Life History Strategy and Population Characteristics of an Unexploited Riverine Cyprinid, Labeo capensis, in the Largest Impoundment in the Orange River Basin

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Life history strategy and population characteristics of an unexploited riverine cyprinid, *Labeo capensis*, in the largest impoundment in the Orange River Basin

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The life history of an endemic riverine African cyprinid, *Labeo capensis,* that dominates the larger ichthyofauna in a large impoundment in the Orange River Basin four decades after damming, was investigated. Both sexes grew at a similar rate until the onset of maturation, after which male growth and survival rates declined. Male mortality rate was significantly higher than estimated for females explaining both the older ages attained by females (12 years) compared to males (9 years) and a female-dominated adult population. Maturation proceeded faster in males than in females, but was considerably delayed in both age and length. Female reproductive contribution was double that of males despite males maturing a year earlier. Intraspecific life history comparisons with riverine and early impoundment populations suggest that *L. capensis* has largely maintained its riverine life history characteristics. These characteristics are common in large fishes that are well-adapted to seasonal riverine environments, but often show high vulnerability to damming or overfishing. The absence of a directed fishery and the availability of periodic floodplains that form when marginal vegetation is inundated by either the unregulated inflow of the Orange River or local erratic rains is suggested to have played a vital role for the successful establishment of *L. capensis* within the impoundment.

Key words: age and growth, reproductive biology, periodic strategist, mortality, gillnet selectivity, population structure.

INTRODUCTION

The construction of man-made lakes or dams creates major hydrological perturbations within river ecosystems (Rosenberg *et al.* 2000). Native riverine cyprinids are often poorly adapted to lentic conditions with several examples of populations declining subsequent to the damming of rivers (Aparicio *et al.* 2000; Clavero *et al.* 2004; Olden *et al.* 2006; Tedesco *et al.* 2008). In Africa, riverine cyprinids of the genus *Labeo* belong to one of the most affected groups (Jackson *et al.* 1988). In Lake Kariba on the Zambezi River, for example, *Labeo altivelis* (Peters 1852) and *L. congoro* (Peters 1852) populations increased shortly after impoundment but declined to negligible levels in the main basin within a few years (Begg 1974). Similar declines following impoundments have been shown for *L. coubie* (Rüppel 1832) and *L. senegalensis* (Valenciennes 1842) in Lake Volta (Vander-puye 1981), for *L. molybdinus* and *L. cylindricus* (Peters 1852) in Lake Itezhi-tezhi on the Kafue River system in Zambia (Cowx & Kapasa 1995), and for *L. niloticus* (Forsskål 1775) in Lake Nasser, Egypt (Abdel-Latif 1984). These declines have been attributed to relatively stable conditions in impoundments interfering with the proximate environmental conditions for spawning (Begg 1974; Vanderpuye 1981; Jackson *et al.* 1988), together with overfishing if directed at spawning aggregations (Begg 1974; Ogutu-Ohwayo 1990; Weyl & Booth 1999; Booth & Weyl 2004). There are no documented cases of any *Labeo* sp. dominating the fish fauna in a large impoundment after a long period after damming. Because fisheries often develop shortly after dam construction in impoundments, it is typically difficult to distinguish between the influence of changes in environmental conditions and the impact of fishing (Vanderpuye 1981; Cowx & Kapasa 1995; Petrere 1996; Hoeinghaus *et al.* 2005; Okada *et al.* 2005).

In South Africa, the westward flowing Orange

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River ranks as the most turbid river system in Africa and the fourth most turbid globally (Bremner *et al.* 1990). One of the most striking features of the system is its depauperate ichthyofauna, which comprises only 16 native fishes. The upper Orange River was impounded by the Gariep hydroelectric dam in 1970 and the Vanderkloof Dam in 1976. Extensive gill net surveys were conducted in Lake Gariep (1971–1978) and the Vanderkloof Dam (1976–1982) to assess the commercial fisheries potential of large cyprinids (Hamman 1980; Tómasson 1983). At this time several studies on the life history and population dynamics of the abundant Orange River mudfish, *Labeo capensis*, populations were conducted in these two newly created impoundments (Fairall & Hamann 1977; Gaigher *et al.* 1980; Hamman 1980; Tómasson *et al.* 1984; Tómasson *et al.* 1985).

