African Journal of Aquatic Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/taas20

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African Journal of Aquatic Science 2020, 45(4): 509–519
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AFRICAN JOURNAL OF AQUATIC SCIENCE
ISSN 1608-5914 EISSN 1727-9364
https://doi.org/10.2989/16085914.2020.1753008

Age and growth of Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) from Lake Tana, Ethiopia

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Age and growth of Nile tilapia, *Oreochromis niloticus*, from Lake Tana were studied from June 2016 to May 2017. In total, 1 597 otoliths were collected from three representative sampling sites for macrozone analysis. Otoliths were ground and examined under a dissecting microscope at 7–40× for the presence of translucent and opaque macrozones using a reflected light source. The age of the fish was determined from the total number of translucent macrozones counted in the otoliths considering the time of translucent zone formation and median hatch date. Two peaks of translucent macrozones were observed in January and February and in June and July. The mean marginal increment was found to be highest (73–85%) in November, December and May, and lowest (0–9.3%) in January, February, June and July. The von Bertalanffy Growth Function was fitted to observed length and age, with L_∞ = 45.1 cm, K = 0.21 y^{-1} and t_0 = −0.514 years. The growth rate for *O. niloticus* from Lake Tana was lower than that previously reported for Ethiopia, warranting additional studies to determine causative factors that would explain the differences.

Keywords: biannuli, growth rate, Lake Tana fishery, macrozone, otolith

Introduction

Lake Tana, the source of the Blue Nile, is the largest lake in Ethiopia. It was formed in the late Pliocene or early Pleistocene epochs, and has been categorized as an oligo-mesotrophic lake containing a truncated fish fauna. The south-north maximum length is ~90 km with an east-west width of ~65 km (Greenwood 1976; Rzoska 1976). Scientific studies on the fishes of Lake Tana date back to 1829 when Rüppell described several cyprinid species (Ameha et al. 2017). The more recent studies on the taxonomy and ecology of the fishes of Lake Tana began in the 1980s as part of fisheries resource development projects implemented by the Ministry of Agriculture (Ameha et al. 2017). Lake Tana is not viewed as species rich, related to other tropical lakes in Africa, but does have a high richness of fishes relative to other Ethiopian lakes (Vijverberg et al. 2012). The relatively large surface area, geographic isolation from other such water bodies and varied microhabitats within the lake and its rivers could be among the reasons for such diversity (Vijverberg et al. 2012).

There are 28 described species of fishes in Lake Tana (Getahun and Dejen 2012). They are divided into four families (Cyprinidae, Balitoridae, Clariidae and Cichlidae) and seven genera (*Labeobarbus*, *Garra*, *Barbus*, *Varicorhinus*, *Afronemacheilus*, *Clarias* and *Oreochromis*). The genus *Labeobarbus* contains 17 species, *Garra* comprises four species and *Barbus* consists of three species, whereas the last four genera, including *Oreochromis*, are each represented by only a single species (de Graaf 2003; Getahun and Dejen 2012). Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is among the most productive and cultured fish species worldwide (World Bank 2012) and has great commercial importance as the base of commercial fisheries in many lakes in Africa (Younes et al. 2015; Hyuha et al. 2017). *Oreochromis niloticus* is spread extensively in most lakes and rivers of Ethiopia, contributing to more than 60% of the total annual landings in the country and ~65% for Lake Tana (Tedla 1973; Reyntjens et al. 1998; Tewabe 2013; Dejen et al. 2017). Therefore, knowledge of age and growth of this species is essential to better understand its stock status and to design optimal management strategies.

Age is a key variable in fish demography because it forms the foundation for calculations of growth and mortality rates and the productivity of populations (Campana 2001). Optimal management strategies are based on information derived from stock assessment models that rely on age data. Important population statistics, such as natural and fishing mortality, age composition of the exploited population, age at first maturity, stock age structure and recruitment success can only be computed when the relationship between length and age is known (Stevenson and Campana 1992). The periodic increments deposited in calcified structures of fishes, such as scales, vertebrae, fin rays, opercula and otoliths, have been used to age different species. Among these, otoliths have become the most popular and widely used source of age information (Campana 2001).

African Journal of Aquatic Science is co-published by NISC (Pty) Ltd and Informa UK Limited (trading as Taylor & Francis Group)

Published online 25 Aug 2020

The growth rate of *O. niloticus* differs between populations depending on environmental conditions and fishing pressure (Kolding 1993; Ojuok et al. 2007). Therefore, recent and local estimations of age are needed to assess growth strategies for stock assessment and management in any given system. For instance, studies in the Nyanza Gulf of Lake Victoria, Kenya showed that growth parameters of *O. niloticus* changed as a result of intensive fishing, with asymptotic length (L_∞) decreasing from 64.6 cm (total length) in 1986 (Getabu 1992) to 56.7 cm in 1999 (Njiru et al. 2000 cited in Ojuok et al. 2007); and the growth rate (K) increasing from 0.25 y^{-1} in 1986 to 0.59 y^{-1} in 1999 (Ojuok et al. 2007).

Many studies on age and growth of *O. niloticus* have been undertaken in Kenya, Mexico and Uganda (Getabu 1992; Gomez-Marquez 1998; Bwanika et al. 2007; Gomez-Marquez et al. 2008) and some studies have also been conducted in the Ethiopian Rift Valley lakes (Tekle-Giorgis 1990; Tekle-Giorgis and Casselman 1995; Admassu 1998; Admassu and Casselman 2000; Tesfaye and Wolff 2015), including Lake Tana. Wudneh (1998) studied age and growth of *O. niloticus* in Lake Tana during 1990–1993, when the fishery of Lake Tana was early in its development and the sampling was restricted to the southern part of the lake. Currently, the Lake Tana fishery is well-developed and age and growth investigations are timely as the data are needed to improved management of *O. niloticus* stock.

The goal of this study was to estimate age and growth parameters of *O. niloticus* in the Lake Tana, Ethiopia to assist with stock assessment and management.

Materials and methods

Description of the study area

The Lake Tana Basin is in the north-western highlands of Ethiopia. It lies between 10°58′–12°47′ N and 36°45′–38°14′ E, at an altitude of 1 800 m above sea level (Figure 1). Lake Tana is a turbid and shallow lake with depths between 8–14 m with a surface area of ~3 050 km^2 and catchment area of 16 500 km^2 (Vijverberg et al. 2009). The lake accounts for ~50% of the freshwater resources of the country.

The Lake Tana region has four climatic variations: 1) the main wet season from June to August (summer); 2) the post-wet season from September to November (spring); 3) the dry season from December to February (winter); and, 4) the pre-wet season with occasional showers from March to May (autumn) (Dejen et al. 2004). Lake Tana's water level fluctuates with the rainfall pattern with levels rising by up to 2 m between the start and end of the rainy season (Wudneh 1998). The lake has a minimum temperature of 20 °C in January and a maximum temperature of 27 °C in May (Dejen 2003).

Three sites were selected in the lake: Bahir Dar (Site 1), Gumara (Site 2) and Gorgora (Site 3; Figure 1). These three sampling sites were assumed to well represent the lake. Bahir Dar (Site 1) represents the southern part of the lake, Gumara (Site 2) represents the eastern part of the lake and Gorgora (Site 3) represents the northern part. The west part of the lake is inaccessible for sampling. Furthermore, insufficient quantities of Nile tilapia exist on the western side of the Lake, despite attempts to sample during the first three months of the sampling period. Permission to perform this research was obtained from the School of Fisheries and Wildlife, Bahir Dar University, Ethiopia.

