Age and growth of sharptooth catfish, *Clarias gariepinus* (Burchell, 1822) (Clariidae), in the Lower Okavango Delta, Botswana

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Abstract. Managing any inland fishery requires reliable age data and accurate estimates of growth rate. *Clarias gariepinus*, the largest catfish species in most tropical African floodplain river systems, is an important constituent of subsistence fishery catches. We used otolith-derived age estimates to describe patterns of age and growth for *C. gariepinus* from the Lower Okavango Delta in northern Botswana. Edge analysis of sectioned sagittal otoliths showed that growth zone deposition occurred during the annual flood peak between July and September. The maximum recorded age was 8 years. Growth was best described by the von Bertalanffy Growth Model of the form $E[L|age] = 528.70\left(1 - e^{-0.72(age+1.35)}\right)$. A comparison of growth parameters from this study with those from previous studies suggests two distinct populations of *C. gariepinus* between the Upper and Lower Okavango Delta, emphasising the importance of regional stock assessment for key fishery species. The fairly short life span and high variability in growth of *C. gariepinus* are important indicators that it is imperative to maintain natural habitat and flow regime for sustainable management of fishery resources in the Lower Okavango Delta.

Additional keywords: Boteti River, edge analysis, otoliths, periodic logistic regression, Thamalakane River.

Introduction

Large-river fisheries represent a key source of nutrition and a critical mechanism by which food security is enhanced across much of sub-Saharan Africa (Dugan *et al.* 2006, 2010; Welcomme *et al.* 2010). Yet these ecosystems are facing a range of growing pressures on their ecological integrity. Key factors include the abstraction of water for energy or crop production, destruction of riparian vegetation cover, and pollution emanating from industrial or domestic waste disposal (Malmqvist and Rundle 2002; Dudgeon *et al.* 2006; Richter *et al.* 2010). Even in rivers with low or negligible levels of flow abstraction or habitat alteration, other factors may still have a significant effect on the population levels of key biota. For example, climate change may alter patterns of flooding such that key life-history cues or access to critical habitats are impeded or lost (Carpenter *et al.* 1992; Eaton and Scheller 1996; Frederick and Major 1997).

Similarly, human fishing pressure may significantly reduce a population's size structure and, thereby, spawning capacity (De Graaf 2003). Riverine fisheries may take up to 30 years to recover if negatively affected (Jackson 2004), and management agencies need robust population descriptors to underpin their monitoring of stock fluctuation and timely intervention. Such stock assessment will be enhanced by including detailed knowledge of population phenomena such as age and growth.

The sharptooth catfish (*Clarias gariepinus* (Burchell, 1822)) is an omnivorous predator (Merron 1991; Winemiller and Kelso-Winemiller 1996; Cambray 2003) that occurs across much of Africa and the Middle East (Kadye and Booth 2012). It is found in a variety of habitats and is a prominent component of the faunal biomass in most rivers throughout its range (Winemiller and Kelso-Winemiller 1996). For this reason, it frequently represents an important fisheries target and source of

local income and protein (Mmopelwa *et al.* 2009). In the Okavango Delta in northern Botswana, *C. gariepinus* contributes substantially to the subsistence fishery catch (van der Bank and Smit 2007; Mmopelwa *et al.* 2009). However, there is a poor understanding of its population biology in key areas of fishing effort throughout the catchment and growth parameters for the Okavango Delta have been derived only for the upper portions of the Delta using length–frequency analysis (Mosepele 2000).

The ability to age fish accurately is fundamental for the estimation of growth and mortality rates and productivity (Campana 2001). Previous studies comparing the ageing accuracy of spines, vertebrae and otoliths of *C. gariepinus* showed a considerable underestimation of longevity from using spines and vertebrae compared with estimates derived from otoliths (Quick and Bruton 1984; Kaunda and Hecht 2003). Weyl and Booth (2008) suggested that this underestimation of longevity was possibly due to the effect of bone resorption, which is more pronounced in spines than in vertebrae. Consequently, otoliths were recommended as the most appropriate structure for ageing adult *C. gariepinus* because they are metabolically inert and not prone to resorption (Weyl and Booth 2008).