Labeo capensis is a large endemic cyprinid that is widely distributed throughout the Orange-Vaal River system and, together with Orange-Vaal smallmouth yellowfish (*Labeobarbus aeneus*), dominates the larger ichthyofauna in the Orange, Vaal and Caledon Rivers (Jubb 1959; Jubb & Farquharson 1965; Skelton 1986). Its life history evolved under the harsh and unpredictable environmental conditions of the Orange River system that is characterized by highly variable physical parameters such as flow, turbidity and temperature (Keulder 1979; Tómasson *et al.* 1984; Skelton 1986). Morphologically, *L. capensis* is characterized by a complex ventral mouth and a long coiled intestine, features suited for specialized feeding on benthic detritus and periphyton (Skelton 1986). Breeding generally occurs in seasonal floodplain habitats during the summer months (Mulder 1973; Tómasson *et al.* 1984). Like many of its congeners, *L. capensis* is fecund, with a large female of 400 mm fork length (L_F) (~1 kg) able to produce in excess of 100 000 eggs (Baird 1976; Tómasson *et al.* 1984).

During the first six years after the impoundments of Lake Gariep and Vanderkloof Dam, *L. capensis* populations exhibited considerable fluctuations in abundance and recruitment (Hamman 1980; Tómasson *et al.* 1985), with a large portion of the reproductive biomass suggested to consist of individuals from the pre-impoundment riverine population (Fairall & Hamann 1977). It was therefore hypothesized that the post-impoundment *L. capensis* populations would need to undergo large-scale demographic changes before stable populations could potentially establish themselves in the newly created impoundments (Fairall & Hamann 1977; Hamman 1980).

A large commercial fishery was never successfully implemented on either impoundment and, to date, the fisheries resource of Lake Gariep is exclusively used by subsistence and recreational anglers who mainly target common carp, *Cyprinus carpio* (Ellender *et al.* 2009; Ellender *et al.* 2010), with *L. capensis* being an insignificant by-catch species with an estimated annual harvest rate of only 0.16 kg/ha/yr (Ellender *et al.* 2010). Lake Gariep therefore presents a unique opportunity to assess the long-term life history response of a *Labeo* sp. to impoundment in the absence of harvesting. To achieve this, this study assesses the age and growth, reproduction, population structure, mortality rates and sex-specific reproductive contribution of *L. capensis* in Lake Gariep some four decades post-impoundment and provides intraspecific life history comparisons with other riverine and early-impoundment populations.

MATERIALS & METHODS

Study Area

Lake Gariep (30°38′S; 25°46′E; 1250 m above mean sea level) has a surface area of about 364 km^2 and is South Africa's largest inland water body (Fig. 1). The impoundment has a mean depth of 16.3 m and a maximum depth of about 50 m at full water level (Hamman 1981). The ~400 km shoreline primarily comprises extensive, gradually sloping shores that are largely devoid of vegetation (Hamman 1981). An estimated 10% of the shoreline is steep and rocky (Cambray *et al.* 1978). During spring and summer, exposed portions of the drawdown zone are colonized by an annual plant community (Cambray *et al.* 1978). The region's climate is semi-arid and rainfall is seasonal, with most of the ~400 mm annual precipitation falling in summer (Keulder 1979). The impoundment's water level fluctuates considerably and is generally a function of the seasonal inflow of the Orange River, usually during either spring or summer, and water release for power and water supply demands. Lake Gariep is naturally highly turbid due to high levels of silt from the Orange River (Keulder 1979). Turbidity levels are positively correlated with seasonal inflow of the Orange River and are therefore typically higher during spring and summer months (Keulder 1979). Routine measurements of Secchi depth and water temperature were taken during bimonthly sampling trips
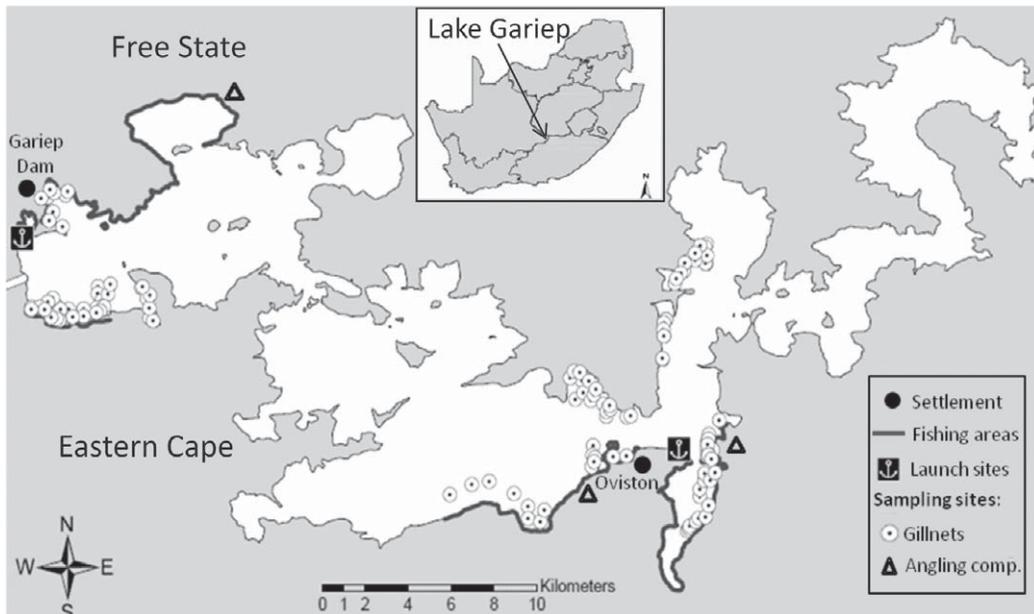
Fig. 1. Map of Lake Gariep showing gillnetting sites and locations of sampled angling competitions.