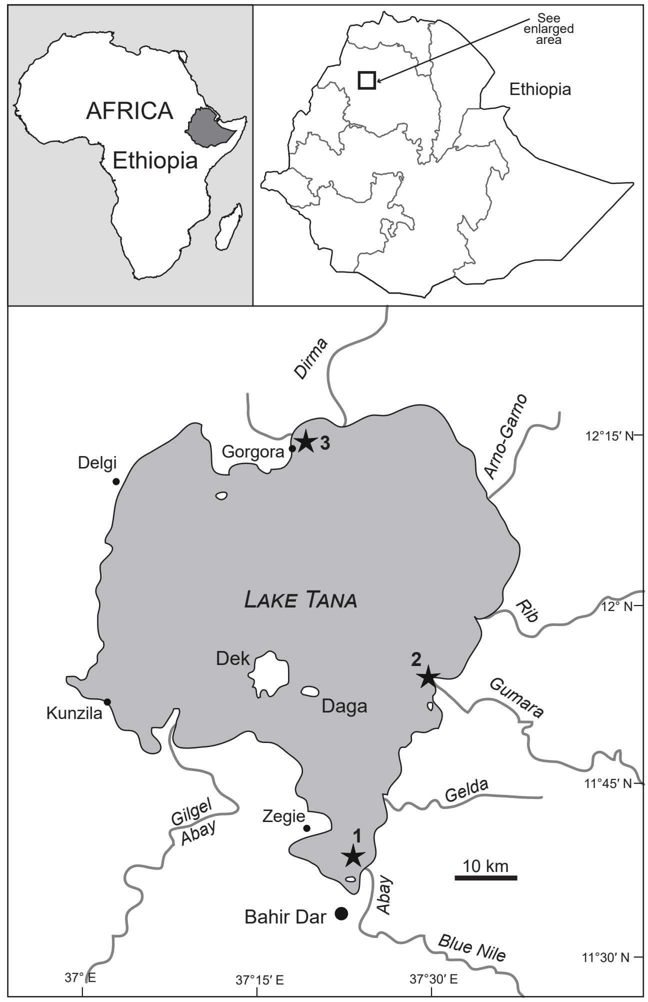

Figure 1: A map showing the location of Lake Tana in relation to Africa, Ethiopia and the study sites (Tefera et al. 2019)

Fish sampling

Fish samples were collected using multifilament gillnets of 6, 8, 10, 12 and 14 cm stretched mesh sizes with an overall size of 1.5 cm × 50 cm. Nets were set every month from June 2016 to May 2017 at the three study sites, and fish were collected. Gillnets were set at approximately 4:00 pm and retrieved at approximately 8:00 am the following day. Upon lifting the nets, almost all of the specimens were deceased. Live specimens were quickly and efficiently sacrificed by severing the spinal cord (as per Ethiopian standards). The total length (TL, cm) and total weight (0.1 g) of each specimen were recorded. Both sagittal otoliths were removed from each fish by making an incision at the dorsal part of the skull right behind the operculum. Once removed, the otoliths were cleaned and placed in 2-ml labelled vials containing 97% ethanol.

Preparation of otoliths for macrozone analysis

Sagittal otoliths were soaked in ethanol for three days, then transferred into 45% glycerol for about a week to enhance the appearance of the macrozones (Tekle-Giorgis and Casselman 1995; Admassu and Casselman 2000). One sagittal otolith was selected randomly from each pair (Panfili 2001; Bokhutlo 2011; Al-Kiyumi 2013) and was ground on the convex side using wet carborundum papers of 400 and 600 grit sizes (Carborundum Universal Limited, India). Macrozones were satisfactorily decipherable when the posterior part of the convex side was ground down (thinned) to a level equal to the canal sulcus acusticus (Tekle-Giorgis and Casselman 1995). During microscope examination, the wider, pale area (opaque zone) was characterised as the fast-growth zone and the narrow, black area (translucent zone) as the slow-growth zone (Admassu and Casselman 2000).

Time of translucent zone formation and age interpretation

Otoliths were examined under a dissecting binocular microscope (Optica Microscope, Italy) for the presence of translucent and opaque macrozones using a reflected light source and a magnification of 7−40× against a black background. To maintain unbiased readings, translucent zones were counted twice for each otolith without knowledge of the fish size and date of capture (Tekle-Giorgis and Casselman 1995; Admassu and Casselman 2000; Panfili 2001). After fixing the magnification of the microscope using a stage micrometer (50 mm units), the maximum posterior radius of each otolith was measured using an ocular micrometer (10-micrometre units). In addition, the width of the opaque zone at the edge of the otolith was measured along the maximum posterior radius. Time of translucent zone formation was determined by the frequency of otoliths with a translucent macrozone at the edge (Tekle-Giorgis and Casselman 1995; Admassu and Casselman 2000). Annuli that were discontinuous i.e. did not form a complete ring and had a faint color, mostly formed in the anterior part of the otolith and were found close to the true zone; they were regarded as false annuli and were not taken into consideration (Admassu and Casselman 2000). A Chi-square goodness of fit test was used to identify months when the percentage of otoliths with a translucent edge was greater than might be expected by chance (calculated by comparing individual Chi-square values for each month with the critical value of 197 (df = 11, α = 0.05).

The age of the fish was determined from the total number of translucent macrozones counted in the otoliths, taking into account the time of translucent zone formation and the breeding season of the fish. In Lake Tana, *O. niloticus* has peak breeding season in June and July (Tadesse 1997; Wudneh 1998) and mid-July was taken as the median hatch date of the fish, had been done for Lake Hawassa (Admassu and Casselman 2000). Accordingly, the number of translucent macrozones was back calculated from the date of capture to hind cast the specific year class of the fish. After categorizing the fish into their specific year classes, the age (in days and then in years) of individuals was determined by calculating the time lapse between the median hatch date of each fish and the date of capture (Tekle-Giorgis 1990; Tekle-Giorgis and Casselman 1995).

Age precision and bias

As a quality control measure for age estimation, tests for precision and bias were applied. Precision, which is the reproducibility of repeated measurements on a given otolith (Chilton and Beamish 1982), was estimated using average percentage error (APE) (Beamish and Fournier 1981) and the average coefficient of variation (CV) (Chang 1982). Between the two readings, ~60 otolith specimens were not satisfactorily decipherable and were excluded from further analyses. The APE and average CV were computed by the following formula:

$$\text{APE} = \frac{1}{N} \times \sum_{j=1}^{N} \left[\frac{1}{R} \times \sum_{i=1}^{R} \frac{\left| X_{ij} - X_j \right|}{X_j} \right] \times 100$$

where N is the number of otoliths examined, R (= 2) is the number of times the fish were aged, X_{ij} is the i^{th} age determination of the j^{th} fish, and X_j is the mean age estimate for the j^{th} fish.

$$\text{CV} = \frac{1}{N} \times \sum_{j=1}^{N} \left[\frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R-1}}}{X_j} \right] \times 100$$

An age-bias plot was produced to visualise the deviation between the two repeated readings from the 1:1 equivalence line (Ogle 2017). Age estimates from the first reading were assumed to be reliable and hence considered as a reference. The mean (± SD) age estimates from the second reading (non-reference age) were plotted against the reference age (Ogle 2017).

