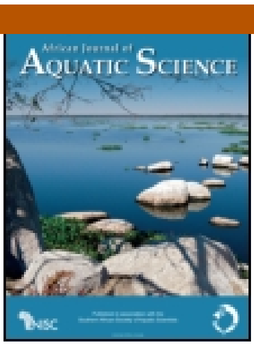

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Growth, reproduction and population structure of *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi

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***Diplotaxodon limnothrissa* is a widely distributed species occurring throughout Lake Malawi from the surface to a depth of at least 220m. It is probably the most abundant cichlid in the lake, with biomass estimates of around 87 000t in the pelagic zone alone. The species is exploited commercially in the southern part of the lake but, since its inception, this fishery has never been assessed. Analysis of sectioned sagittal otoliths revealed that *D. limnothrissa* is a slow-growing and relatively long-lived species, attaining ages in excess of 10 years. Length-at-age was described using the von Bertalanffy growth model, with combined-sex growth described as $L_t = 211.21(1 - exp(-0.24(t + 1.36)))$mm *TL*. Females matured at 139mm TL at an estimated age of 3.18 years. Total, natural and fishing mortalities were estimated at 0.63yr^{-1}, 0.38yr^{-1} and 0.25yr^{-1} respectively.**

Keywords: Cichlidae, length-at-maturity, mortality**,** Ndunduma, von Bertalanffy growth model

Introduction

With a surface area of *ca* 28 800km^2, Lake Malawi (9°30'S–14°30'S) is the second largest of the African Rift Valley lakes, supporting at least 500, and possibly 2 000, fish species (Turner 1995). The ichthyofauna is dominated by haplochomine cichlids, most of which are confined to the demersal and littoral zones. As a result of over-fishing, the abundance of many of these species has declined (Turner 1994a, 1995, Bulirani *et al.* 1999, Allison *et al.* 2002). In contrast, the lake's offshore fish stocks are considered to be unexploited or only lightly exploited (Thompson and Allison 1997, Turner *et al.* 2000) and the redirection of fishing effort to these stocks is a high priority (Thompson and Allison 1997, Turner *et al.* 2000, Allison *et al.* 2002). Consequently, the Malawi government is currently collaborating with the African Development Bank to develop the deepwater/ offshore fishery in order to increase yields by an estimated 11 000 tons (MC Banda, National Research co-ordinator, pers. comm.).

The most abundant cichlid species in the pelagic zone is the small (<210mm TL) zooplanktivorous *Diplotaxodon limnothrissa* (Turner 1994, Thompson and Allison 1997). It has been recorded throughout the lake at depths ranging from 20 metres down to the anoxic zone at *ca* 220 metres (Turner 1994b, Thompson *et al*. 1996, Duponchelle *et al*. 2000a) and it makes up *ca* 52% to the total fish biomass (Thompson and Allison 1997). *Diplotaxodon limnothrissa* will therefore be a major target species in the pelagic fishery, and already comprises in excess of 50% of the mid-water trawl fishery in the southeast arm (SEA) of the lake (Turner 1996).

Since a major objective of the Malawi fisheries policy is 'regulating production within safe sustainable limits for each fishery' (Government of Malawi 2001, page 5), 'safe' harvest levels for *D. limnothrissa* must be determined if the resource is to be utilised sustainably. This requires an understanding of its biology and life history, as well as the application of quantitative methods which require age-based estimates of growth, maturity and population structure.

In a lake-wide investigation of the reproductive biology of *D. limnothrissa*, Thompson *et al.* (1996) observed a spawning peak from May to June and determined that the average size of females at maturity was 14 cm total length (TL). Duponchelle *et al.* (2000b), working in the southwest arm (SWA) of the lake, obtained similar results, with a spawning peak between April and June and a female length at 50% maturity of 105mm standard length (SL) (*ca* 140mm TL).

