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Age validation, growth and mortality of introduced *Tilapia zillii* in Crater Lake Nkuruba, Uganda

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Abstract Periodicity and timing of opaque zone formation in otoliths of introduced redbelly tilapia, *Tilapia zillii* (Gervais), in Crater Lake Nkuruba, Uganda, were validated using marginal increment. Age and growth were assessed through readings of biannuli in thin-sectioned sagittal otoliths. Deposition of opaque zone formation in *T. zillii* otoliths was bimodal (March–May and September–November), corresponding to two seasonal peaks of precipitation characteristic of this equatorial region. Ages of *T. zillii* ranged from 2 to 8 years, with fish gillnetted offshore having a faster growth and attaining larger size-at-age than fish captured inshore in minnow traps, suggesting that use of multiple gears is needed when estimating the growth of *T. zillii*. Total instantaneous mortality (*Z*), estimated using catch curve analysis, was 0.74 for gillnetted fish and 0.71 for trapped fish. These estimates were at the low end of the total mortality reported for other tilapia species. Natural mortality (*M*) was estimated as 0.52–0.54 by applying Rikhter and Efanov's maximum age at maturity and Hoenig's maximum age methods, respectively. Fishing mortality (*F*) in Lake Nkuruba was 0.17–0.22, indicating a low exploitation level in the lake.

KEYWORDS: ageing, cichlid fishes, growth, life history, tropical lakes.

Introduction

While the African Great Lakes, such as lakes Victoria, Tanganyika and Malawi, have been the focus of numerous scientific investigations (Beadle 1981; Lowe-McConnell *et al.* 1992), much less attention has been paid to minor water bodies in the region that can be reservoirs for diverse natural fish stocks that also provide protein, employment, income and contribute to improved rural livelihoods. In Uganda alone, there are about 160 minor lakes that collectively contribute about 416 757 t of fish to the national fish production (Department of Fisheries Resources 2010/2011). Of these, approximately 89 are small volcanic crater lakes that lie along the foothills of the Rwenzori Mountains that separate East Africa from the Congo basin. Three tilapia species, Nile tilapia *Oreochromis niloticus* (L.), blue-spotted tilapia *Oreochromis leucostictus* (Trewavas) and redbelly tilapia *Tilapia zillii* (Gervais), were introduced into several of these lakes in the 1940s, 1960s and sporadically in later years to increase available protein to the local communities. Of the three introduced tilapia species, *T. zillii* is the most abundant in the catches of the artisanal fisheries (Efitre 2007; Efitre *et al.* 2009). The lakes also vary in their limnological features, accessibility, extent of catchment deforestation and fishing pressure. Physical and chemical properties, primary productivity, phytoplankton, and zooplankton communities of many of these lakes have been studied in the last 50 years (Beadle 1963, 1981; Visser 1965; Melack 1978; Kizito *et al.* 1993;

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Kizito & Nauwerck 1995, 1996; Chapman *et al.* 1998; Efitre 2007; Efitre *et al.* 2009; Saulnier-Talbot *et al.* 2014), but the fish faunas of these lakes (both native and introduced) have received little attention. Currently, many of these lakes are producing stunted tilapia populations, causes of which remain unknown but may reflect resource limitations associated with the crater lake environment and/or low mortality leading to high levels of intraspecific competition resulting in density-dependent growth. An understanding of variation in important life-history traits of tilapias such as growth and mortality is of great importance to management of introduced and native populations. Validated age and growth studies of *T. zillii* in African natural waters using otolith microincrement structure are not available, but critical to understanding life-history variation within and across lakes.

The paucity of validated age and growth studies in tropical fish species using otoliths and other calcified structures has been attributed to a widespread assumption that growth of tropical fish is rather consistent due to the weak temperature fluctuations characteristic of many tropical environments (Brothers 1979). However, recent studies of tropical fish species have demonstrated that variation in climatic conditions in tropical regions may lead to the deposition of one annulus (one macrozone per year) such as in *Tropheus moorii* (Boulenger) in Lake Tanganyika (Egger *et al.* 2004) and *Tilapia mariae* (Boulenger) in northern Australia (Russell *et al.* 2013) or biannuli (2 macrozones per year) such as in the Nile tilapia in Ethiopian lakes (Yosef & Casselman 1995; Admassu & Casselman 2000) and in Lake Nabugabo in Uganda (Bwanika *et al.* 2007). Both abiotic and biotic factors have been suggested as possible causes of formation of these growth zones (Beckman & Wilson 1995) including wet-and-dry seasonal cycles (Bwanika *et al.* 2007), regular seasonal variation in temperature in some tropical regions (Blake & Blake 1978; Panella 1980; Yosef & Casselman 1995; Russell *et al.* 2013), variation in total dissolved solids (Fagade 1974), photoperiod, feeding patterns, and spawning period (e.g. Morales-Nin & Ralston 1990), and spawning activity and associated body condition (Nekrasov 1980; Booth *et al.* 1995). These studies emphasise the need to validate the deposition of macrozones on calcified structures of tropical species on a species- and region-specific basis (Beamish & McFarlane 1983, 1987), prior to applying ages to growth or mortality estimates.