Validation

Marginal increment analysis (MIA) was used to validate the periodicity of growth zone formation. The marginal increment is the width of the opaque macrozone on the edge divided by the mean width of that particular opaque zone in *O. niloticus* that were caught later having a similar number of growth zones and had completed their seasonal growth (Tekle-Giorgis and Casselman 1995). That time, when the relative marginal increment was lowest, was taken as the time of translucent zone formation. In addition, the time when there is a slight increase in a relative marginal increment is considered to be the period of completion of translucent zone formation (Tekle-Giorgis and Casselman 1995). The mean relative marginal increments widths per month were compared using a single factor ANOVA and a post hoc Tukey test. In addition to MIA, an edge analysis model was used to validate the periodicity of growth zone formation using R statistical software (detailed procedure in Okamura and Semba 2009). The model was fitted for scenarios with no peaks, one peak and two peaks per year. The model was fitted to the total number of otoliths examined and the number of otoliths in each month that had their translucent zone at the edge. The model with the lowest Akaike information criterion (AIC) value was taken as the best fit.

Back calculation

A regression analysis was used to test the relationship between the length of a fish and the radius of its otolith (Admassu and Casselman 2000). According to Maceina and Betsill (1987), the relationship between the otolith radius and fish length is expected to be proportional. A linear function was used to describe the relationship: $lj = bX_j + \alpha$, where: l_j = length of the fish (j) (cm), X_j = size of the corresponding otolith radius (mm) (Admassu and Casselman 2000; Gomez-Marquez et al. 2008). The parameters 'a' and 'b' were estimated using linear regression of log-transformed length measurements on the log-transformed radius of the otolith. Back calculations of a fish length corresponding to growth rings on otoliths were made using the Fraser-Lee formula (Maceina and Betsill 1987):

$$l_i = \left(\frac{D_i}{D_j}\right)^b \times l_j$$

where: l_i = back-calculated fish length at the ith macrozone, b = coefficient of the regression of ln (l_j) on ln (X_j), l_j = length at the capture of the fish, D_i = distance from the origin to i^{th} macrozone of the otolith, D_j = distance from the origin to the edge of the otolith (i.e. the radius of the otolith at the time of capture).

Fitting the von Bertalanffy growth curve to length at age data and estimation of growth parameters

The von Bertalanffy Growth Function (VBGF; von Bertalanffy 1938) was applied to sex-disaggregated length and age data and the results were tested for differences in at least one of the VBGF parameters between males and females. The hypothesis was examined for:

1. fitGen = $L_\infty(1 - \exp^{-K[sex] \times (age - t_0[sex])})$ — All of the VBGF parameters (L_∞, K and t_0) were different for both sexes,
2. fitKT = = $L_\infty \times [sex] \times (1 - \exp^{-K(age - t_0[sex])})$ — K and t_0 vary with sex,
3. fit1LT = $L_\infty \times [sex] \times (1 - \exp^{-K(age - t_0[sex])})$ — L_∞ and t_0 vary with sex,
4. fit1LK = $L_\infty \times [sex] \times (1 - \exp^{-K[sex] \times (age - t_0)})$ — L_∞ and K vary with sex,
5. fit2T = $L_\infty(1 - \exp^{-K(age - t_0[sex])})$ — only t_0 varies with sex,
6. fit2K = $L_\infty(1 - \exp^{-K[sex] \times (age - t_0)})$ — only K varies with sex,
7. fit2L = $L_\infty \times [sex] \times (1 - \exp^{-K(age - t_0)})$ — only L_∞ varies with sex, and,
8. fitCom = $L_\infty(1 - \exp^{-K(age - t_0)})$ — when all VBGF parameters were constant for both sexes.

The model fits were carried out using R statistical software and the model with lowest AIC was considered the best fit (Okamura and Semba 2009).

The VBGF was fitted to both observed and back-calculated length-at-age data (von Bertalanffy 1938): $L_t = L_\infty(1 - \exp^{-K(t - t_0)})$, where: L_t = length (TL) at age 't' (cm), L_∞ = asymptotic length of fish (cm), K = growth rate constant (per year), t = age of fish (years), t_0 = theoretical age of fish at 'zero' length (years). The parameters for this function were estimated with a non-linear curve fitting procedure using individual length at age datapoints instead of mean values of length at age. The value of growth performance in length ($Ø'L$) was calculated according to Munro and Pauly (1983): $Ø'L = \log(K) + (2 \times \log(L_\infty)$ and maximum age T_{max} was calculated as:

$$T_{max} = \frac{3}{K}$$

An age-at-length key was constructed by rounding the age to the nearest year and constructing a frequency table of samples for each age, where the age of fish could be reliably estimated from its length (Bwanika et al. 2007). Data for age-at-length keys were pooled without regard to sex, because *O. niloticus* in Lake Tana showed no difference in growth between male and female fish. The data for the age-at-length key were grouped into 1-cm length classes.

Results

Sampled specimen characteristics

In total, 1 597 fish samples were collected; 730 fish from Bahir Dar, 575 fish from Gumara and 292 fish from Gorgora. The total collection comprised 794 males and 803 females. The fish sizes ranged from 3.8 to 44 cm TL and from 1 to 1 594 g total weight (TW). Of the fish sampled 72% were ≤ 22 cm and 28% were ≥ 24 cm (Figure 2).

Time of translucent zone formation and age interpretation

Growth zones were visible as alternating opaque and translucent bands. Visibility of the translucent zones decreased as the fish length increased (Figure 3).

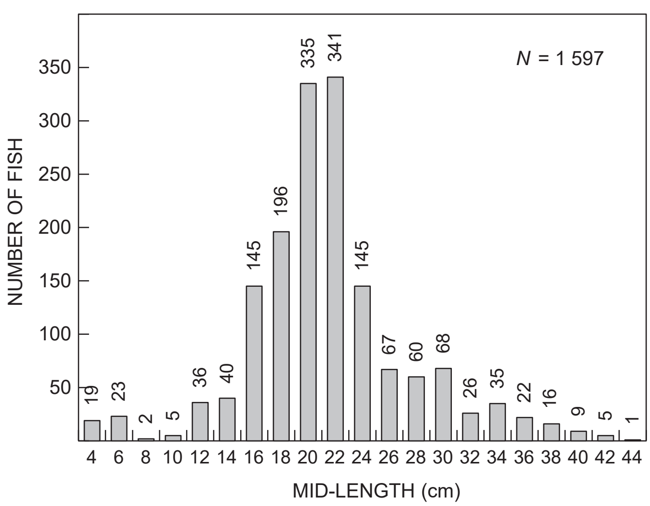

Figure 2: Length frequency distribution of *Oreochromis niloticus* in Lake Tana sampled from June 2016 to May 2017. Note: The numbers at the top of each bar represent the number of samples in each length group

Otoliths that had translucent zones at the margin were present in all sampling occasions, but their frequency of occurrence varied with season (Figure 4). Significantly higher percentages (monthly Chi-square values >197) of translucent zone occurrence were recorded in the main wet and dry seasons (June/July [summer] and January/ February [winter], respectively), ranging from 55 to 90%; percentages in remaining months were 10−35%.

The bimodal distributions of translucent zones with a first maximum in January/February and a second one in June/July (Figure 4), suggest that two translucent and two opaque zones were formed per year. There was a significant difference in the relative frequency of occurrence across months ($p < 0.05$, df = 11 and Chi-square ~264).

Age precision and age bias

The calculated values of the average percent error (APE) and the average coefficient of variation (CV) were 5.2% and 7.4%, respectively. In 71.4% of the otolith readings, the two readings were identical; in 28.4% of the readings they differed by only one annulus and in only 0.2% of the readings did they differ by two annuli. There was very little indication of bias in the age-bias plot (Figure 5), with most values close to the 1:1 line.