Growth-zone deposition rate in the otoliths of African freshwater fishes has been validated by several authors (see Weyl and Booth 2008 for a review) and successfully utilised for ageing *C. gariepinus* in several African populations (Bruton and Allanson 1980; Quick and Bruton 1984; Chimatiro 2004; Richardson *et al.* 2009; Wartenberg *et al.* 2013). However, in large catchment areas, variability in fish life-history parameters may exist for the same species between regions and between connected rivers of the same system (Duponchelle *et al.* 2007). For example, by comparing growth rates of several cichlid species, Mosepele *et al.* (2005) suggested that the Upper and Lower Okavango Delta may harbour two or more distinct subpopulations with significant variation in growth rates. For the downstream end of the catchment, there is a pressing need to establish a clearer picture of the population biology of key species ahead of predicted upstream water resource developments and the likely effects on downstream hydrology (Ramberg 1997; OKACOM 1998).

The present study is the first to utilise otolith structures to assess the age and growth of *Clarias gariepinus* in the Okavango Delta. Using age data from sectioned otoliths, we provide estimates of these key parameters for comparison with populations upstream in the Okavango River and from elsewhere in southern Africa.

Materials and methods

Study area

The Okavango River originates in the Angolan highlands, and flows through Namibia before ending in a large delta in northern Botswana (hereafter, 'Delta') (Fig. 1). The Delta is characterised by a semi-arid climate, with one distinct wet season from November to March (Neuenschwander *et al.* 2005), which is asynchronous with the winter timing of the annual flow peak from Angola at Mohembo (Ringrose *et al.* 1988). It is divided into two broad regions, classified as the Upper and Lower Delta (Mosepele *et al.* 2005). Flows at the end of the Lower Delta

terminate in the Thamalakane and Boteti rivers in the northern Kalahari Desert.

In the Upper Delta, the flood pulse increases steadily from November and peaks in April (McCarthy *et al.* 1998; Wolski *et al.* 2006) (Fig. 2). The Lower Delta is made up of low-gradient seasonal swamps whose permanence varies from year to year and depends on the magnitude of winter flood peak (McCarthy *et al.* 1998). Water levels in the terminal Thamalakane and Boteti rivers peak between August and October, $\sim$5 months after peaking at the onset of the Upper Delta at Mohembo (McCarthy *et al.* 1998) (Fig. 2). The total annual input of water into the Okavango system is estimated at 15.339×10^9 m^3, of which only 2.36×10^8 m^3 (1.5%) is discharged into the Thamalakane River (McCarthy *et al.* 1998).

Data collection

Specimens of *C. gariepinus* were collected opportunistically during weekends from commercial fishers operating along the Thamalakane River and at Chanoga Lagoon on the Boteti River between March and September 2010 (Fig. 1). The fishers used gill-nets of 100-mm stretched mesh size which were set overnight for a typical duration of $\sim$12 h. Upon capture, total length (TL) of each specimen was measured (to the nearest millimetre) and its sex was determined. The sagittal otoliths were removed from the cranium and stored dry in 1.5-mL Eppendorf tubes for later processing and age determination. Procedures for otolith removal and preparation followed those used in previous studies of *C. gariepinus* (Weyl and Booth 2008; Richardson *et al.* 2009).

Data analysis

Sex ratio and size structure

To test for differences in sex ratio, a Chi-Square test for goodness of fit was used. The Tukey multiple comparisons of means was used to determine the difference in mean length between sexes. Analyses were performed in R using packages multcomp and FSA (Hothorn *et al.* 2008; Ogle 2013*a*).

Determining age

For ageing, one otolith from each pair was selected at random and mounted in clear polyester casting resin. Each otolith was sectioned transversely through the nucleus using a double-bladed diamond-edged saw to a thickness of 0.3–0.4 mm, and then mounted on a microscope slide using DPX mountant. Growth zones were identified as alternating opaque and translucent bands. Age was estimated by counting the number of opaque rings from the nucleus to the edge of the otolith under transmitted light.