The goal of this study was to estimate growth and mortality of *T. zillii* in the equatorial Crater Lake Nkuruba, Uganda, as a means to evaluate the potential of crater lakes to contribute to local fish production. The specific objectives were as follows: (1) to develop criteria for interpreting opaque zones and growth at the edge of the otoliths, (2) to validate the periodicity and timing of opaque zone formation within otolith sections and (3) to use the validated ageing method to estimate growth and mortality of the *T. zillii* population within Crater Lake Nkuruba.

Materials and methods

Study area

Crater Lake Nkuruba is a small (surface area 3 ha) mesotrophic freshwater lake that belongs to the Kasenda cluster of volcanic crater lakes in western Uganda, located at 0° 32′ N and 30° 19′ E. Maximum and mean depths of the lake are 37 and 16 m, respectively. Surface water temperature in Lake Nkuruba has averaged 23.7 °C between March 1992 and February 2012 (range = 21.4–25.5 °C), dissolved oxygen concentration has averaged 6.3 mg L^{-1} or 92.3% saturation (range = 0.4–12.1 mg L^{-1}, 5.7–179.9% saturation), and water transparency (Secchi disc range) has averaged 2 m (range = 1.4–2.9, Saulnier-Talbot *et al.* 2014; L. Chapman, unpublished data). The lake is anoxic below 8–15 m depending on the season (Kizito *et al.* 1993; Chapman *et al.* 1998; Saulnier-Talbot *et al.* 2014). Total phosphorus concentration of surface water ranged from 38 to 43 µg L^{-1} during the period 1990–1992 (Kizito *et al.* 1993) during which time chlorophyll a concentration of surface water was low (range 9–22 µg L^{-1}). Aquatic macrophytes are limited to a very small area on the eastern shore of the lake and the crater wall, averaging about 48 m above the water surface, is characterised by a rich forest of large tropical trees.

Rainfall is bimodal, with two wet seasons from March to May and September to November (Chapman *et al.* 2010), with an average of 1643 mm of rainfall received annually (1990–2013; data recorded at the Makerere University Biological Field Station in Kibale National Park, C. A. Chapman and L. J. Chapman, unpublished data). Between 1990 and 2013, the mean daily minimum air temperature was 15.5 °C, and the mean daily maximum air temperature was 23.7 °C.

Two tilapia species, *O. leucostictus* and *T. zillii*, as well as the guppy *Poecilia reticulata* (Peters), were introduced into the lake in the 1940s and 1960s to improve protein sources for the local people and to control malaria-causing mosquitoes, respectively; there are no records of further introductions in Lake Nkuruba since that time. There is no gillnet fishery in Lake Nkuruba; harvest is regulated through activities of the Lake Nkuruba Nature Reserve and Ecotourism project. A small number of fishers (<30) use hook-and-line to fish in the lake.

Fish collections and processing

A total of 450 *T. zillii* were collected during a 12-month period between July 2005 and July 2006, with fish captured approximately every 2 weeks. Fishing gears used included the following: (1) two experimental monofilament gillnets, each 30 m long comprised of four panels of 25.4, 50.8, 76.2 and 101.6 mm stretched mesh, respectively; (2) one artisanal fisher multifilament gillnet (1800 m long) comprised of mesh sizes 25.4, 50.8, 63.5 and 76.2 mm; and (3) 20 metal minnow traps (450 mm long and 7-mm square wire mesh, with an opening size of 25.4–38.1 mm). The experimental gillnets and traps were set between 14:00 and 16:00 h and lifted the following morning between 08:00 and 10:00 h. To obtain samples representative of the entire fish population in the lake, one experimental gillnet was set parallel to the shoreline (about 20 m offshore), the second experimental gillnet was set offshore in deeper waters, and the minnow traps were set in the shallow shoreline areas. The long multifilament net was set around the perimeter of the lake and then into the middle of the lake. Individual fish were measured to the nearest 1 mm total length (*TL*), and total weight (*TW*) was determined to the nearest 0.1 g using an Ohaus hand-held electronic scale; fish >320 g were weighed using a spring balance (±1 g). Fish were sexed and categorised as male, female or immature by visual inspection of their gonads. Sagittal otoliths were removed from a length-stratified subsample of fish, wiped clean, air-dried and stored in labelled plastic vials until processed for age determination.