Validation

The marginal increment analysis revealed that, each year, two translucent and two opaque zones were formed in otoliths of *O. niloticus* in Lake Tana. The highest mean marginal increment ratios were observed in November,

Figure 3: Whole sagittal otolith of a 35.5 cm TL *Oreochromis niloticus* from Lake Tana with 12 translucent zones. Note: The otolith was viewed under reflected light and annuli are indicated by white dots

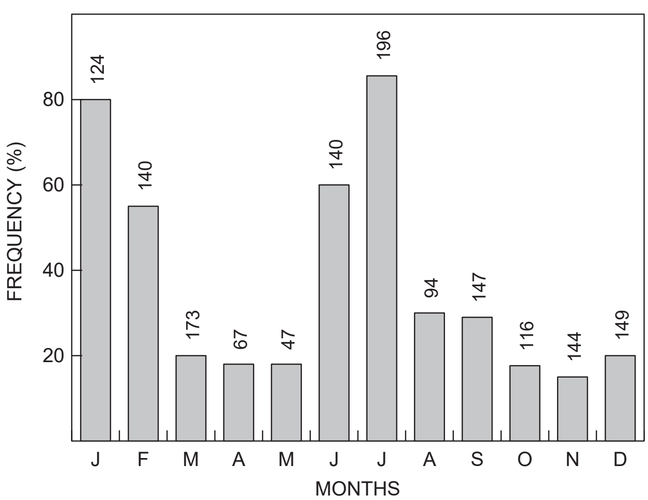

Figure 4: The relative frequency (%) in each month from June 2016 to May 2017 of otoliths of *Oreochromis niloticus* from Lake Tana with a translucent zone at the edge. Note: The number at the top of each bar is the number of otoliths examined in that month

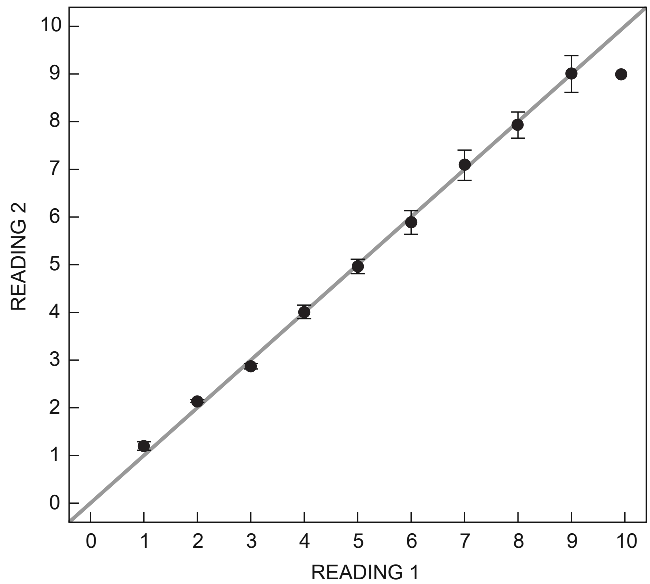

Figure 5: Age-bias plot of two readings per otolith of *Oreochromis niloticus* from Lake Tana from June 2016 to May 2017. Reading 1 was taken as reference. The numbers on the top horizontal axis indicate the number of otolith samples examined in each reference age group; the bars indicate the confidence interval

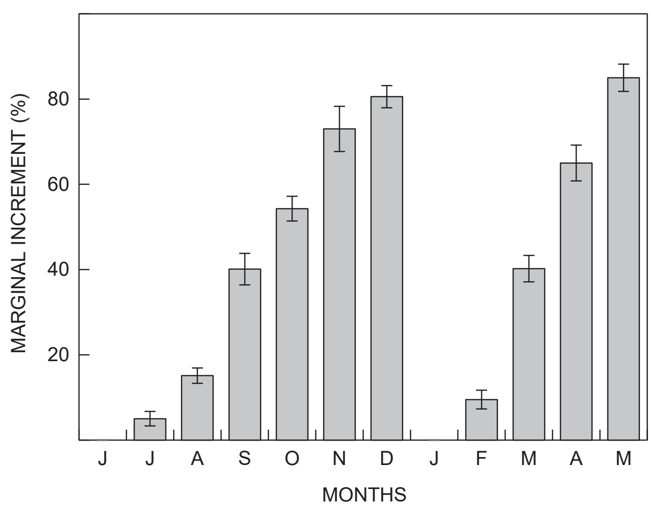

Figure 6: The mean (± SD) ratio (%) of the marginal increments in each month from June 2016 to May 2017 of otoliths of *Oreochromis niloticus* from Lake Tana

December and May (range 73–85%, $F_{(11,48)} = 259$, $p < 0.01$) and the lowest in June, July, January and February (range 0–10%) (Figure 6). The months with low marginal increment ratios were considered to be periods of translucent zone formation. The first translucent zone was formed in January/February, whereas the second was formed in June/July; an approximate six-month interval (Figure 6). The time when there was a slight increase in marginal increment ratios (March and August) was considered to be the period of completion of translucent zone formation. Accordingly, the number of translucent macrozones was back calculated from the date of capture to hind-cast the year class of each fish.

Edge analysis showed similar results to MIA, with two peaks formed; one in June/July and the other in January/February (Figure 7). This was confirmed by the edge analysis model fits, which gave the lowest AIC number (1758) for two peaks formed y^{-1} (Figure 7c), compared with no peaks (2079) and one peak (2026).

A linear regression between log-transformed TL (cm) and log-transformed otolith radius was significant (ANOVA, $F_{(1,119)} = 5\,917$, $p < 0.01$), indicating a close synchronisation between growth of somatic tissue and otoliths. The coefficient ($b = 1.26$) and intercept ($a = 0.55$) of the relationship were also significantly different from zero (t-test, $p < 0.01$) (Table 1).

