the lake, where the fishery is well established in the productive shallow southern part, and in Lake Malombe (FAO 1993, Banda *et al.* 2005). The chambo fishery in the SEA of Lake Malawi at Mangochi (Figure 1), is intensively exploited by both artisanal (traditional) and commercial fishers (FAO 1993, Weyl 2001, Weyl *et al.* 2004a, Banda *et al.* 2005). Catches of *Oreochromis 'Nyasalapia'* species (*O. karongae, O. lidole* and *O. squamipinnis*) in the SEA were dominated by juveniles (Weyl 2004a), suggesting recruitment overfishing (i.e. excessive reduction of spawner biomass). Weyl (2001) reported that, at the prevailing fishing mortality (F_{cur}) in area A of the SEA of Lake Malawi, the spawner-biomass-per-recruit (SBR) for chambo had reduced to 37% of pristine levels, which he described as too low to sustain the chambo stock.

This study suggests that, except for Lake Malombe where the sizes at 50% maturity may have been greatly reduced by heavy fishing, *O. karongae* populations throughout Lake Malawi, with the exception of those in the southeast arm, have similar breeding (size at 50% maturity) and growth patterns. The hypothesis that the growth rate of *O. karongae* differs along the lakeshore is therefore accepted because of the observed differences in mean length-at-age between populations of *O. karongae* (Table 5). This further supports findings that fishing mortality affects the growth of *O. karongae* (Trippel 1995, Law 2000). Although low sample sizes for small fish at Nkhotakota could have influenced the data for growth parameters, dominance of large fish in the sample could not be avoided because the fishery in the northern part of Lake Malawi is not over-exploited, as it is in the southern part and in Lake Malombe where the adult fish population has nearly been fished out (Weyl *et al.* 2004a, Weyl *et al.* 2004b, Banda *et al.* 2005).

It is suggested, therefore, that timely and appropriate management strategies for the sustainable exploitation of chambo in Lake Malombe, and possibly those in the southeast arm of Lake Malawi, should be implemented. It is also concluded from this study that the current management strategies for the chambo fish populations in Lake Malawi cannot be applied for chambo populations in Lake Malombe.