Otolith processing, age determination and validation

In the laboratory, otoliths were prepared for ageing and measurement using thin sectioning. The left sagittal otolith from each fish was secured to a frosted glass slide using melted thermoplastic quartz cement. The mounted otolith was then thin-sectioned (~0.5 mm thick) through its core along a transverse plane using a Buehler® Isomet 1000 digital sectioning saw (Buehler®, Lake Bluff, IL, USA) with a diamond wafering blade (7.6 cm diameter × 0.15 mm blade width) at 3.8 g. Resulting thin sections were rinsed in ethyl alcohol and deionised water, blotted dry and mounted on glass slides with thermoplastic glue Crystalbond® (Electron Microscopy Sciences, Hatfield, PA, USA)). To improve readability, sections were ground down to the core on one side using Gatorgrit® (Electron Microscopy Sciences, Hatfield, PA, USA) wet–dry sandpaper (grit sizes 400 and 600 μ) and then polished with a Buehler® (Buehler®, Lake Bluff, IL, USA) microcloth using 0.3 μ alpha Buehler® micropolish alumina polishing powder paste.

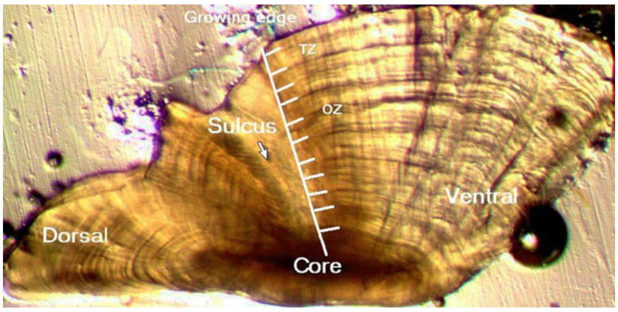

Figure 1. Transverse section of a sagittal otolith from a 6-year-old (with 12 biannuli) *Tilapia zillii* from Crater Lake Nkuruba, western Uganda. Otolith viewed using transmitted light, showing bi-biannuli, opaque zones (OZ), as well as the translucent zones (TZ) between opaque zones, and the sulcus.

Slides with otolith sections were placed in a petri dish filled with water to improve their clarity and examined with a stereomicroscope (10–40×) using transmitted light to count opaque growth zones. A combination of one narrow opaque zone (dark brown) with one broad translucent zone (clear to light brown) was interpreted as a complete annulus under transmitted light. If ‘false annuli’ merged with true annuli at the sulcus region, it was counted as one annulus. Annuli were read and counted along the sulcus that was chosen as the primary reading axis because the annuli were most visible along this axis (Fig. 1).

Following established ageing criteria, the primary reader (JE) read all otoliths twice, without knowledge of collection date, fish length and other sampling information. The second reading was carried out after approximately 1 month. To determine between-reader agreement, a random subsample of 100 otoliths covering the complete age range of the *T. zillii* population in Lake Nkuruba was read by a secondary reader (DJM) experienced in examination of transverse sagittal otolith sections. Ageing precision between the primary and secondary reader was then estimated using three methods: (1) percent agreement between the two independent readers, (2) the coefficient of variation (CV) (Kimura & Lyons 1991) and (3) the average percent error (APE) (Beamish & Fournier 1981).

Validation of opaque zone formation in Tilapia zillii

Edge interpretation and marginal-increment analysis was used to validate the periodicity of opaque zone formation by analysis of the temporal pattern of the marginal increment of growth in the otoliths. For edge analysis, the type of zone (opaque or translucent) at the growing edge of the otolith was identified in each month. The percentage of otoliths with opaque zones at the growing edge was then computed and plotted against month over a 12-

month cycle. For marginal-increment analysis, the periodicity of opaque zone formation was quantified using (Tanaka *et al.* 1981): $C = (W_n/W_{n-1})$ x100, where W_n is the distance from the otolith growing edge to the centre of the outermost complete (ultimate) opaque zone, and W_{n-1} is width of the previously complete increment (the distance from the centre of the ultimate opaque zone to the centre of the penultimate opaque zone) (Fig. 1). Measurements were made using calibrated digital callipers on a *Motic® Image System* (version 2.0; Motic, Inc., Richmond, BC, USA*)* under transmitted light at magnifications ranging from 20 to 40×. The average index of completion for each month was plotted over a 12-month period and checked for the number of minima. In both edge analysis and marginal-increment analysis, the presence of one minimum and one maximum would indicate that only one complete annulus (one opaque zone and one translucent zone) was deposited each year (12-month period). The presence of two minima and two maxima would indicate the deposition of biannuli, with two complete annuli deposited each year.