Otoliths were read twice at least 2 weeks apart by a single reader without prior knowledge of the length and sex of the fish. If the two readings matched, the age estimate was accepted. If the readings failed to match, a third reading was taken. A match between two of the three readings meant acceptance of the age estimate from the two matching readings. If the three readings differed by not more than 2 years they were averaged, otherwise the otolith was rejected as unreadable (Booth and Merron 1996).

Validation

Accuracy of the age estimates obtained in this study was validated using edge analysis as described by Winker *et al.* (2010*a*, 2010*b*). In edge analysis the monthly percentage
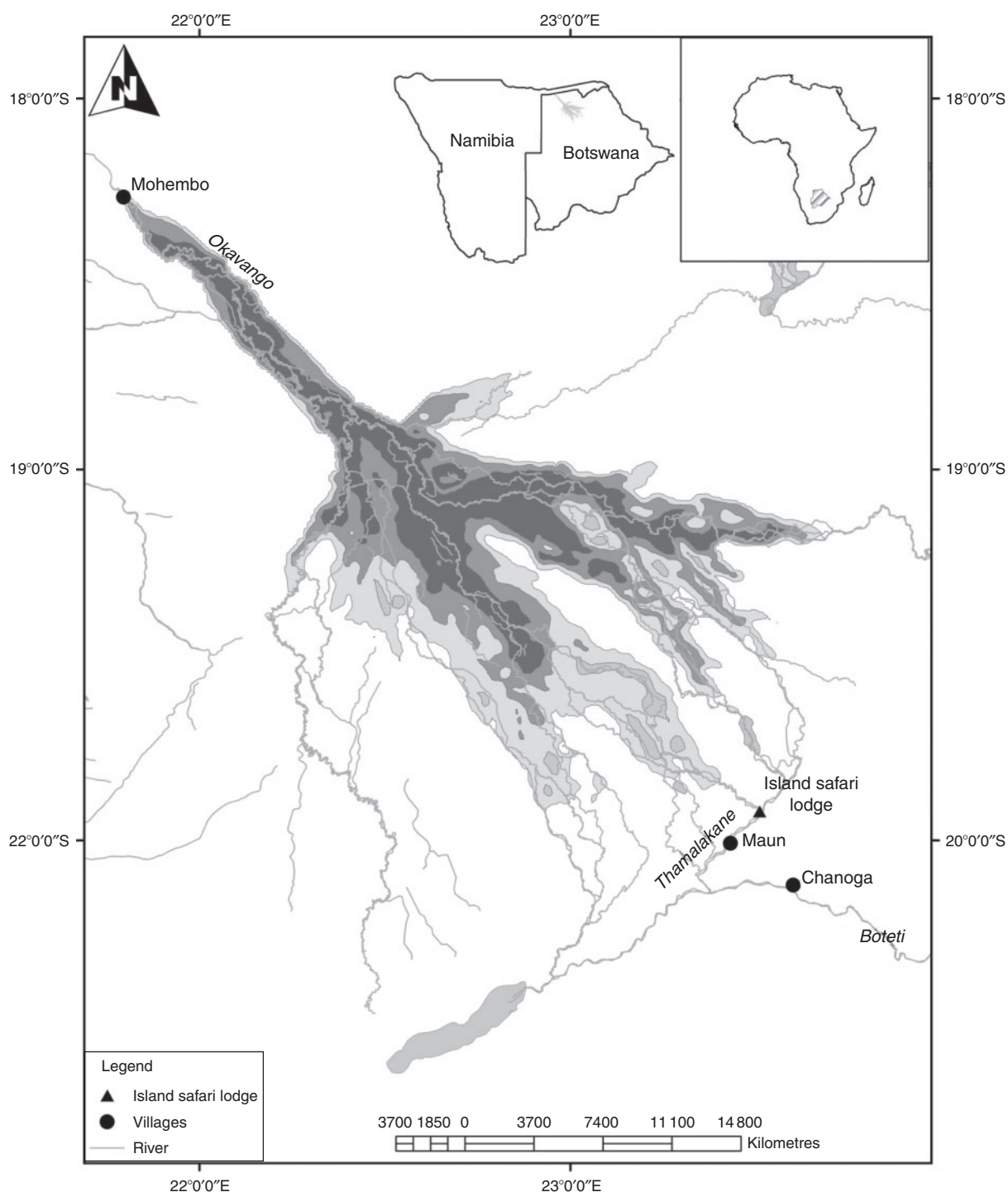
Fig. 1.   The Okavango Delta in northern Botswana and the sampling sites used in the present study.