Obtaining reliable estimates of age was more complicated. Thompson *et al*. (1995) found no annual rings on otoliths, scales or opercular bones from *ca* 10 fish, and therefore used length-frequency analysis in an attempt to determine growth rate. Dupochelle *et al.* (2000b) also used length-frequency methods to describe growth. Both studies described growth using the von Bertalanffy growth function (VBGF), but their estimates of the parameters differed considerably.

The accurate determination of age in fishes is a fundamental requirement for determining the population age structure and growth rate (Beamish and McFarlane 1987), both of which are needed for reliable stock assessments. The lack of reliable estimates of growth constrains the provision of management advice, especially in species-rich but poorly-known systems such as Lake Malawi. Length-frequency methods used to age fish may be inaccurate if species have protracted spawning seasons and/or are long-lived, which precludes accurate discrimination between older cohorts. Consequently, using this method, estimates of age at any length tend to be lower, resulting in a significant positive bias and the overestimation of growth and mortality rates. Hard-structures such as otoliths have been used to age fish and sectioned otoliths are currently considered the most suitable hard tissue for age and growth determination in tropical and subtropical areas (Campana 2001).

Whereas Thompson *et al.* (1990) failed to find annual growth rings in a limited sample of whole otoliths, this study successfully used sectioned otoliths to age *D. limnothrissa* in the SEA of Lake Malawi, and age-based estimates for growth, maturity and population structure were obtained.

Materials and Methods

Age and Growth

For the determination of age and growth, 522 fish ranging in size from 25mm to 195mm TL were selected between May 2001 and June 2002 from the catches of Maldeco Fisheries Ltd. Fish were measured to the nearest mm and weighed whole to the nearest gram. Both sagittal otoliths of each fish were removed, cleaned and stored dry in marked manila envelopes for later processing. As no asymmetry in otolith shape was apparent, sagittae from either left or right of each fish were arbitrarily selected for ageing. Otolith length (OL) (distance from anterior tip of rostrum to antirostrum) was measured to the nearest 0.01mm, using a digitised calliper for the larger sagittae and a calibrated ocular eyepiece fitted to a compound light microscope for those <2mm OL.

To enhance the visibility of otolith growth zones, each otolith was burnt to a light brown colour over an electric hotplate. Burnt sagittae were embedded in clear polyester casting resin and sectioned transversely through the nucleus to a thickness of *ca* 0.5mm using a double-bladed diamond saw. Sections were mounted with DPX mountant on microscope slides and viewed with a stereo microscope. Under transmitted light, alternate opaque and translucent zones were visible (Figure 1) which, together, were taken to comprise a complete growth zone. Since interpretation was relatively difficult for sagittae with >8 growth zones, an index of readability (Table 1) was used to classify the sagittae according to growth zone appearance. All sagittae were read twice, at an interval of three weeks, without reference to the date of capture or length of the fish. If the number of opaque zones given by both readings was equal, the age estimate was accepted, whereas if the difference between the two readings was less than or equal to two, a mean age was taken, otherwise the otolith was rejected as unreadable. The precision of age determination was assessed using the average percent error method outlined by Beamish and Fournier (1981).

The periodicity of growth zone formation was validated indirectly by marginal zone analysis (MZA). Sectioned otoliths collected from monthly samples of at least 30 fish were examined and the optical appearance of the marginal zone noted. The detection of an opaque zone on the margin was found to be problematic as the optical appearance was often difficult to interpret. This problem was overcome by also noting those otoliths with a thin hyaline margin, as this marks the period soon after opaque zone deposition. The presence of a periodic trend in the monthly proportion of otoliths with opaque and narrow hyaline zones was tested statistically using autocorrelation and autoregressive integrated moving average models (Priestley 1981).