Growth of Tilapia zillii

The regression equation: $TW = aTL^b$ was used to describe the length–weight relationships for the gillnetted and trapped fish; where TW = total fish weight in grams, TL = total length in mm, a = regression constant and b = exponent. Length and weight data were log-transformed due to heteroscedasticity and the relationship was fitted by least square regression.

Growth was estimated by calculating the mean length of fish at each age for each gear type and using a two-way ANOVA to test for differences in mean length-at-age between gears, where age and gear were main effects and length-at-age the response variable. Age-related growth differences between gears were determined for ages 3–7 years; ages <3 and >7 years were excluded due to low sample size. Analyses were performed using SPSS® software, version 12 (IBM, Chicago, IL, USA) and at significance level = 0.05.

Estimates of total mortality, natural mortality and apparent survival rates

Instantaneous total annual mortality (Z) and total annual apparent survival (S) rates for gillnetted and trapped *T. zillii* were estimated using standard catch curve analysis (Ricker 1975) based on the assumption that samples from each gear represented the actual age distribution from the population across the sizes selected by the gears. Total mortality and apparent survival estimates were computed using the regression method of plotting ln (N) vs age for the descending limb of the regression for ages fully recruited to the gear. Apparent survival was then estimated from: $S = e^{-Z}$, where Z is the instantaneous total annual mortality.

Instantaneous rate of natural mortality was estimated using two methods. The first was computed using FISAT software (version 1.0.0) following the empirical method developed by Rikhter and Efanov (1976) with the equation described by: $M = 1.521/t^{0.72}_{\text{mass}} - 0.155$, where t_{mass} is 'the age at which the share of mature specimens exceeds 50%'. For *T. zillii*, an age at maturity of 3 years was used based on the range of 2–3 years reported by Lévêque (1977).

The second approximation of M was based on Hoenig's (1983) longevity–mortality relationship where the mortality rate is computed from the oldest individual encountered in the data set as: $\ln(M) = 1.46 - 1.01 \times \ln(t_{\max})$, where $t_{\max}$ is the maximum age for the species. There are no known maximum ages for *T. zillii* from a completely unexploited population near Lake Nkuruba, so the observed maximum age of 8 years for *T. zillii* in Lake Nkuruba was used in the calculation of M. This was assumed to be reasonable given the low directed fishing effort on Lake Nkuruba.

Results

Fish collections and processing

A total of 450 *T. zillii* were collected, with 80 (17.8%) gillnetted and 370 (82.2%) trapped (Fig. 2). To detect potential effects of gear on TL, length frequencies were plotted for males and females collected using gillnets or

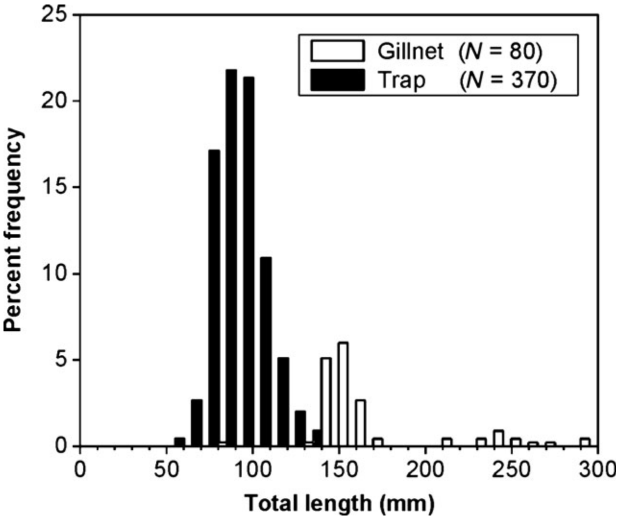

Figure 2. Length frequencies (% of total catch) of gillnetted and trapped *Tilapia zillii* from Lake Nkuruba between July 2005 and June 2006.

traps separately. A visual assessment of the length frequency plots revealed no differences between female and male size frequencies for each gear. Therefore, length frequency data were pooled for all fish (males, females and immature fish) by gear type, and length frequencies of gillnetted and trapped fish were compared using the Kolmogorov–Smirnov test.

Length frequencies of gillnetted and trapped *T. zillii* were significantly different (Kolmogorov–Smirnov test; $Z = 3.94$; $P = 0.0001$). Gillnets caught larger fish than minnow traps, with virtually no overlap in sizes of fish caught by the two gears (Fig. 2).