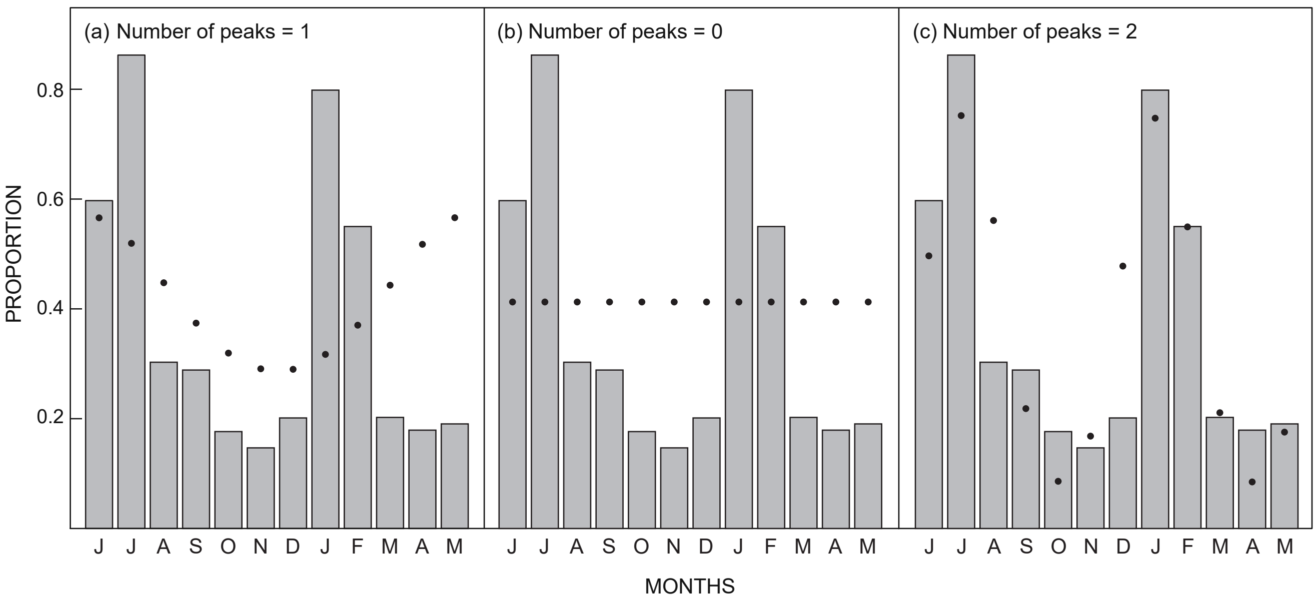

Figure 7: Results of the edge analysis showing the proportion in each month from June 2016 to May 2017 of otoliths with a translucent zone at the edge for *O. niloticus* from Lake Tana when (a) predicted number of peaks to be formed is one, (b) predicted number of peaks to be formed is zero, and (c) predicted number of peaks to be formed is two. Predicted values from three models fitted to the data are shown as circles; the best-fit model with the lowest AIC number is when two peaks formed per year

Table 1: Estimates of '*a*' and '*b*' from a linear regression relationship between log-transformed total length (TL, cm) and log-transformed otolith radius for *Oreochromis niloticus*

	Coefficients	Standard error	*t*-value	*p*-value	Lower 95%	Upper 95%
Intercept	0.554158	0.009113	60.81073	1.79 $\exp^{-91}$	0.536114	0.572203
x-variable	1.258664	0.016363	76.92254	2.6 $\exp^{-103}$	1.226264	1.291064

Table 2: The outputs of the VBGF parameters test for both sexes of *Oreochromis niloticus* from Lake Tana

Name of equation	Explanation	AIC
fitGen	All parameters were different for both sexes	6 692
Fit1KT	*K* and to varies with sex	6 690
fit1LT	L_∞ and to varies with sex	6 691
fit1LK	L_∞ and *K* varies with sex	6 692
fit2T	Only t_0 varies with sex	6 691
fit2K	Only *K* varies with sex	6 691
fit2L	Only L_∞ varies with sex	6 690
fitCom	All parameters were constant for both sexes	6 688*

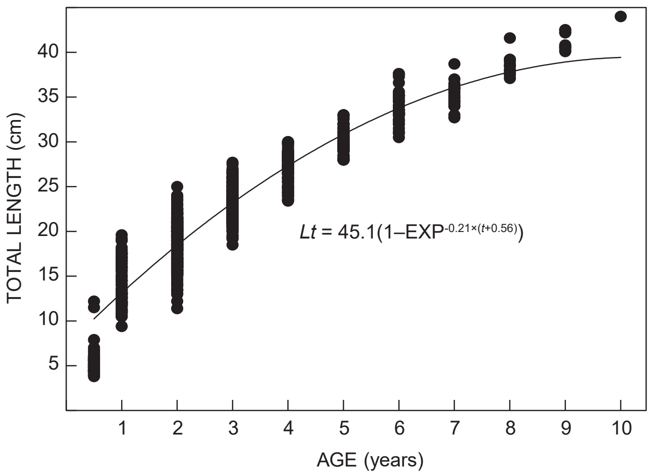

Figure 8: von Bertalanffy growth curve fitted to observed length-at-age data for *O. niloticus* in Lake Tana (June 2016 to May 2017)

Fitting the von Bertalanffy growth curve

The hypotheses that were tested for identifying sex-dependent VBGF parameters are summarised in Table 2, with the lowest AIC for the equation (fitCom) when all parameters were the same for both sexes.

The von Bertalanffy growth function (VBGF) was fitted to the observed length-at-age data (Figure 8, Table 3a), and back-calculated length-at-age data (Table 3b). The measured maximum TL value (44 cm) was between the calculated asymptotic length (L_∞) value (45 cm) and the back-calculated L_∞ value (43 cm). The fish had a relatively fast growth rate for the first four years, attaining 62% of their estimated L_∞; whereafter, the growth rate slowed down with an increase in age.

The maximum age or longevity estimated for *O. niloticus* in Lake Tana was 14.3 years. The value of growth performance in length (Ø′L) was 2.63 cm y^{-1}. The length-at-age key of *O. niloticus* is presented in Table 4. Because estimated parameters were similar for both males and females, the two sexes were pooled.

Table 3: Estimated von Bertalanffy growth parameters for observed (a) and back-calculated (b) length-at-age data for *Oreochromis niloticus* with a 95% confidence interval

Parameter	Estimated parameter	SE	95% Confidence interval	
			Lower bound	Upper bound
(a)				
K (y^{-1})	0.208	0.006	0.197	0.219
L_∞ (cm)	45.100	0.571	43.900	46.200
t_0 (years)	−0.565	0.031	−0.625	−0.504
(b)				
K (y^{-1})	0.226	0.004	0.217	0.234
L_∞ (cm)	43.400	0.427	42.600	44.200
t_0 (years)	−0.514	0.013	−0.540	−0.488

Table 4: Length-at-age-key for combined sexes of *Oreochromis niloticus* from Lake Tana (June 2016 to May 2017) giving the number of fish in 1–cm length categories as a function of age

Length	Age (years)											
Group	0+	1	2	3	4	5	6	7	8	9	10	Total
3–4	19											19
5–6	23											23
7–8	2											2
9–10		5										5
11–12		29	6									35
13–14		17	23									40
15–16		14	129									143
17–18		13	171	1								185
19–20		7	295	21								323
21–22			122	196								318
23–24			14	111	14							139
25–26			1	45	20							66
27–28				3	46	9						58
29–30				1	9	56	2					68
31–32						15	10	1				26
33–34						3	21	10				34
35–36							8	14				22
37–38							4	2	10			16
39–40									3	6		9
41–42									1	4		5
43–45											1	1
Total	44	85	761	378	89	83	45	27	14	10	1	1 537

Age groups 2 and 3 years were dominant in the catch and constituted ~49.5% and 24.6%, respectively, whereas age groups 8, 9 and 10 years contributed only 0.9%, 0.7% and 0.1%, respectively (Table 4).

Discussion

Biannuli formation

In the current study, the translucent zone was formed twice y^{-1} in otoliths of *O. niloticus* from Lake Tana. This was validated with marginal-increment and edge analyses. Translucent zones associated with biannuli were formed in January/February and June/July. Several investigators have shown the formation of two annuli y^{-1} in calcified tissues of fish (Willoughby 1974; Warburton 1978; Admassu 1998; Tekle-Giorgis 1990; Alemu 1995; Tekle-Giorgis and Casselman 1995; Admassu and Casselman 2000; Bwanika et al. 2007). However, in another cichlid species (*Tropheus moorii*) Egger et al. (2004) reported formation of a single annulus y^{-1}. Clearly, there is variation among species, and several hypotheses explaining the timing of annulus formation have been reported, including seasonal changes in temperature (Tekle-Giorgis and Casselman 1995; Admassu 1998; Grammer et al. 2012), annual variation in food quality (Tekle-Giorgis 1990; Alemu 1995; Tekle-Giorgis and Casselman 1995), and fluctuation of body condition associated with spawning (Tekle-Giorgis and Casselman 1995; Jiménez Badillo 2006; Gomez-Marquez 2008).