occurrence of opaque zones on the edge of the otolith was recorded and the distribution was then tested as either unimodal or bimodal using a periodic logistic regression model (Flury and Levri 1999). The model fit was obtained using the glm() function in R (R Core Team 2013). Exponentiation was used to convert the model regression coefficients from the log (odds) scale to the odds scale so that the magnitude of change in the

odds of ring deposition in response to a unit change in predictor variables could be determined (Kabacoff 2011).

Precision

The precision of the age estimates was assessed using three commonly applied statistical measures: the index of average percentage error (*IAPE*), the coefficient of variation (*CV*) and
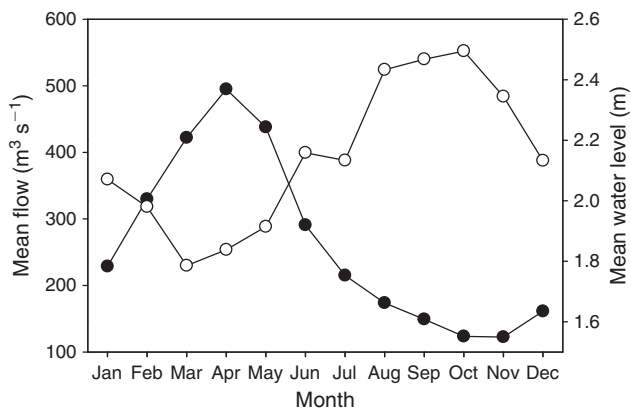
Fig. 2. Mean monthly water levels (m³) recorded at Island Safari Lodge (Lower Delta, 2001–09) (white circles) and mean monthly flows (m³ s⁻¹) at Mohembo (Upper Delta, 2001–08) (black circles). Low flows at Mohembo correspond to high water levels in the Thamalakane River.

the index of precision (*D*). The *IAPE* in aging the *j*th fish was determined after Beamish and Fournier (1981) as:

$$IAPE = \frac{1}{n}\sum_{j=1}^{n}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - \bar{X}_j|}{\bar{X}_j}\right] \cdot 100$$

where X_{ij} is the *i*th age determination of the *j*th fish, X_j is the mean age of the readings, *R* is the number of readings and *n* is the number of fish aged. The *CV* was calculated as in Kimura and Lyons (1991):

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

where the definitions for X_{ij}, X_j and *R* are those previously described for *IAPE*.

The percentage error contributed by each observation to the average age class was estimated by an index of precision (*D*) (Chang 1982). The index is defined as:

$$D = \frac{1}{n}\sum_{j=1}^{n}\left[\frac{CV_j}{\sqrt{R}}\right]$$

If multiplied by the average age for the *j*th fish, the index of precision (D_j) gives the error in age determination made for each observation.

To objectively test the observed positive relationship between water levels and growth ring deposition on *C. gariepinus* otoliths, Kendall's Tau, a non-parametric measure of rank correlation (McLeod 2011), was applied to monthly edge analysis *v.* mean monthly water level data. Hydrological data were obtained from the Island Safari Lodge flow gauge (Fig. 1) near the Okavango Research Institute, University of Botswana, Maun, and daily water level measurements were averaged

by month over 8 years (2001–09) to obtain the mean monthly water levels.