Otolith processing, age determination and validation

Thin sections of otoliths showed faint and indistinct alternating translucent and opaque zones when viewed under transmitted light. Sanding of transverse otolith sections with wet–dry sand paper and subsequent polishing with 0.3-μ alumina polishing powder improved the readability of the sections and identification of the zones (Fig. 1). The core of thin sections of *T. zillii* otoliths was easily recognisable as a fairly dense, large opaque structure (Fig. 1), separated by a large translucent zone that corresponded to the first complete annulus (combination of the first opaque zone and the translucent zone). Thin sections of *T. zillii* otoliths displayed considerable variation in size and structure of the opaque zone, from narrow and distinct opaque zones extending throughout the otolith sections to broad and split-opaque zones with cross-checking or false annuli along the dorso-ventral axis of the sulcus (Fig. 1).

Marginal-increment and edge analyses indicated that *T. zillii* in Lake Nkuruba deposit biannuli or two annuli (two opaque zones and two translucent zones) in their otoliths each year. Mean indices of completion (width of translucent zones at the otolith edge) were highest during the dry seasons between January–February (peaking in January) and between June–August (peaking in August (Fig. 3). Indices of completion were lowest between September–November and between March–May, indicating that the two opaque zones were deposited during the peak of the first wet season and about 1 month after the peak of the second wet season (Fig. 3). Edge analysis results further confirmed the bimodal pattern, with the highest percentage of opaque zones at otolith edges occurring between September and November and between March and May (Fig. 3). There was a significant positive correlation between mean monthly rainfall and percentage of otolith sections with opaque edges ($r^2 = 0.70$, $P = 0.005$, $n = 12$).

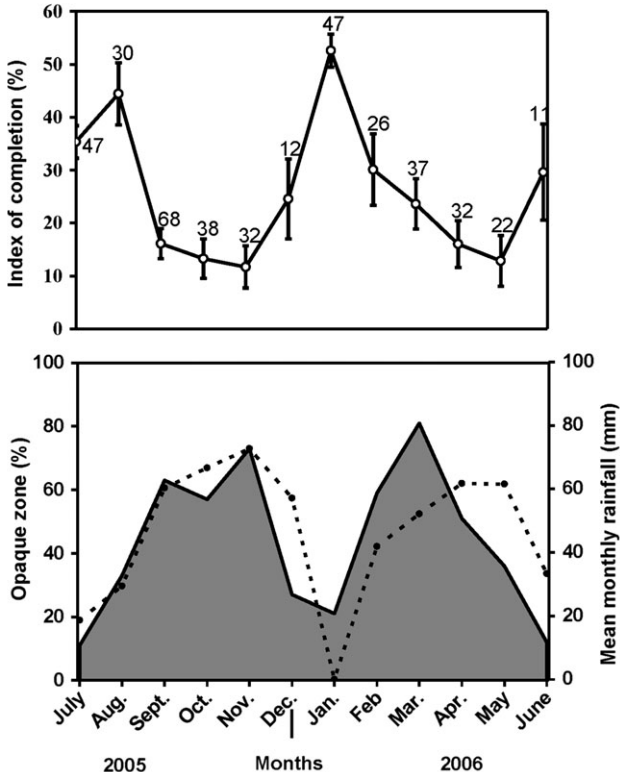

Figure 3. Marginal-increment and edge analyses for *Tilapia zillii* from Lake Nkuruba. Top panel gives the mean index of completion of the marginal increment of thin-sectioned otoliths over a 12-month period, showing two minima. Vertical bars denote standard errors and the numbers above the bars indicate sample size (*n*). Bottom panel gives the percentage of otoliths with opaque growth at the margin (line), showing two minima and mean monthly rainfall (grey area) measured at Makerere University Biological Field Station, Kibale National Park, during the study period, also showing two minima.

To account for *T. zillii* depositing two annuli per 12-month period (biannuli), all original counts were divided by 2 to determine the age of the fish. Between-reader agreement for the primary reader (JE) and secondary reader (DJM) showed no difference in the annuli counts for 36.0% of the otoliths ($n = 75$ random and independent age estimates), with 70.7 and 86.7% of the otolith readings differing by ≤1 annulus (equivalent to 0.5 year) and ≤2 annulus (equivalent to 1.0 year), respectively. More thorough, age-independent estimates of precision indicated a relatively high level of ageing precision for *T. zillii* (APE = 6.6% and CV = 9.3%).

Age and growth of Tilapia zillii

Length–weight relationships for gillnetted (size range 73–284 mm *TL* and 6.0–425 g *TW*) and trapped *T. zillii* (size range 51–138 mm *TL* and 4.1–48.8 g *TW*) were significant (gillnet: $TW = 0.000016\ TL^{3.01}$, $r^2 = 0.99$, $n = 78$, $P < 0.0001$; minnow trap: $TW = 0.00002\ TL^{2.98}$, $r^2 = 0.96$, $n = 362$, $P < 0.001$). Slopes ($P = 0.07$) and intercepts ($P = 0.09$) of the regression lines for gillnetted and trapped *T. zillii* did not differ and data were therefore pooled for both gears, where $TW = 0.00021\ TL^{2.97}$, $r^2 = 0.99$, $n = 440$.