Length-at-age was modelled using the VGBF, which is described as $L_t = L_\infty (1 - \exp(-(t - t_0)))$, where L_t is length at

Figure 1: Sectioned sagittal otolith from a six year old, 180mm TL *Diplotaxodon limnothrissa* with 12 opaque zones

Table 1: Criteria used for classifying otolith readability in *Diplotaxodon limnothrissa*

Category	Description
1	Believed to be reliable. Good definition between translucent and opaque zones
2	Zonation relatively clear but not well defined, error margin expected to be ± 0.5 year (i.e. ± 1 ring)
3	Zones vaguely marked, error margin possibly ±1 year or more (i.e. ± 2 rings)

Table 2: Macroscopic criteria used to stage *Diplotaxodon limnothrissa* ovaries

Stage	Development	Macroscopic appearance
1	Immature	Sex indistinguishable. Gonad a thin, translucent, gelatinous strip.
2	Undeveloped to early developing	Sex distinguishable. Ovaries white, slightly yellowish, or pinkish in appearance. Texture of ovary varies from granular to oocytes being readily distinguishable.
3	Developing	Oocytes enlarged and readily visible.
4	Ripe	Oocytes of maximum size, fully hydrated and loose within ovary.
5	Mouthbrooding or spent	Ovary with few ripe eggs and/or mouthbrooding evident. Ovaries sac-like, flaccid.

time t, L_∞ is the theoretical asymptotic length, K is the Brody growth coefficient and t_0 is the age of a zero-length fish. Parameters were estimated using a non-linear minimisation of a Normal log-likelihood function. Parameter variances were calculated using parametric bootstrap resampling (Efron and Tibshirani 1986) with 1 000 bootstrap replicates. Confidence intervals were obtained from the sorted bootstrap data using the percentile method (Buckland 1984).

Maturity

To determine reproductive seasonality, a total of 604 female fish (TL > 140mm) were collected at monthly intervals from the catches of mid-water and demersal trawlers between June 2001 and May 2002. All fish were weighed to the nearest 0.01g and the condition of their gonads was staged macroscopically (Table 2). Gonads were dissected from the fish and weighed to the nearest 0.01g. Reproductive activity was assessed using a monthly gonadosomatic index (GSI), where gonad weight (g) was expressed as a percentage of the somatic weight of the fish excluding its gonads.

To determine the length and age at maturity, 461 female fish, ranging in length from 88mm to 190mm TL, were collected during peak reproductive activity (March–April 2002). The length-at-50%-maturity (l_{50}) was determined by fitting a logistic function of the form $P_a = (1 + \exp^{-(l - l50/\delta)})^{-1}$ to the proportion of reproductively active female fish (stages 4 and 5, Table 2). The function, where P_a is percentage of mature fish at length l, and δ the steepness of the logistic, was fitted by non-linear minimisation of a Binomial log-likelihood function.

Population structure

A first estimate of total annual mortality in the SEA was calculated by catch curve analysis (Ricker 1975). Length-frequencies obtained from the Department of Fisheries' trawl surveys conducted in the SEA during 1999 and 2000 (Malawi Department of Fisheries, unpublished survey data) were transformed to age-frequencies using the age-length key summarised in Table 4. Total mortality was estimated by fitting a linear regression to the descending limb of the combined data. Natural mortality was calculated from Pauly's (1980) empirical formula.

Results

Age and Growth

The relationship between otolith length and fish length was best described as: OL (mm) = 0.4451 + 0.02615TL(mm) ($r^2 = 0.95$, n = 268); and the length weight relationship as Wt (g) = $0.000019\text{TL(mm)}^{2.85}$ ($r^2 = 0.99$, n = 508).

Of the 522 sagittae examined, 31% could not be aged reliably. Of the remaining 351 otoliths, 21%, 43% and 26% were classified as having a readability of 1, 2 and 3 respectively (Table 3).

An examination of the otolith margins revealed that two opaque zones were deposited annually, one between April–May and the other during September–October (Figure 2a). The corresponding autocorrelation plot is illustrated in Figure 2b. The peaks at lags 0 and 6 indicate that two opaque growth zones were deposited annually. An autoregressive model with a periodicity of 6 indicated that the periodicity was significant ($P < 0.05$, $r^2 = 0.95$). Growth ring counts were therefore divided by two to obtain an estimate of age in years. Age estimates had an average percent error of 10.5%, a CV of 7.4% and an index of precision of 5.3.