between May 2007 and March 2008. Secchi depth from offshore areas ranged from 5 cm to 34 cm (mean = 14.6 cm, *n* = 40) between May 2007 and March 2008. Mean surface water temperature was 21.4°C (range: 16.6–26°C) in summer and 10.2°C (8.7–11.3°C) in winter.

Sampling

The majority of the data used in this study were obtained from gillnet surveys conducted bi-monthly between May 2007 and March 2008. Supplementary samples for biological examination were collected from anglers in November 2006, January 2007, April 2007 and October 2007.

The experimental gillnet fleet comprised five multifilament nets (45 m × 3 m constructed of green, knotted nylon netting. Each net consisted of five randomly positioned panels (9 m long × 3 m deep) with stretched mesh sizes of 47, 65, 77, 105 and 152 mm. The fleet of five gillnets was deployed parallel to the shore along the 2.5–3 m depth contour and the GPS coordinates of each net was noted. The fleet was set between 17:00 and 19:00 in the evening and lifted between 05:00 and 07:00 the following morning. During routine gillnet surveys, the gillnet fleet was set on two nights within 10 km of the small settlement Oviston (Fig. 1). During winter (June 2007) and summer (January 2008), sampling was intensified and extended to other lake areas (Fig. 1). Each

seasonal gillnet survey comprised eight gillnet fleet nights. This resulted in a total sample size of 40 net nights per summer and winter season and a total of 130 net nights over the study period.

All fish caught in each gillnet mesh size were identified and weighed to the nearest 0.1 kg. The relative abundance of fishes caught by gillnets was expressed by the index of relative importance (IRI, (Kolding 1993):

$$IRI = (\%N + \%W) \times \%F ,$$

where %N and %W are the percentage mass and number of each species of total catch, and %F is the percentage frequency of occurrence per fleet night (percentage of all fleet nights containing a given species).

For biological analysis, all *L. capensis* were measured to the nearest mm fork length (L_F). Depending on feasibility and sample size demands, sub-samples of measured specimens were selected at random, weighed to the nearest gram, and then dissected and sexed. The developmental stage of gonads was macroscopically determined according to the criteria presented in Weyl & Booth (1999). Astericus otoliths, the largest and most suitable ageing structure of the three pairs of otoliths in cyprinids (Vilizzi & Walker 1999; Phelps *et al.* 2007; Winker *et al.* 2010), were removed, dried and stored in Eppendorf tubes for later age determination.

Age and growth

A total of 512 astericus otolith pairs was used for age determination. To enhance the visibility of opaque (dark) and translucent (light) growth zones, whole otoliths were submerged in methyl salicylate and examined under transmitted light using varying magnifications (×10–40) according to the procedures outlined in Winker *et al.* (2010).

The consistency of growth zone counts was assessed using the average percentage error (APE) method (Beamish & Fournier 1981) and by calculating the average coefficient of variation (CV), as suggested by Chang (1982). The otolith readings were undertaken twice without reference to the length of the specimen, at random and at least two weeks apart.