Water temperature is one of the most prominent factors in annulus formation in calcified tissues of fish, and previous studies have indicated strong effects of water temperature on the growth of *O. niloticus*. For example, Teichert-Coddington et al. (1997) showed that *O. niloticus* achieved optimal growth at 28−36 °C, and growth declined with decreasing temperature; and Admassu (1998) showed that a temperature change of ~−5 °C affected the growth of *O. niloticus*. Lake Tana has a minimum and maximum water temperature of 20 °C in January and 27 °C in May, respectively (Dejen 2003). The minimum water temperature recorded coincided with the time of one of the two biannuli formation during January and February. Seasonal fluctuations in water temperature were also proposed to explain the formation of biannuli in the otoliths of the immature *O. niloticus* from Lake Hawassa (Tekle-Giorgis and Casselman 1995). One of the two annuli was formed in *O. niloticus* of Lake Ziway with the difference between the yearly maximum and minimum temperature between 5 °C and 6 °C. Moreover, Admassu (1998) confirmed that a temperature variation of approximately 3 °C to 5 °C, had affected the growth of *O. niloticus*. In addition, Gomez-Marquez (1998) reported the formation of two translucent zones in *O. niloticus* with one formed in December-January when the water temperature was 21 °C. Furthermore, the maximum temperature (27.7 °C) and minimum temperature (24.4 °C) of the year in Lake Tanganyika decelerated growth rate of *T. moorii* and caused growth zone formation (Egger et al. 2004). Therefore, the lower temperature in Lake Tana from January to February, recorded by Dejen (2003), may account for the formation of the translucent zone in the otoliths of *O. niloticus* seen in this study during this period.

Availability of food is another factor that may contribute to annuli formation. Admassu (1998) and Tekle-Giorgis (1990) reported the formation of checks on scales and translucent zones on otoliths of *O. niloticus* from Lake Hawassa, with slow growth due associated with reduced quality of food consumed. This observation is also supported by the study by Alemu (1995) in Lake Hayq (Ethiopia). In Lake Tana, *Aulacoseira*, *Navicula*, *Nitzschia*, *Microcystis*, *Scenedesmus*, *Pediastrum* and *Chroococcus* spp. are the most important algal groups consumed by *O. niloticus* (Tadesse 2011). These phytoplankton species, mainly bloom in post-rainy and dry seasons, whereas they are rare in the rainy season of the year (Wondie and Akoma 2008). It is during the latter period that one of the two biannuli is formed in the otoliths of *O. niloticus.*

The breeding season for *O. niloticus* is typically from April to August with a peak spawning in June/July (Tadesse 1997), which corresponds with one period of translucent zone formation. This is most likely related to the mouthbrooding behaviour of *O. niloticus,* resulting in reduced feeding by the female, whereas males are engaged in building and guarding spawning sites, as well as fertilizing numerous females during this period (Jiménez Badillo 2006; Gomez-Marquez 2008). Therefore, in Lake Tana, the reproductive period could be one of the factors contributing to one of the two translucent zone formations on *O. niloticus* otoliths. In addition, in Lakes Hawassa, Hayq and Ziway formation of translucent macrozones in *O. niloticus* otoliths also corresponded with the major spawning seasons of the species (Admassu 1998).

Growth parameters estimation

The estimated age-length relationship for *O. niloticus* in Lake Tana was comparable to that in Lake Hayq (Admassu 1988), lower than in Lake Koka (Tesfaye and Wolff 2015; Table 5) and higher that at least two other Ethiopian Rift Valley lakes (Admassu 1998; Tesfaye and Wolff 2015). Under favourable conditions, *O. niloticus* in tropical lakes can attain lengths of 14–16 cm in a year (Rinne 1976). Variation in food quantity and quality, water temperature, and population densities of *O. niloticus* among water bodies may result in variation in the growth of this species. Additional information on the quality and quantity of food consumed by Lake Tana *O. niloticus* is needed to compare and contrast its growth with fish in other habitats (i.e. the same species in other places). Fishing pressures also affect the growth of fish (Ojuok et al. 2007).

The value of L_∞ estimated in this study is within the range of that reported for *O. niloticus* in Ethiopian and other African water bodies (Getabu 1992; Admassu 1998; Tesfaye 2006; Tesfaye and Wolff 2015; Table 6). The estimated L_∞ value approximated the size of the largest fish caught in this study. Similar results were reported from Lake Ziway with L_∞ of 28.1 cm and maximum length of 27 cm (Tesfaye 2006). When comparing growth parameters of *O. niloticus* to a previous study in Lake Tana (Wudneh 1998), the L_∞ value was lower and the *K*-value was higher than in the earlier study. This could be related to differences in sampling and method of calculation. Wudneh (1998) restricted his study to the southern Gulf of the lake and used a bottom trawl. Although Wudneh (1998) did not mention the depth (in

Table 5: Length attained (cm) by *Oreochromis niloticus* at age one to five years in Ethiopian water bodies

Waterbody authority	Lake Tana Current study	Ziway Admassu (1988)	Hawassa Admassu (1988)	Hayq Admassu (1988)	Koka Tesfaye and Wolff (2015)
Age					
1	12.5	8.1	9.1	14.0	19.0
2	18.6	13.2	15.7	21.4	27.6
3	23.6	17.2	20.4	26.3	33.3
4	27.6	20.2	23.4	29.5	37.1
5	30.9	22.6	26.0	31.6	39.6

*NB. Estimated lengths were calculated from respective von Bertalanffy growth equations and not from the observed length at age data

Table 6: von Bertalanffy growth parameters and growth performance of *Oreochromis niloticus* from different African waterbodies lakes according to different authors

L_∞ (cm)	K (y^{-1})	Ø'L	Lakes	Reference
45.1	0.21	2.63	Tana	Current study
35.7	0.50	2.83	Tana	Wudneh (1998)
36.6	0.80	3.00	Hayq	Admassu (1998)
32.1	0.31	2.51	Langano	Tesfaye (2006)
36.6	0.40	2.73	Koka	LFDP (1997)
44.1	0.26	2.70	Koka	Tesfaye (2006)
44.5	0.41	2.90	Koka	Tesfaye and Wolff (2015)
28.1	0.43	2.53	Ziway	Tesfaye (2006)
30.2	0.50	2.70	Ziway	Admassu (1998)
35	0.28	2.54	Hawassa	Admassu (1998)
64.6	0.25	3.00	Victoria	Getabu (1992)
71.5	0.14	2.80	Itassy	Moreau (1979) in Getabu 1992

metres) of the lake nor the depth that the trawling occurred, trawling was performed at the open part of the lake with the greatest depth. *Oreochromis niloticus* lives in the shallow periphery of the lake and it may have been inadequately sampled with a bottom trawl in their study (Kayanda et al. 2009). During this study period, Nile tilapia were also observed to inhabit the periphery of the lake, where vegetation was available. In addition, large fish were rare in Wudneh's (1998) study (range: 8–30 cm TL), compared with the current study (range: 3.8–44 cm TL). Moreover, estimates of L_∞ and K were made from back-calculated lengths in Wudneh (1998).

In Lake Koka, different growth parameters were estimated for *O. niloticus* at different times. L_∞ and K estimated by LFDP (1997) and Tesfaye (2006) were 36.6 cm, 0.40 and 44.1 cm, 0.26, respectively. A recent investigation in the same waterbody reported 44.5 cm and 0.41 values for L_∞ and K, respectively (Tesfaye and Wolf 2015). Sampling methods and method of ageing (age-based or length-frequency) could have contributed to the difference in growth parameters. In Lake Koka, the estimated values of L_∞ and K using an age-based method (44.1 cm y^{-1} and 0.26 cm y^{-1}) were lower than from a length frequency method (45.5 cm y^{-1} and 0.36 cm y^{-1}), respectively (Tesfaye 2006). It is also possible that the growth rate varied, because of variation in food conditions or *O. niloticus* population densities.