The length-at-age key for *D. limnothrissa* is provided in Table 4. The oldest fish sampled in this study, with an age of 10 years, measured 180mm TL. The fitted VBGF is shown in Figure 3 and the growth parameters are summarised in Table 5.

Maturity

Monthly GSI and the progression of the various macroscopic stages of maturity are shown in Figure 4. The proportion of ripe females increased from 23% in January to *ca* 65% in April, and subsequently decreased to *ca* 19% between May and June when 47% of the female fish were in the 'spent' condition (Figure 4b). Thereafter the proportion of ripe females continued to decline, with no ripe females being recorded in November. Subsequently, a gradual increase in the proportion of ripe females was noticed from December to April. A similar trend was observed in the mean monthly GSI, which ranged from a minimum of 0.23% in August to a maximum of 1.20% in April (Figure 4a). The maturity logistic

Table 3: The percentage of *Diplotaxodon limnothrissa* otoliths in each readability category, by age group

Age (years)	n	Readability category		
		Type 1	Type 2	Type 3
1	43	26%	56%	18%
2	124	30%	38%	32%
3	91	12%	35%	53%
4	42	7%	40%	52%
5	19	5%	68%	26%
6	14	29%	50%	21%
7	7	43%	43%	14%
8	3	0%	100%	0%
9	2	50%	50%	0%
10	1	100%	0%	0%

curve (Figure 4c) shows that female fish attained l_{50} at 139mm TL, which corresponded to an estimated age of 3.18 years.

Population structure

The age structure sampled during the 1999 and 2000 monitoring surveys and the corresponding catch curves are shown in Figure 5. Using catch-curve analysis, total mortality was estimated at 0.63yr^{-1}. Natural mortality was estimated at 0.38yr^{-1}, with fishing mortality calculated by subtraction at 0.25yr^{-1}.

Discussion

Despite the earlier failure to age *D. limnothrissa* using hard parts (Thompson *et al.* 1995), in this study clear, biannually-deposited growth zones were visible in sectioned and burnt sagittal otoliths, leading to the first hard-part-based estimate of age and growth for this species.

Opaque growth zone formation in otoliths has been attributed to one or more environmental variables which reduce metabolic rate, resulting in a slowing of the growth rate (Gauldie and Nelson 1990). In cichlids from tropical and subtropical areas, growth zone formation has been linked to temporal variation in feeding intensity (Bruton and Allanson 1974), reproductive periodicity (Bruton and Allanson 1974, Hecht 1980, Booth *et al.* 1995, Booth and Merron 1996) and temperature variation (Hecht 1980, Weyl and Hecht 1998). Whilst MZA, the most commonly used indirect validation method, has been criticised as being subjective (Campana 2001), direct methods such as mark-recapture and fluorochrome marking could not be applied here because of barotrauma and the extremely low probability of recapture. Nevertheless, MZA did show that two opaque zones, representing periods of slow growth, were deposited in *D. limnothrissa* otoliths per year. It is acknowledged that the deposition of opaque (and the opaque-thin hyaline) zones are lagged, as the respective protein and calcium carbonate components (otolin and aragonite) take time to deposit. Therefore, the periodicity of growth-zone deposition could be assessed, but the correlation of this to causative factors was not possible.

This study's estimated growth rates from sectioned sagittae differed considerably from earlier estimates based on length-frequency analysis (Thompson *et al.* 1995, Duponchelle *et al.* 2000b, Figure 6). If one assumes that otolith-based estimates of age are the most accurate, both Thompson *et al.* (1995) and Duponchelle *et al.* (2000b) appear to have overestimated the initial growth rate of the species. Their faster growth estimates can be attributed to the rapid growth of the species in its first 3–4 years of life and to the lack of discernible modes in the length-frequency distributions after *ca* 1.5 years (Thompson *et al.* 1995, Duponchelle *et al.* 2000b). This study has shown that *D. limnothrissa* is a relatively slow-growing species, which matures in its third year of life and which attains its maximum length after 3–4 years. The species is relatively long-lived, with a maximum recorded age of 10 years, and growth rate reducing significantly after the fourth year of life (Figure 3).