In cases where the two readings differed, a third reading was conducted. If this resulted in two identical readings, then the counts were accepted. If the three readings differed by no more than two growth zones (e.g. 2, 3, 4), then the median was accepted, otherwise the otolith was considered unreadable and therefore excluded from the analysis (Campana 2001).

Mark–recapture of adult *L. capensis* chemically tagged using oxytetracycline hydrochloride and corroboration by edge analysis provided evidence that one growth zone is deposited annually (Winker *et al.* 2010). To avoid false year class identification, monthly age estimates were back-calculated by assuming that all fish were born during the peak of the determined spawning season in November, and that opaque zone formation occurred between June and August (Winker *et al.* 2010). This involved adding the number of months between November and capture date to specimens that were caught before June, and subtracting the number of months between the next spawning events to capture date if caught after August. For specimens that were captured during the assumed transition period between June to August, the number of months between spawning and the date of capture was either added or subtracted, depending on whether their otoliths were categorized as translucent or opaque, respectively.

Length-at-age was described by the three-parameter von Bertalanffy growth model of the form:

$$L_t = L_\infty(1 - \exp(-K(t - t_0))) ,$$

where L_∞ is the predicted asymptotic length of the fish, K is the Brody growth coefficient and t_0 is the theoretical age of a zero-length fish. The model

was fitted by minimizing the negated normal log-likelihood function. Likelihood ratio tests were used to test the null hypotheses that growth was equal between sexes. Parameter variability was estimated using the conditioned parametric bootstrap resampling technique described by Efron & Tibshirani (1986). The percentile method (Buckland 1984) was applied to estimate 95% confidence intervals from resulting bootstrap vectors, where the 2.5% and 97.5% percentiles were chosen to obtain the lower and upper 95% confidence intervals, respectively.

Reproduction

Length-at-maturity was expressed as the proportion of reproductively active fish (developing, ripe and spent reproductive stages) in each 10 mm size class for each sex separately. The length-at-(50%) maturity (Lm_{50}) was estimated by fitting the data to a logistic model of the form:

$$\psi(L) = m_\infty(1 + \exp(-(L - Lm_{50})\delta_L^{-1}))^{-1} ,$$

where $\psi(L)$ is the predicted proportion of reproductively active fish in size class L and Lm_{50}, δ_L is the steepness parameter of the logistic ogive and m_∞ is asymptotic maturity. The model was fitted by minimizing the negated binomial log-likelihood function. For species where all mature individuals are in reproductively active condition at the same time, it is conventional to set $m_\infty = 1$. However, if smaller proportions of the adult population mature at different times over an extended period, as has been reported for *L. capensis* (Gaigher *et al.* 1980; Tómasson *et al.* 1984), it may be desirable to estimate m_∞ as an additional parameter (Quinn & Deriso 1999). Mathematically, Lm_{50} then denotes the size at which half the sampled population attained m_∞. Based on the results by Gaigher *et al.* (1980), the spawning season of *L. capensis* in Lake Gariep was assumed to occur mainly from October until March. However, monthly samples from this period were only considered if at least 50% of adult fish (>female Lm_{50}) were in reproductively active stages. Likelihood ratio tests were used to test the null hypotheses that maturity was equal between sexes.

Length-at-maturity was converted to age-at-maturity using the reformulation of the von Bertalanffy equation

$$tm_{50} = t_0 - K^{-1} \ln(1 - Lm_{50} L_\infty^{-1}) .$$

According to Booth & Weyl (2004), the steepness parameter of the logistic ogive for age t, δ_t, can

then be calculated as:

$$\delta_t = (2K \ln(3))^{-1} \ln((L_\infty - Lm_{50})(L_\infty - Lm_{50} - \delta_L \ln(3))^{-1}).$$

The proportion of mature fish at age t was then calculated as:

$$\psi_t = (1 + \exp(-(t - tm_{50})\delta_t))^{-1}.$$

Temporal patterns of spawning activity were assessed on the basis of the proportion of maturity stages per sampling month for adult fish (>female Lm_{50}), which were plotted against lake water levels and mean monthly temperatures. The sex ratio of adult fish was determined and then compared to a 1:1 ratio using a contingency table.

Population structure

To assess the size and age structure of the *L. capensis* population, it was necessary to first determine the gillnet selectivity such that sampled length frequencies from gillnet fleets, the most effective capture method, could be corrected to provide an unbiased estimate of the length structure in the population.