Growth

To compare the growth of males and females, separate von Bertalanffy growth curves were fitted for each sex. The separate growth curves were expressed following Ogle (2013b) as:

$$L(t) = L_\infty[sex]\left(1 - e^{-K[sex](t - t_0[sex])}\right)$$

where *sex* is either male or female.

This is the general model with separate parameter estimates for individuals of each sex (i.e. the model assumes that (L_∞, *K*, t_0) are different between sexes). After fitting the general model, its subset models were fitted in order of increasing parsimony. Models that assumed that one parameter was common between sexes were considered first followed by those that assumed two parameters were common to both sexes (i.e. (L_∞ and *K*), (L_∞ and t_0), (*K* and t_0)). The model that assumed all parameters were common to both sexes was fitted last. To determine the best subset model, model fits were ranked hierarchically using the Akaike Information Criterion (AIC) (Ritz and Streibig 2008). The model with the lowest AIC was chosen as the best model.

From applying the AIC, the best model assumed that all parameters were the same for both sexes, implying no significant difference in the growth of males and females. Therefore, data for both sexes were pooled and growth was modelled by fitting the three-parameter von Bertalanffy Growth Model (VBGM) to observed length-at-age data (Beverton and Holt 1957). The model was defined as:

$$E[L|t] = L_\infty\left(1 - e^{-K(t - t_0)}\right)$$

where $E[L \mid t]$ is the expected or average length at age *t*, L_∞ is the asymptotic average length, *K* is the Brody growth-rate coefficient (year⁻¹), and t_0 is the age when the average length was zero.

Parametric bootstrap resampling (Efron and Tibshirani 1986) with 1000 bootstrap replicates was used to estimate growth parameters, 95% confidence intervals and prediction bounds for the model. To establish whether *K* was less than 0.5, the null hypothesis, $H_0 : K = 0.5$ was tested on the bootstrapped estimates of *K* *v.* the alternative hypothesis, $H_A : K < 0.5$. Analyses were implemented in R using packages nlstools and FSA (Baty and Delignette-Muller 2012; Ogle 2013a).

Results

Sex ratio and size structure

The overall sex ratio of females to males was 1 : 0.7, which was not significantly different from unity (χ^2 goodness-of-fit test: $\chi^2 = 3.44$, d.f. = 1, $P = 0.06$). There was no significant difference in mean length between sexes (Tukey multiple comparison of means: $P = 0.62$).

Age and growth

Precision

In total, 114 *C. gariepinus* otoliths were examined. Only four otoliths could not be aged reliably and these were therefore
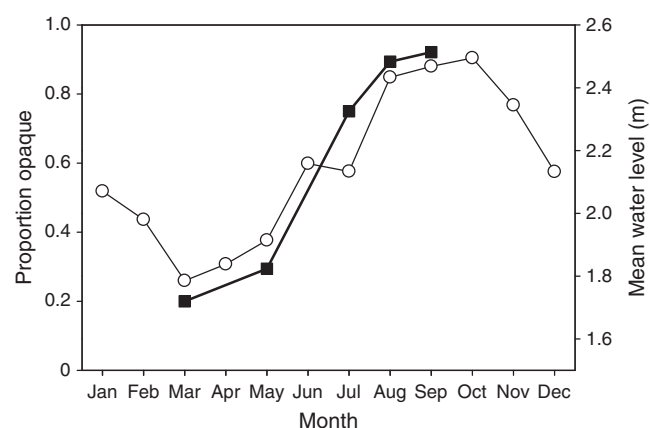
Fig. 3. Predicted frequency of occurrence of opaque rings (black squares) on the edge of otoliths by month of capture in the Thamalakane and Boteti rivers of the Lower Okavango Delta. Peak ring deposition occurs once per year between July and September during the annual flood peak (white circles).

Table 1. Parameter estimates from the periodic logistic regression model predicting the proportion occurrence of opaque margins on the otoliths of *Clarias gariepinus* from the Thamalakane and Boteti rivers in the Lower Okavango Delta, Botswana over a period of 1 year

Parameter	Estimate	s.e.	Exp(Estimate)
β_0	0.57	0.40	1.77
β_1	0.48	0.68	1.62
β_2	−1.98	0.31	0.14
d.f.	3		

excluded from the analysis. For the readable otoliths, *IAPE* was 8%, *CV* was 11% and *D* was estimated at 6%.