The age of *T. zillii* collected from Lake Nkuruba ranged from 2 to 8 years (Fig. 4). There was no interaction between age and gear type as a function of *TL* ($F = 0.7$; $P = 0.65$), and within each gear type, there was no difference in *TL* as a function of age ($F = 1.04$; $P = 0.4$). There was a significant difference in mean *TL* between gears, however, with gillnetted fish being larger-at-age compared to trapped fish (ANOVA: $F = 40.63$; d.f. = 1.8; $P < 0.0001$). On average, a 3-year-old gillnetted *T. zillii* was 137.8 mm *TL* compared with 87.1 mm *TL* for a 3-year-old trapped fish. Both gears exhibited unimodal distributions in age frequency with gillnetted fish having a modal age of 5 years (4.1% of the total catch) and trapped fish dominated by 4-year-old individuals (16.7% of total catch) (Fig. 5).

Estimates of total mortality, natural mortality and apparent survival rates

Tilapia zillii were fully recruited to the fishing gear at age 5 for gillnetted fish and at age 4 for the trapped fish (Fig. 5). Instantaneous annual mortality (*Z*) was estimated as 0.74 (age range: 4–8 years) for gillnetted fish and 0.71 for trapped fish (Fig. 5) corresponding to apparent survival rates of 0.36 and 0.39, respectively. Estimates of natural mortality (*M*) for *T. zillii* were similar for both the Rikhter & Efanov and Hoenig methods, at 0.52 and 0.54, respectively.

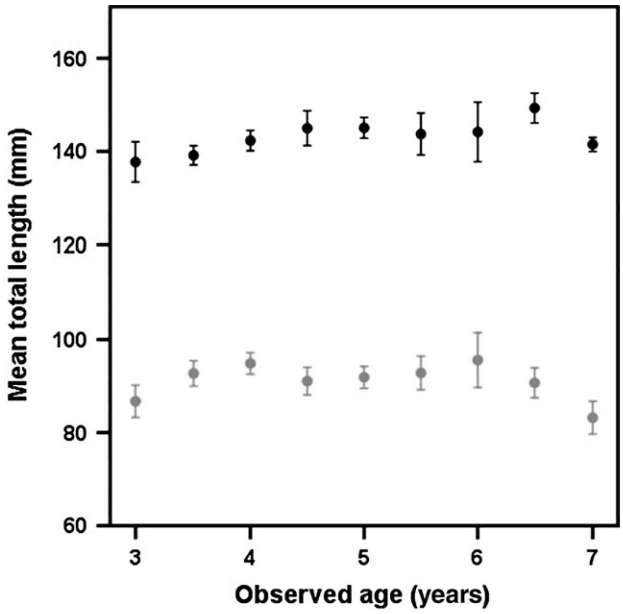

Figure 4. Mean total length-at-age (±SE) of *Tilapia zillii* (3–7 years) captured with gillnets and minnow traps in Lake Nkuruba, western Uganda, between July 2005 and June 2006. The black circles are gillnetted fish and the grey circles represent trapped fish.

Discussion

Otolith processing, age determination and validation

Despite the labour-intensive and time-consuming process of otolith preparation and analysis, sanding and polishing of transverse thin-sectioned sagittal otoliths seems to be the best way to age both juvenile and adult *T. zillii* in Lake Nkuruba. The biannual pattern of opaque zone formation in otoliths of *T. zillii* is consistent with studies of other tilapia species in the tropical regions that have reported opaque zone formation associated with wet-and-dry seasonal cycles (Warburton 1978; Bwanika *et al.* 2007). Opaque zone deposition is thought to occur