In Lake Tana, *O. niloticus* attained L_∞ rather slowly (K = 0.21 y^{-1}), compared with other tilapia populations in Ethiopian lakes (Table 6). This could be owing to the oligo-meso trophic nature of the lake (Dejen et al. 2004), resulting in the low growth of *O. niloticus*. Furthermore, the gross primary production rates of Lake Tana are among the lowest reported for tropical lakes (Wondie et al. 2007). Of all the 100 stocks evaluated by Moreau et al. (1986), the K values of *O. niloticus* ranged from 0.14 y^{-1} in Lake Itassy to 0.59 y^{-1} in Lake Mariut. Hence, our estimated value of K is within the range mentioned in tropical African lakes.

Conclusions and recommendations

In Lake Tana, the *O. niloticus* population deposited biannuli each year, one in January/February and the other in June/July. Edge analysis and MIA confirmed the formation of biannuli and their frequency was the lowest in months when the frequency of translucent zones at the edge of the otolith was highest and vice versa. The values of L_∞, K, and t_0 from the observed age-at-length data were 45.1 cm, 0.21 y^{-1} and −0.56 years, respectively. These may be used for additional mortality analyses and stock assessment of *O. niloticus* in Lake Tana. Future studies should include slicing of otoliths from mature *O. niloticus* and inclusion of more immature fish for microzone analysis for accurate estimation of existing stocks and their age.

References

Admassu D. 1998. Age and growth determination of tilapia, *Oreochromis niloticus* L. (Pisces: Cichlidae) in some lakes in Ethiopia. PhD thesis, Addis Ababa University, Ethiopia.

Admassu D, Casselman J. 2000. Otolith age determination for adult tilapia, *Oreochromis niloticus* L. from Lake Awassa (Ethiopian Rift Valley) by interpreting biannuli and differentiating biannual recruitment. *Hydrobiologia* 418: 15–24. https://doi.org/10.1023/A:1003883419105.

Alemu K. 1995. Age and growth of *Oreochromis niloticus* (Pisces: Cichlidae) in Lake Hayq, Ethiopia. MSc thesis, Addis Ababa University, Ethiopia.

Al-Kiyumi F. 2013. Biology and fisheries assessment of the Arabian Pandora (*Pagellus Affinis*) (Boulenger, 1887) in the Arabian Sea, Sultanate of Oman. PhD dissertation, University of Tasmania, Sultanate of Oman.

Ameha A, Aragaw C, Mingist M, Goshu G. 2017. The fish and the fisheries of Lake Tana. pp.157–177. In: Stave K, Goshu G and Aynalem S (Eds). *Social and ecological system dynamics: Characteristics trends, and integration in the Lake Tana basin, Ethiopia*. Cham, Switzerland: Springer International Publishing Ag.

Beamish R, Fournier D. 1981. Method for comparing the precision of a set of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*. 38: 982–983. https://doi.org/10.1139/f81-132.

Bokhutlo T. 2011. Life-History and Stock Assessment of *Clarias gariepinus* in the Okavango Delta, Botswana. MSc thesis, Rhodes University, South Africa.

Bwanika GN, Murie DJ, Chapman LJ. 2007. Comparative age and growth of Nile tilapia (*Oreochromis niloticus* L.) in lakes Nabugabo and Wamala, Uganda. *Hydrobiologia* 589: 287–301. https://doi.org/10.1007/s10750-007-0746-y.

Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59: 197–242. https://doi.org/10.1111/j.1095-8649.2001.tb00127.x.

Chang W. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1208–1210. https://doi.org/10.1139/f82-158.

Chilton D, Beamish R. 1982. Age determination methods for fisheries studies by the groundfish program at the pacific biological station. *Canadian Special Publication of Fisheries and Aquatic Sciences* 60: 1–102.

de Graaf M. 2003. Lake Tana's Piscivorous Barbs (Cyprinid, Ethiopia) PhD thesis, Wageningen University, The Netherlands.

Dejen E. 2003. Ecology and potential for fishery of the small barbs (Cyprinidae, Teleostei) of Lake Tana, Ethiopia. PhD thesis, Wageningen University, The Netherlands.

Dejen E, Vijverberg J, Sibbing F. 2004. Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (Lake Tana, Ethiopia). *Hydrobiologia.* 513: 39−49. https://doi.org/10.1023/B:hydr.0000018163.60503.b8.

Dejen E, Anteneh W, Vijverberg J. 2017. The decline of the Lake Tana (Ethiopia) fisheries: causes and possible solutions. *Land Degradation & Development* 28: 1842–1851. https://doi.org/10.1002/ldr.2730

Egger B, Meekan M, Salzburger W, Mwape L, Makasa L, Shapola R, Sturmbauer C. 2004. Validation of the periodicity of increment formation in the otoliths of a cichlid fish from Lake Tanganyika, East Africa. *Journal of Fish Biology* 64: 1272–1284. https://doi.org/10.1111/j.0022-1112.2004.00390.x.

Getabu A. 1992. Growth parameters and total mortality in *Oreochromis niloticus* (Linnaeus) from Nyanza Gulf, Lake Victoria. *Hydrobiologia* 232: 91–97. https://doi.org/10.1007/BF00014617.

Getahun A, Dejen E. 2012. Fishes of Lake Tana, a guide book. Addis Ababa, Ethipia: Addis Ababa University Press

Gomez-Marquez J. 1998. Age and growth of *Oreochromis niloticus* (Perciformes: Cichlidae) in Mexico. *Revista de Biologia Tropical* 46: 929–936.

Grammer G, Slack W, Mark S, Peterson, M, Dugo M. 2012. Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) establishment in temperate Mississippi, USA: multi-year survival confirmed by otolith ages. *Aquatic Invasions*. 7: 367–376. http://dx.doi.org/10.3391/ai.2012.7.3.008

Greenwood PH. 1976. Fish fauna of the Nile. (pp 127–141). In: Rzoska J (Ed.). *The Nile, biology of an ancient river.* The Hague, The Netherlands: Dr. W. Junk Publishers. https://doi.org/10.1007/978-94-010-1563-9_18.

Gomez-Marquez JL, Pena-Mendoza B, Salgado-Ugarte IH, Arredondo-Figueroa JL. 2008. Age and growth of the tilapia, *Oreochromis niloticus* (Perciformes: Cichlidae) from a tropical shallow lake in Mexico. *Revista de Biologia Tropical* 56: 1–9.

Hyuha T, Ekere W, Egna H, Molnar JJ. 2017. Social and economic performance of tilapia farming in Uganda. (pp 127–144). In: Cai J, Quagrainie KK, Hishamunda N (Eds). *Social and economic performance of tilapia farming in Africa.* FAO Fisheries and Aquaculture Circular No. 1130. Rome, Italy: FAO.

Jiménez Badillo L. 2006. Age-growth models for tilapia *Oreochromis aureus* (Perciformes, Cichlidae) of the Infiernillo reservoir, Mexico and reproductive behaviour. *Revista de Biología Tropical* 54: 577–588. https://doi.org/10.15517/rbt.v54i2.13923.

Kayanda R, Anthony M, Taabu A, Tumwebaze A, Muhoozi L, Jembe T, Muhoozi E, Nzungi P. 2009. Status of the major commercial fish stocks and proposed species-specific management plans for Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries* 12: 15–21.