Validation

The distribution of opaque zones on the edge of the otolith was unimodal with a maximum in September (Fig. 3). Therefore, it was assumed that one opaque and one hyaline zone was deposited each year and that counts of growth zones corresponded to the age of the fish. Parameter estimates for the periodic logistic regression model predicting the proportion of occurrence of opaque margins on the otolith edges of *C. gariepinus* are presented in Table 1. Assuming a unimodal shape, the odds of ring deposition were increased by a factor of 0.14 for a unit change in the sinusoidal wave (the flood pulse) that occurred once per year. There was a very strong, positive and significant correlation between monthly mean water levels and the proportion of opaque margins on otolith edges (tau = 1, 2-sided *P* value = 0.03) (see Fig. 3).

Growth

The maximum estimated age for *C. gariepinus* from the lower Delta was only 8 years. The VBGM parameter estimates are presented in Table 2 and the fitted growth model is shown in Fig. 4. The null hypothesis that $K = 0.5$ could not be rejected ($P = 0.77$).

Table 2. Von Bertalanfy growth model parameter estimates, standard error (s.e.) and 95% confidence intervals (95% CI), of *Clarias gariepinus* from the Thamalakane and Boteti rivers in the Lower Okavango Delta, Botswana
$n = 106$

Parameter	Estimate	s.e.	95% LCI	95% UCI
L_∞	528.70	13.07	510.99	579.95
K	0.72	0.31	0.25	1.68
t_0	−1.35	0.99	−4.90	0.02
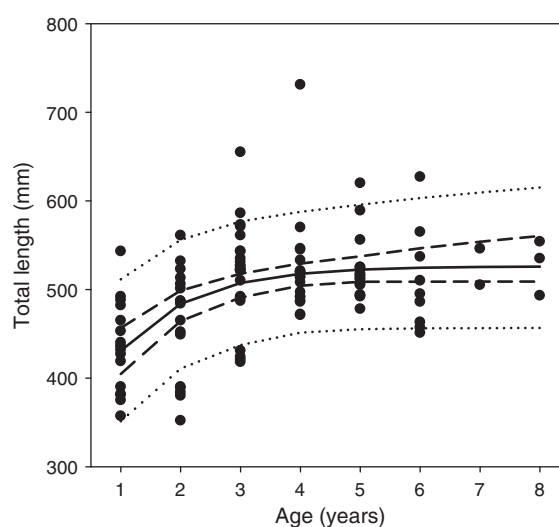
Fig. 4. Fitted line plot for the fit of the VBGM with ~95% bootstrap confidence bounds (inner dashed lines) and 95% bootstrap prediction bounds (outer dashed lines).

Table 3. Sample size, range and observed mean lengths at age (±s.d.) of *Clarias gariepinus* from the Thamalakane and Boteti rivers in the Lower Okavango Delta, Botswana

Age	n	Length (mm)			
		Mean	s.d.	Minimum	Maximum
1	16	435.12	50.95	357	543
2	17	462.00	62.12	352	561
3	23	517.91	56.93	418	655
4	19	523.00	56.59	471	731
5	17	522.24	35.86	478	620
6	9	510.11	57.82	451	627
7	2	525.50	28.99	505	546
8	3	527.33	31.21	493	554

The mean lengths at age from the observed age frequencies are presented in Table 3. There was noticeable variation in length at age across all age classes. For example, 3-year-old fish varied from 418 to 655 mm TL. The largest fish recorded was a 4-year-old at 731 mm TL whereas the smallest fish sampled was a 2-year-old at 352 mm TL. Early growth was rapid, with

fish reaching lengths greater than 300 mm TL in their first year of life.