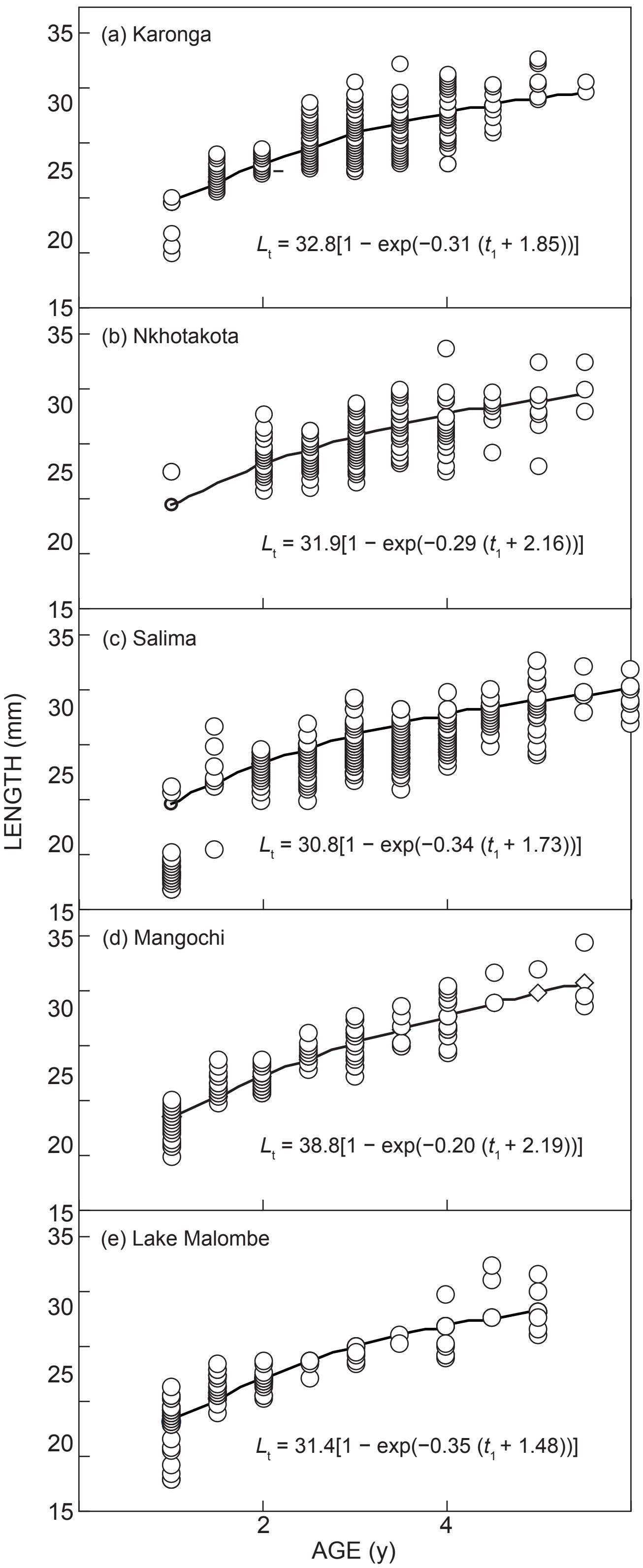

Figure 4: Observed individual lengths-at-age of *Oreochromis karongae* from Karonga, Nkhotakota, Salima, Mangochi and Lake Malombe, using opercula, and fitted using the von Bertalanffy growth model

Table 4: Comparative growth parameters (L_∞, K and t_0), and estimated growth performance index (ϕ′), for *Oreochromis karongae* from Lakes Malombe and Malawi, after Lowe-McConnell (1952), Banda (1992), Seisay *et al.* (1992) (using length frequency), and from this study. FW = Ford-Walford, G&H = Gulland and Holt, vB = von Bertalanffy, M = Munro, LS nlreg. = Least Square non-linear regression

	Banda (Lake Malombe)				Lowe (Lake Malawi)				Seisay (Lake Malombe)				This study Lake Malombe				This study Lake Malawi			
Method	L_∞	K	t_0	ϕ′	L_∞	K	t_0	ϕ′	L_∞	K	t_0	ϕ′	L_∞	K	t_0	ϕ′	L_∞	K	t_0	ϕ′
FW & vB	40.5	0.21	−1.20	2.54	31.9	0.72	0.26	2.86												
G & vB	41.0	0.21	−1.26	2.55	31.9	0.69	0.25	2.85												
M & vB	41.3	0.18	−1.34	2.49	30.8	0.56	0.56	2.73												
G & H									39.4	0.50		2.89								
LS nl reg									39.8	0.24	−1.58	2.58								
vB													31.4	0	35–1.48	2.54	35.1	0.29	−1.98	2.49

Table 5: Pair-wise comparison of mean total lengths by age of *Oreochromis karongae* for all sites (KARO = Karonga, MALO = Lake Malombe, MANG = Mangochi, NKK = Nkhotakota, SAL = Salima): means scored with the same letter are the same; mean pair-wise comparison was by Duncan's multiple range test (DMRT)

	Means					
SITE	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
KARO	17.08 ± 0.90 b	22.84 ± 0.12 b	25.22 ± 0.15 a	26.97 ± 0.23 a	29.56 ± 0.47 ab	30.50 ± NA
MALO	18.00 ± 0.34 b	21.61 ± 0.16 c	23.59 ± 0.30 b	25.41 ± 0.76 b	29.33 ± 0.97 ab	–
MANG	18.12 ± 0.25 b	21.70 ± 0.16 c	24.80 ± 0.29 a	26.97 ± 0.36 a	30.67 ± 0.94 a	30.70 ± 1.72
NKK	22.60 ± 0.0 0 a	23.92 ± 0.22 a	24.76 ± 1.17 a	26.61 ± 0.31 a	28.11 ± 0.44 b	30.10 ± 1.30
SAL	13.94 ± 0.33 c	22.74 ± 0.29 b	24.45 ± 0.14 ab	25.39 ± 0.15 b	27.99 ± 0.30 b	29.28 ± 0.53
F-value	30.8	24.79	4.46	10.42	3.35	0.48
p-value	<0.0001	<0.0001	0.0016	<0.0001	0.0137	0.7024

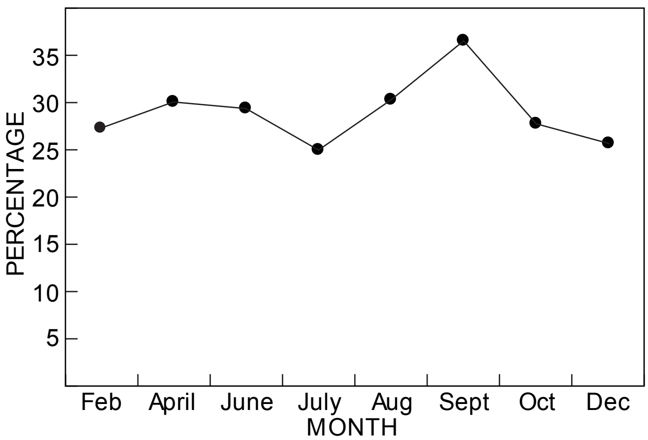

Figure 5: Monthly percentage occurrence of an opaque margin on opercula of *Oreochromis karongae* from all sample collection sites (*n* = 958)

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