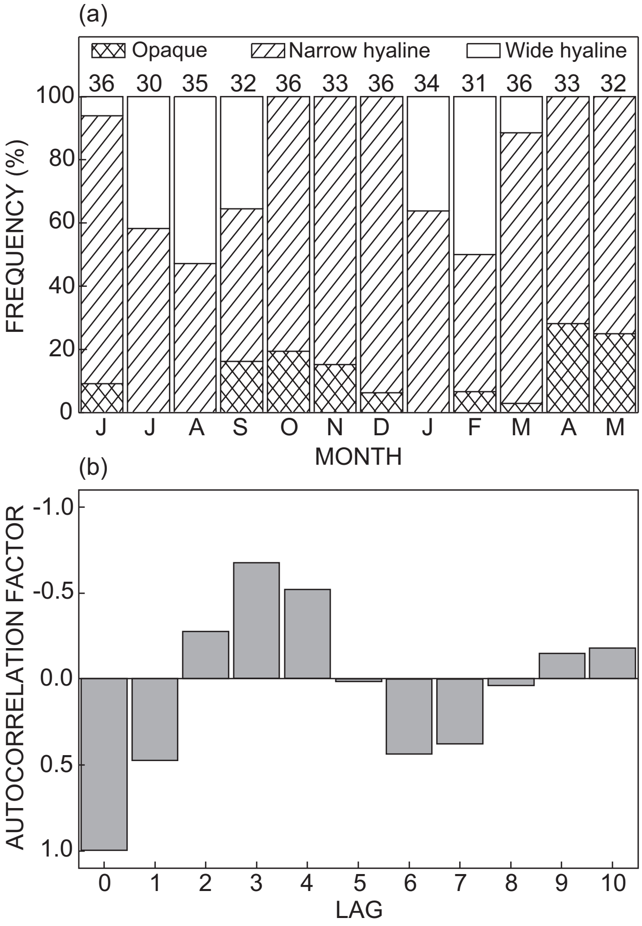

Figure 2: (A) Marginal zone analysis and (B) autocorrelation plot for marginal zone deposition in otoliths from *Diplotaxodon limnothrissa* collected from the southeast arm of Lake Malawi between June 2000 and March 2001

This being the first study using sectioned otoliths to age a haplochromine cichlid from Lake Malawi, direct comparisons with closely-related species were not possible. However, estimates for the VGBF parameters K and L_∞, determined using length-frequency analyses, are available for seven haplochromine species from the lake (Iles 1971, Tweddle and Turner 1977, Table 7). As there is interaction and dependence between the VGBF parameters K and L_∞, direct

Table 4: Age-length key for *Diplotaxodon limnothrissa* from the southeast arm of Lake Malawi

Length class	Age (years)										
(mm TL)	0	1	2	3	4	5	6	7	8	9	10
20–39.9	5										
80–99.9		13	35	7							
100–119.9		25	59	16							
120–139.9		5	22	14							
140–159.9			8	35	19	3					
160–179.9				18	22	15	6	5	1		
180–199.9				1	1	1	8	2	2	2	1
N	5	43	124	91	42	19	14	7	3	2	1