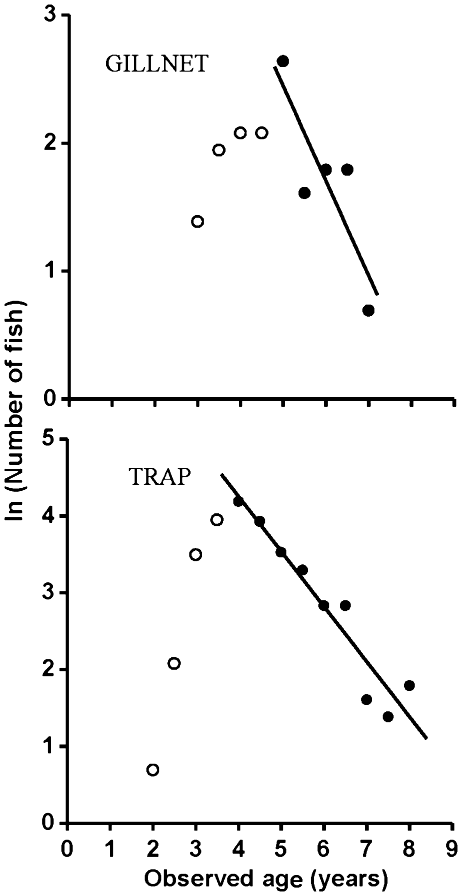

Figure 5. Linearised catch curves for estimating total mortality (*Z*) for gillnetted ($Z = 0.74$; $r^2 = 0.72$) and trapped ($Z = 0.71$; $r^2 = 0.91$) *Tilapia zillii* from Lake Nkuruba, Uganda, between July 2005 and June 2006. Open symbols indicate ages not fully recruited to the gear and therefore excluded from the regression analyses.

during periods of increased growth, whereas the corresponding translucent zone is formed during periods of low metabolic activity (Beckman & Wilson 1995). Studies of other tilapia species (e.g. *O. niloticus*) also associate opaque zone formation with faster growth (Yosef 1990; Yosef & Casselman 1995). In reviews of otolith studies in tropical latitudes, Beckman and Wilson (1995) and Fowler (1995) found that the period of opaque zone formation coincided with spring and summer months in temperate fishes. The present study determination of the biannuli was based on both Marginal Increment Analysis (MIA) and edge analysis. Campana (2001) pointed out some limitations of MIA, including difficulties associated with viewing increments at the margin due to refraction or reflection of light by the curved surface of the otolith, difficulties distinguishing a yearly cycle of formation from other frequencies, and problems associated with the application of marginal-increment results determined in young, fast-growing fish to older fish. The validity of the current approach was maximised by following established ageing criteria (no prior knowledge of fish sample characteristics) and application of quantitative analyses to detect biannuli.

Median values for CV of 7.6% and APE of 5.5% have been reported for various fish species aged using otoliths (Campana 2001). The present estimates of CV = 9.3% and APE = 6.6% for *T. zillii* are slightly higher but comparable to studies of other tilapia species in the region. For example, in a study of Nile tilapia in lakes Wamala and Nabugabo in Uganda, Bwanika *et al.* (2007) reported similar ageing precision (CV = 7.9%, APE = 5.6%). The present ageing precision shows that *T. zillii* can be aged reliably using otoliths but it is just harder to consistently do so. The difficulty of ageing tropical fishes using calcified structures has been noted in other studies (e.g. Yosef & Casselman 1995). The between-reader agreement for *T. zillii* was 64% in this study (86.7% differing by 1 year); whereas in temperate species, between-reader agreement above 90% is commonly reported (e.g. Barger 1985; Beckman *et al.* 1988; Dutka-Gianelli & Murie 2001).

There are several factors suggested to influence growth zone formation in tropical fishes, including seasonal variation in temperature, rainfall, photoperiod, food quality, reproductive activity and changes in other environmental parameters (Blake & Blake 1978; Warburton 1978; Nekrasov 1980; Morales-Nin & Ralston 1990; Booth *et al.* 1995; Yosef & Casselman 1995; Bwanika *et al.* 2007; Russell *et al.* 2013). In Lake Nkuruba, the mean annual surface water temperature over the study period was 23.9 °C and the range was relatively small (21.7–25.1 °C), although it is possible that small changes in temperature could affect oxygen consumption and allocation of energy to growth. Day length in the crater lakes region is relatively constant, because the lakes lie astride the equator, and therefore, photoperiod is unlikely to trigger growth zone formation. The effect of spawning activity on the formation of growth zones was not evident in this study as growth zones were observed in otoliths of immature and mature *T. zillii*. In addition, *T. zillii* are also known to breed all year round in the equatorial regions with slightly higher breeding intensity during March–May and July–August (Welcomme 1967; Siddique 1977). Given the correlation in opaque zone formation with the two wet seasons, it is most probable that opaque zone formation in *T. zillii* from Lake Nkuruba may be driven by rainfall and associated availability of food driven by nutrient influx.