Discussion

Validation and precision

In any growth study, precision and accuracy are important prerequisites and using edge analysis for age validation is important in determining the timing of growth zone deposition within 1 year (Campana 2001). Otoliths of *C. gariepinus* revealed a discernible and repeatable pattern of opaque zone deposition. Growth rings were deposited between July and September, with one opaque and one hyaline ring formed annually. This was consistent with case studies reviewed by Weyl and Booth (2008) and indicates that *C. gariepinus* from the Lower Okavango Delta deposit a single annual growth zone in their otoliths.

The seasonal timing of ring formation between July and September coincided with the peak water levels, an increase in temperature, and an increase in daylength. A similar pattern has been documented for other Okavango fishes. For example, in *Oreochromis andersonii* and *Oreochromis macrochir*, annulus deposition occurred in summer when temperatures were high and annulus deposition was attributed to reproductive activity (Booth *et al.* 1995; Booth and Merron 1996). Booth *et al.* (1995) and Booth and Merron (1996) obtained their samples from perennial floodplain lagoons that received the annual flood peak between May and August. Therefore, growth ring deposition for *C. gariepinus* may also be associated with the energetic costs of reproduction because breeding generally occurs between July and December in the Lower Okavango Delta (Merron 1991).

On comparison with other studies, the age estimates obtained in the current study were comparable with those obtained for sectioned otoliths of *C. gariepinus* from Xonxa Dam in South Africa (*IAPE* = 8.5%: Richardson *et al.* 2009), and the closely related *B. nyasensis* from Lake Malawi (*IAPE* = 14.2%, *CV* = 10%, *D* = 7.1%: Kaunda and Hecht 2003).

Growth

Growth was adequately described by the three-parameter VBGM, with an asymptotic length of 528.7 mm TL. This was consistent with Chimatiro (2004), who estimated L_∞ at 502.9 mm TL for this species in the Lower Shire floodplain river system in Malawi. However, Mosepele (2000) derived a much higher L_∞ estimate of 905 mm TL for this species in the Upper Okavango Delta. The latter finding suggests that growth in *C. gariepinus* may differ substantially between the Upper and the Lower Okavango Delta regions. Indeed, Mosepele *et al.* (2005) also reported lower asymptotic lengths for three cichlid species (*Oreochromis andersonii*, *O. macrochir* and *Tilapia rendalli*) in the Lower Okavango Delta compared with the Upper Delta. Generally, it has been hypothesised that fish populations in the Upper Delta grow slowly and reach larger sizes compared with those in the Lower Delta (Merron 1991; Tweddle *et al.* 2003). This is supported by the current study which shows that in the Lower Delta L_∞ was approached more rapidly ($K = 0.72$) than in fish from the Upper Delta, where Mosepele (2000) estimated a much lower von Bertalanffy K of 0.26 for *C. gariepinus*.

Clarias gariepinus in the Lower Okavango Delta grow rapidly in their first year of life, reaching lengths of over 300 mm TL. Similar observations were made in the Elands River in South Africa (van der Waal and Schoonbee 1975) and the Shire valley in Malawi (Willoughby and Tweddle 1978) where the species respectively reached 426 and 200 mm TL in the first year. In contrast, Bruton and Allanson (1980) observed total lengths of up to 144 mm in the first 6 months of life for *C. gariepinus* in South Africa's Lake Sibaya. Fast growth in the first year is typical of organisms that have to go through a succession of different mortality rates and it is hypothesised that this strategy may help to reduce the susceptibility of juveniles to predation (Craig 1985; McKaye 1986). Owing to the ephemeral nature of rivers such as the Thamalakane and Boteti and their associated floodplains in the Lower Okavango Delta, rapid attainment of a larger size may be essential for migration back into the main river channels during the February to May draw-down period (Welcomme 1979).

Lengths at age were highly variable, resulting in large error rates around the fitted growth function. Booth *et al.* (1995) also observed large variation in length at age data for *O. andersonii* from the Okavango Delta. This variability was mainly attributed to the variable environmental conditions experienced by individual fish in different parts of the floodplain (particularly fluctuations in food availability) as well as intrinsic genetic variation between the individuals themselves (Booth *et al.* 1995).