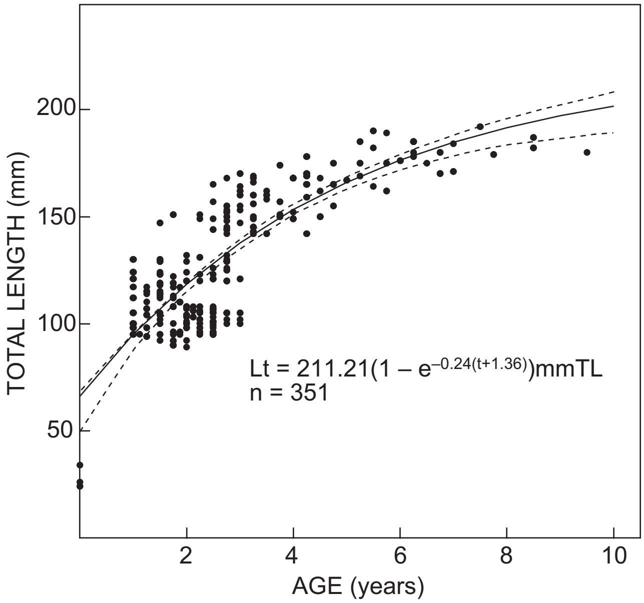

Figure 3: Observed individual lengths-at-age, and the expected von Bertalanffy growth curve (solid line, with dashed lines denoting 95% confidence intervals) for combined sex *Diplotaxodon limnothrissa* determined from sectioned sagittal otoliths sampled from the southeast arm of Lake Malawi between May and June 2002 (n = 351)

Table 5: Point estimates, associated coefficients of variation (CV) and 95% confidence intervals (CI) for combined sex length-at-age data fitted using the von Bertalanffy model for *Diplotaxodon limnothrissa* sampled from the southeast arm of Lake Malawi during May/June 2002

Parameter	Point estimate	CV	95% CI
L_∞	211.21mm TL	5.4%	[194.95, 235.21]
K	0.24 year^{-1}	15.3%	[0.17, 0.32]
t_o	–1.36 year	19.3%	[–1.97, –0.93]

comparisons of parameter values between species are meaningless because species with different growth parameters may have similar growth performances. However, the parameter phi-prime (Pauly and Munro 1984) takes the interaction and dependence between the VBGF parameters into consideration and provides a useful basis for comparison. Since the methods used by Iles (1971) and Tweddle and Turner (1977) did not allow for the estimation of the parameter t_o, comparisons of growth performance necessitated the fitting of a 2-parameter nested form of the full VBGF, with t_o fixed at 0, to the *D. limnothrissa* length-at-age data from this study. Subsequent comparison between phi-prime values showed that the growth performance of *D. limnothrissa* did not differ significantly from that of the other species (Students t-test; P > 0.05).

Sectioned otoliths showed that *D. limnothrissa* attain ages of at least 10 years. While the length-frequency analysis system used in the previous studies does not allow for a direct estimate of age for any of the haplochromine species (Iles 1971, Tweddle and Turner 1977), Iles (1971) presents evidence for at least 5 year-classes in *Copadichromis virginalis* and *C. quadrimaculatus*. Further, *D. limnothrissa*'s longevity is not unusual for African cichlids, since studies using sectioned otoliths to age tilapiine cichlids have produced longevity estimates in excess of 10 years (Booth *et al*. 1995, Booth and Merron 1996, Weyl and Hecht 1998).

Female *D. limnothrissa* matured at a mean length of 139mm TL, which was similar to the maturity estimates obtained by Thompson *et al*. (1995), Turner (1996) and Duponchelle *et al*. (2000a). Using length-at-age data from this study, age-at-maturity was estimated at *ca* 3.2 years, which is similar to that estimated by Iles (1971) for *Copadichromis pleurostigmoides* and by Tweddle and Turner (1977) for *Lethrinops longipinnis* (Table 6). Reproductively active female *D. limnothrissa* have been recorded throughout the year, whilst the reproductive activity peaks between March and May (Thompson *et al*. 1995, Duponchelle *et al*. 2000a). Thompson *et al*. (1995) observed that peak spawning in the SEA occurred between April and June and off-shore between February and April. In the SWA arm of the lake Duponchelle *et al.* (2000a) also observed that peak spawning occurred between April and June. These data suggest that, within the southern part of the lake, there is no temporal variation in the spawning seasonality, but that it does vary in intensity.