Growth of Tilapia zillii

The size and growth differences in gillnetted and trapped *T. zillii* in Lake Nkuruba may be influenced by shifts in diet and dietary differences between the fish captured in the different gears and/or density-dependent factors. Growth of tilapia species is known to be affected by the quality and quantity of food (Lowe-McConnell 1982). A qualitative assessment of the diet of *T. zillii* in Lake Nkuruba ($n = 25$ fish) showed that detritus (macrophytes) constituted the greatest percentage of the food items in the stomachs of fish of all sizes caught in both gillnets and minnow traps (Efitre 2007). Phytoplankton was also found in gillnetted and trapped fish; however, zoobenthos (Chironomidae larvae) and newly hatched fish larvae were only found in the stomachs of gillnetted *T. zillii* (Efitre 2007). This difference in diet may contribute to faster growth in gillnetted fish. Density dependence due to intraspecific competition for food resources may also have contributed to the observed difference in growth rate between fish collected, especially in the trapped fish. Shallow littoral areas containing macrophytes that form the major diet of the trapped fish are limited in Lake Nkuruba, and this may contribute to density-dependent growth in this region of the lake. The source of the variation between the trapped and gillnetted fish may reflect plastic variation and/or genetic differences that could represent ecologically driven diversification within the lake or different stocks. This is an interesting area for future study and presents a unique opportunity to explore the possibility of local adaptation within the crater lake systems.

The maximum age of *T. zillii* reported in the present study is within the range of maximum ages reported for the species in other previous studies. Maximum life span for *T. zillii* has been reported to range between 8 years (De Silva 1991) and 11 years old (Fryer & Iles 1972;

James 1989). Lévêque (1977) also reported a maximum age of 7 years for *T. zillii* in Lake Kinneret in Israel. Longevity of tilapia has been reported to decline with decreased environmental quality (James 1989). Hodgkiss and Mann (1977) reported that most tilapia species in a thermally harsh reservoir were <5 year old. Similarly, Hecht and Zway (1984) reported stunted tilapia mostly 5 year old or less in a hot spring. The low level of exploitation in Lake Nkuruba may contribute to their intermediate longevity compared to those reported for other lakes.

Estimates of total mortality, natural mortality and apparent survival rates

The estimated total instantaneous mortality (Z) (0.71–0.74) and natural mortality (M) (0.36–0.39) rates for *T. zillii* in Lake Nkuruba are at the low end of the range of values reported for other tilapia species. Getabu (1992) estimated Z of 0.818 yr^{-1} for *O. niloticus* in the Kenyan part of Lake Victoria using length-based methods. Estimates of Z and M for *O. niloticus* in Lake Victoria were estimated at 1.67 and 0.63 yr^{-1} by LVFRO (UNECIA 2002), and 1.84 and 0.72 yr^{-1} (Muhoozi 2002), respectively. In Kandulla Reservoir, Amarasinghe and De Silva (1992) estimated $Z = 1.399\ yr^{-1}$ and 1.707 yr^{-1} for *O. mossambicus* and *O. niloticus*, respectively. In a study of *T. mariae* in a Nigerian wetland stream using the seasonalised, length-converted catch curve method, King and Etim (2004) computed Z and M of 1.75 yr^{-1} and 0.99 yr^{-1}, respectively. Despite biases associated with the different methods used for estimation of mortality rates, Z from a seasonalised length-converted catch curve is often comparable with Z from an age-structured catch curve (Pauly 1990). Estimates of Z for *T. zillii* in Lake Nkuruba using the linearised catch curve are extremely low due to the low fishing mortality in Lake Nkuruba. Natural mortality accounts for most of the reduction in population density in Lake Nkuruba and may be due to a number of factors, including low levels of surface dissolved oxygen concentration caused by periodic overturns (Saulnier-Talbot *et al.* 2014), which have caused fish kills in Lake Nkuruba in recent years. Predation by fish-eating waterfowl may also contribute to natural mortality in Lake Nkuruba, but this is likely not significant because their number is low in the lake (Efitre personal observation).

Conclusions

This is the first otolith-based study of *T. zillii* in Uganda and the East African region. The study adds to the growing list of tropical species for which otolith ageing methods have been successfully validated. The results also represent the first estimates of growth and mortality for *T. zillii* in the crater lakes and provide an essential first step in appropriate management of the small-scale fishery for local communities within the vicinity of these lakes. Gillnetted fish captured a component of the *T. zillii* population that was larger and faster growing, while the traps captured smaller and slower-growing fish, suggesting that the *T. zillii* stock in Lake Nkuruba may be composed of two components living in different (offshore, inshore) habitats. This can only be resolved by future studies that apply both gears in inshore and offshore habitats and/or use of experimental gill nets that integrate smaller mesh sizes set in both habitats, but it raises the possibility of habitat-associated divergence in key life-history traits over a very small spatial scale. The use of multiple gears should be applied and periodically evaluated in future studies of *T. zillii* populations in the crater lakes to ensure the data obtained accurately reflect *T. zillii* population parameters.

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