In floodplain river systems, rising water levels usually result in inundation of the floodplain and therefore an increase in the surface area of the habitat available for exploitation by fishes (Junk *et al.* 1989; Merron 1991; De Graaf 2003). However, during the flood recession period, this expanded habitat may become fragmented, resulting in cut-off pools that form micro-habitats with spatial variability in abundance of food, density of fish, physicochemical characteristics and species assemblages (Lamberts 2001). For this reason, the availability and quality of food to an individual inhabiting the different microhabitats is likely to be highly variable and, because food availability affects growth (Hislop *et al.* 1978), the growth history of individual fish will differ. Hence, a small old fish may have inhabited a food-poor environment before being sampled whereas a relatively young large fish may have inhabited a food-rich environment. As *C. gariepinus* is highly tolerant of different environmental conditions and is able to utilise the full range of microhabitats available, this is likely to result in the large variation in individual growth rates observed in this study.

Longevity

The present study showed that *C. gariepinus* in the Thamalakane and Boteti rivers are fairly short lived. The estimated maximum age (8+ years) is close to that estimated by Chimatiro (2004) for the same species in the Lower Shire floodplain river in Malawi (9 years), although considerably lower than otolith estimates from South African impoundments (12 years: Richardson *et al.* 2009; 15 years: Weyl and Booth 2008; 25 years: Wartenberg *et al.* 2013). Booth *et al.* (2010) attributed the variation in longevities between impoundments to the age of the reservoirs. Moreover, fishing pressure in these impound-ments is low and there are few natural predators, and so

C. gariepinus inhabiting these water bodies tend to be considerably longer lived than those in rivers systems (Wartenberg *et al.* 2013). However, the causal factors that may influence such large disparities in longevities between floodplain river systems and man-made impoundments may, in part, be due to differences in environmental variability between the two habitats that may result in divergent life-history strategies.

Conclusions and management recommendations

Findings from the present study support previous assertions (Mosepele *et al.* 2005) that there may be two or more sub-populations of fish stocks in the Okavango Delta. Furthermore, Mosepele *et al.* (2011) reported a significant difference in mean lengths of fish between lagoons in the Upper Delta and those in the Lower Delta. It is recommended that future studies aim to supplement these length-based regional analyses with robust age-based comparisons between regions where age data are available. Furthermore, phylogenetic analyses should establish whether the observed regional life-history variation is a result of genetic drift or adaptive phenotypic plasticity (Duponchelle *et al.* 2007).

From extant information, it is imperative that regional stock assessments be undertaken to underpin the development of spatially explicit management strategies. To this end, the present study provides first estimates of growth parameters for *C. gariepinus* in the downstream portions of the Okavango Delta. These should be used as input parameters in resource modelling for future fisheries and flow-management planning for this part of the catchment. Resource modelling in the form of stock assessment is essential because it will provide fishery managers with information on sustainable utilisation and management of the resource, particularly with regard to sustainable take levels and size limits (Cadima 2003).

The fairly short life span of *C. gariepinus* in the lower Okavango Delta shows that the species may be vulnerable to changes in the flow regime even over short periods. The annual peak water levels will be critical in determining access to key habitats, food resources and, thereby, interannual growth rate (Poff *et al.* 1997). Decrease in both the flood peak and duration could negatively affect growth and increase the time spent in suboptimal habitats. In turn, the latter may concentrate the stock in limited areas available for fishing and, thereby, see an increase in fishing pressure and the likelihood of stock decline. If substantial flow reduction occurred over four successive years, with concomitant recruitment failure, Lower Delta populations of the species would be at a substantial risk of collapse.

Biodiversity in the lower Delta is faced with potential threats from land-use activities such as urbanisation and livestock grazing (Mbaiwa 2004). Moreover, potential water extraction from the upstream portion of the catchment may play a major role in altering flow regimes in future. Changed riparian land use and flow alteration should be given top priority in the development of the fisheries policy and management plans for the Okavango Delta, and consideration given to the effects on fish population structure and growth.

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