Like all haplochromine cichlids, *D. limnothrissa* is a maternal mouth brooder and, although its spawning behaviour has never been observed, this is presumably similar to that of other haplochromines, which exhibit elaborate spawning behaviour, with the males actively defending territories (Turner 1996). Feeding activity in both male and female fish is therefore likely to be reduced during

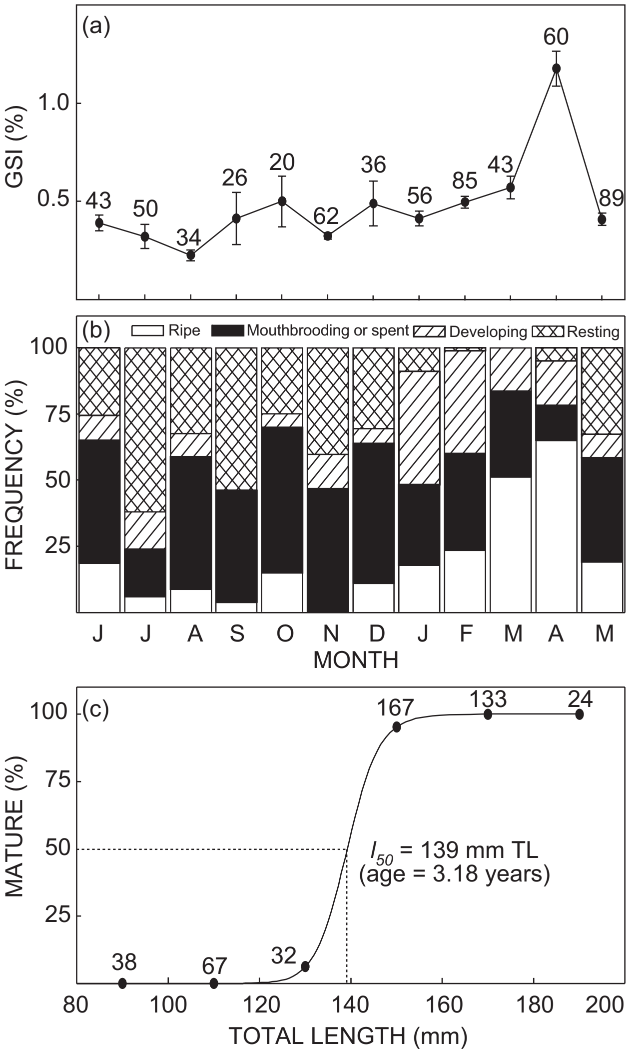

Figure 4: *Diplotaxodon limnothrissa* female (A) monthly mean gonadosomatic index (GSI), (B) monthly proportion of fish with gonads in ripe, spent, developing and resting condition; and (C) fitted logistic maturity ogive to the proportion of reproductively active female fish (ripe and spent) at length. Error bars denote standard errors. Numbers above data points = number of fish examined

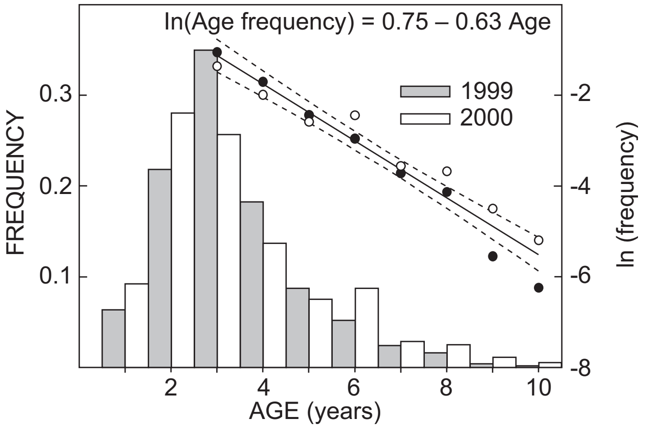

Figure 5: Age frequency distribution (bars) and catch curve (solid line, with dashed lines denoting 95% confidence intervals) fitted to data for *Diplotaxodon limnothrissa* caught during the Department of Fisheries' annual monitoring surveys in 1999 (solid circles) and 2000 (open circles) in the southeast arm of Lake Malawi. The slope of the descending limb of the catch curve provides an estimate of total mortality (Z)