Kolding J. 1993. Population dynamics and life-history styles of Nile tilapia, *Oreochromis niloticus*, in Ferguson's Gulf, Lake Turkana, Kenya. *Environmental Biology of Fishes* 37: 25–46. https://doi.org/10.1007/BF00000710.

LFDP (Lake Fisheries Development Plan). 1997. National fisheries seminar working paper, No.25. Ethiopia: Ethiopian Ministry of Agriculture.

Maceina J, Bestil RK. 1987. Verification and use of the whole otoliths to age white crappie. (pp 267–278). In: Summerfelt C, Hall G (Eds). *Age and Growth of Fish*. Ames, Iowa State University Press.

Moreau J, Bambino C, Pauly, D. 1986. A comparison of four indices of overall fish growth performance based on 100 tilapia (Cichlidae) populations. (pp 201–206). In: Maclean J, Dizon L, Hosillos L (Eds). *First Asian Fisheries form*. Manila, Philippines: Asian Fisheries Society.

Munro J, and Pauly D. 1983. A simple method for comparing the growth of fishes and Invertebrates. *The World Fish Center* 1: 5–6.

Ogle D. 2017. Modified age bias plot. Available at http://derekogle.com/fishR/2017-04-14-Modified_AgeBiasPlot. [Accessed 10 May 2018].

Ojuok JE, Njiru M, Ntiba MJ, Mavuti KM. 2007. The effect of overfishing on the life-history strategies of Nile tilapia, *Oreochromis niloticus* (L.) in the Nyanza Gulf of Lake Victoria, Kenya. *Aquatic Ecosystem Health & Management* 10: 443–448. https://doi.org/10.1080/14634980701708107.

Okamura H, Semba Y. 2009. A novel statistical method for validating the periodicity of vertebral growth band formation in elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 66: 771–780. https://doi.org/10.1139/F09-039.

Panfili J. 2001. Validation of age estimation and back-calculation of fish length based on otolith microstructures in tilapias (Pisces, Cichlidae). *Fish Bulletin* 99: 139–150.

Reyntjens D, Mengistu T, Wudneh T. 1998. Fisheries development in Ethiopia-Which way now? *European Commission Fisheries Bulletin* 11: 20–22.

Rinne JN. 1976. Coded spine clipping to identify individuals of the spiny-rayed fish Tilapia. *Journal of the Fisheries Board of Canada* 33: 2626–2629. https://doi.org/10.1139/f76-313.

Rzoska J (Ed.). 1976. *The Nile, biology of an ancient river*. The Hague, The Netherlands: Dr W Junk Publisher. https://doi.org/10.1007/978-94-010-1563-9.

Stevenson DK, Campana, SE (Eds). 1992. *Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences* 117: 126 p. Ottawa, Canada: Canada Communication Group Publishing.

Tadesse Z. 1997. Breeding season, fecundity, length-weight relationship and condition factor of *Oreochromis niloticus* L. (Pisces: Cichlidae) in Lake Tana, Ethiopia. *Sinet. An Ethiopian Journal of Science* 20: 31–47. https://doi.org/10.4314/sinet.v20i1.18090.

Tadesse Z. 2011. Diel feeding rhythm, ingestion rate and diet composition of *Oreochromis niloticus* L. in Lake Tana, Ethiopia. (pp 59–66). In: Lemma B, Getahun A (Eds). *Impacts of climate change and population on tropical aquatic resources*. Proceedings of the 3rd International Conference of the Ethiopian Fisheries and Aquatic Sciences Association (EFASA). Addis Ababa, Ethiopia: AAU Printing Press.

Tedla S. 1973. Freshwater Fishes of Ethiopia. Haile Selassie I University, Addis Ababa.

Tefera D, Zerihun M and Wolde-Meskel Y. 2019. Catch distribution and size structure of Nile tilapia (*Oreochromis niloticus*) in Lake Tana, Ethiopia: implications for fisheries management. *African Journal of Aquatic Science* 44: 273–280. https://doi.org/10.2989/16085914.2019.1637710.

Teichert-Coddington DR, Popma TJ, Lovshin LL. 1997. Attributes of tropical pond cultured fish. (pp 183–198). In: Enga HS, Boyd, CE (Eds). *Dynamics of pond aquaculture.* Boca Raton, Florida, USA: CRC Press.

Tekle-Giorgis Y.1990. Age determination and growth estimation of immature *Oreochromis niloticus* Linn. (Pisces: Cichlidae) in Lake Awassa, Ethiopia. MSc thesis, University of Waterloo, Waterloo, Canada.

Tekle-Giorgis Y, Casselman JM. 1995. Increasing the precision of otolith age determination for tropical fish by differentiating biannual recruitment. (pp 247–269). In: Dean JM, Campana SE (Eds). *Recent developments in fish otolith research*. Columbia: University of South Carolina Press.

Tesfaye G. 2006. Population dynamics and stock assessment of Nile tilapia *Oreochromis niloticus* L. in three Rift Valley Lakes (Koka, Ziway and Langano), Ethiopia. MSc thesis, University of Bremen, Germany.

Tesfaye G, Wolff M. 2015. Stock assessment of fishery target species in Lake Koka, Ethiopia. *International Journal of Tropical Biology and Conservation* 63: 755–770.

Tewabe D. 2013. Status of Lake Tana commercial fishery, Ethiopia. *ABC Research Alert* 1: 1−16.

Vijverberg J, Sibbing F, Dejen E. 2009. Lake Tana: Source of the Blue Nile. (pp 163–192). In: Dumont H (Ed.). *The Nile: Origin, environments, limnology and human use.* Springer Science + Business Media BV. Dordrecht, The Netherlands: Springer Science + Business Media BV.

Vijverberg J, Dejen E, Getahun A, Nagelkerke L.2012. The composition of fish communities of nine Ethiopian lakes along a north-south gradient: threats and possible solutions. *Animal Biology (Leiden, Netherlands)* 62: 315–335. https://doi.org/10.1163/157075611X618246.

von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Human Biology* 10: 181–213.

Warburton K. 1978. Age and growth determination in marine catfish using an otolith check technique. *Journal of Fish Biology* 13: 429–434. https://doi.org/10.1111/j.1095-8649.1978.tb03451.x.

Willoughby NG. 1974. The ecology of the genus Synodontis (Pisces: Silluroidei) in Lake Kainji, Nigeria. PhD thesis, University of Southampton, United Kingdom.

Wondie A, Akoma O. 2008. Seasonal variation of phytoplankton biomass in Lake Tana (Ethiopia). *Tropical Freshwater Biology* 17: 21–31.

Wondie A, Mengistu S, Vijverberg J, Dejen. 2007. Seasonal variation in primary production of a large high-altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency. *Aquatic Ecology* 41: 195–207. https://doi.org/10.1007/s10452-007-9080-8.

World Bank. 2012. The Hidden Harvests: The Global Contribution of Capture Fisheries. management and development. FAO Fisheries Representatives, (289) Supply 2. Washington DC, USA: World Bank.

Wudneh S. 1998. Biology and management of fish stocks in Bahir Dar Gulf, Lake Tana, Ethiopia. PhD thesis, Wageningen Agricultural University, the Netherlands.

Younes A, Mohamed L, Eida MF, Gaafar A. 2015. Characterization and pathogen challenge of Pseudomonas species from *Oreochromis niloticus* in Egypt. *Research Journal of Pharmaceutical, Biological and Chemical Sciences* 6: 312–317.

Manuscript received: 19 February 2019; revised: 10 March 2020; accepted: 26 March 2020
Associate Editor: L Chapman