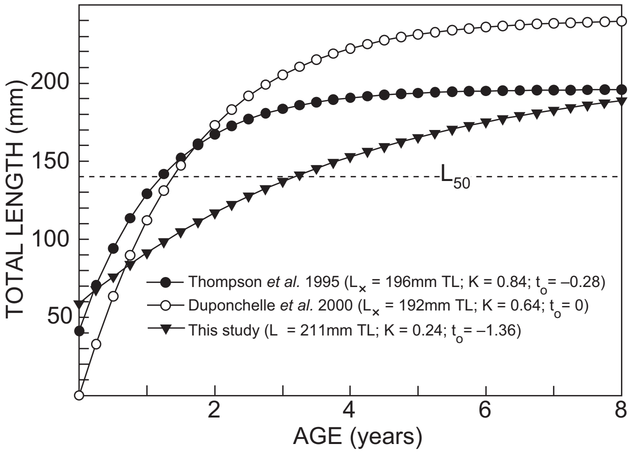

Figure 6: Comparison of growth curves for *Diplotaxodon limnothrissa* derived from sectioned otoliths in this study with those derived from length-frequency analysis by Thompson *et al* (1995) and Duponchelle *et al.* (2000b)

the reproductive period, leading to slower growth, especially in females, which brood juveniles until they reach a length of *ca* 30mm TL (Turner 1994b).

The determination of age and growth rates in this study enabled the estimation of total mortality in the *D. limnothrissa* population at 0.63yr^{-1}. This estimate differs substantially from a previous estimate of 3.48yr^{-1} in the SWA arm of the lake (Duponchelle *et al.* 2000b), which is a direct result of the overestimation of growth rate.

In conclusion, this study has shown that burnt sagittal otoliths can reliably be used to age *D. limnothrissa.* The age and growth information showed that this species is long-lived and, from a cichlid perspective, slow-growing, reaching sexual maturity after three years. These factors, in conjunction with the species' low fecundity of 15 eggs per fish (Thompson *et al.* 1996) and its mouthbrooding its young to a large size (23mm SL) (Duponchelle *at al.* 2000a), imply vulnerability to harvesting pressure. If overfished, and depending on the extent of overfishing, it would require a relatively long period for the stock to recover. It is therefore recommended that any expansion of the pelagic trawl fishery needs to be carefully monitored. For long-term monitoring, it is suggested, that fish samples be collected between July and August and between February and August, respectively, in order to reduce measurement error in both, age determination and size/age at sexual maturity. Ageing studies need to avoid the introduction of measurement error in counting growth zones by circumventing the periods when opaque zone deposition is

Table 6: Comparison of *Diplotaxodon limnothrissa* von Bertalanffy growth function (VGBF) parameters (t_o, K and L_∞), estimated age-at-maturity (a_{mat}) and calculated phi-prime (Pauly and Munro 1984) derived in this study, with length-frequency analysis-based estimates for other haplochromine cichlid species from Lake Malawi. To allow for a direct comparison between species, a 2-parameter nested form of the full VBGF, with t_o fixed at 0, was fitted to *D. limnothrissa* length-at-age data (*D. limnothrissa* 2-parameter nested VBGF). (nd = not determined)

Species	t_o	K	L_∞	a_{mat}	*Phi-prime*
Copadichromis pleurostigmoides[1]	nd	0.764	144	3+	4.20
Copadichromis quadrimaculatus[1]	nd	0.650	190	2+	4.37
Copadichromis virginalis[1]	nd	0.775	121	2+	4.05
Ctenopharynx intermedius[3]	nd	0.571	229	2+	4.48
Diplotaxodon limnothrissa[2]	–1.36	0.240	211	3+	
D. limnothrissa (2-parameter nested VBGF)[2]	0	0.560	176		4.24
Lethrinops longipinnis[3]	nd	0.571	202	3+	4.37
Lethrinops parvidens[3]	nd	0.487	208	2+	4.32
Maravichromis anaphyrmis[3]	nd	0.671	196	2+	4.41

[1] Iles (1971), [2] This study, [3] Tweddle and Turner (1977)

highest. Similarly, while reproductive activity is highest in February to April, errors in categorising mature fish into the immature category can be minimised by sampling over the period of peak reproductive activity.

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