The SELECT method of Millar & Holst (1997) was employed to estimate the gillnet selectivity of *L. capensis.* All individuals caught in the experimental multifilament gillnet fleet were grouped into 10 mm L_F size classes L for any given mesh size m_i. Assuming that the retention probability is normally distributed, the selectivity of mesh m_i is given by

$$S_i(L) = \exp(-(L - \mu_i))/(2\sigma_i^2)).$$

The mean μ_i can then be expressed as a linear function of mesh size m_i and the spread σ_i is assumed to be proportional to m_i such that $\mu_i = m_i k_1$ and $\sigma_i = m_i \sqrt{k_2}$, where k_1 and k_2 are the scaling parameters for the selectivity curves, which are estimated from a log-linear Poisson model as described in detail by Millar & Holst (1997) and Booth & Potts (2006). The pseudo-coefficient of determination (r^2) (Swartzman *et al.* 1992) was used to assess how much the variance in the gillnet catch data could be explained by the model. As each gillnet had the same five mesh sizes with equal surface areas, it was assumed that the fishing intensity of each mesh size was equal (Millar & Fryer 1999) and that the selectivity of a multi-mesh gillnet catching a fish of length L can therefore be calculated as $S_{GN}(L) = \sum_i S_i(L)$.

The size structure of the *L. capensis* population was determined by pooling the bi-monthly gillnet length frequency samples and correcting them for gillnet selectivity. The expected frequency of fish in length class L, $\hat{f}_L$, was calculated as $\hat{f}_L = f_L / S_{GN}(L)$, where f_L is the observed length frequency.

Mortality

To obtain sex-specific mortality estimates, the selectivity-corrected length frequencies were multiplied by the observed proportion of females and males in each 10 mm L_F size class and converted into age-frequencies by means of normalized age-length keys for each sex. Estimates of the instantaneous total mortality (Z) were obtained from catch curve analysis (Ricker 1975) and by applying the maximum likelihood estimator of Chapman & Robson (1960). Because *L. capensis* is not directly targeted by the hook and line fishery at Lake Gariep (Ellender *et al.* 2010), Z was assumed to be equal to natural mortality (M).

A non-parametric bootstrap procedure (Efron & Tibshirani 1986) was used to estimate the standard error (S.E.), the coefficient of variation (CV) and confidence intervals (CI) for Z. For this purpose, random data sets were generated by resampling length-at-age data with replacement based on a dynamic age-length-key. The Ricker (1975) and the Chapman & Robson (1960) mortality estimator were executed 1000 times and the percentile method (Buckland 1984) was used to estimate the 95% confidence intervals from the resulting bootstrap vectors.

Reproductive contribution

Under the assumptions that recruitment is constant and all fish have the same natural mortality rate throughout their lifespan, the reproductive contribution of an individual of each sex over its life span can be calculated as a function of its growth in weight and survival as

$$RC_t^s = \sum_{t=0}^{max} \left(w_t^s \psi_t^s \exp\left(- \sum_{t'=0}^{max-1} Z^s\right)\right) + \frac{w_{max}^s \psi_{max}^s \exp(-Z^s)}{1 - \exp(Z^s)},$$

where $w_t^s = \alpha L_t^{s\,b}$ is the mass of an animal at age t and sex s, L_t^s is length-at-age for each sex s, α and β are the parameters of the length–weight relationship, ψ_t^s is the proportion of mature females and males at age t and sex s, and Z^s is the sex-specific instantaneous rate of total mortality.

Intraspecific life history comparison

Available age-derived life history parameters for riverine and early impoundment populations of *L. capensis* from various locations were collated

from literature. For ease of comparison between this study and growth studies conducted on other populations of *L. capensis,* the growth performance index was calculated as $\Phi' = \log K + 2 \log L_\infty$ (cm L_F) (Pauly & Munro 1984). This index was proposed to account for the interaction and dependence of the von Bertalanffy parameters L_∞ and K and it has been found that similar populations, species or families often have similar Φ' estimates although their growth parameters may differ.

RESULTS

A total of eight species were sampled during the bi-monthly gillnet surveys including one rainbow trout (*Oncorhynchus mykiss*) (Walbaum 1792) and one rock catfish (*Austroglanis sclateri*) (Boulenger 1901), which were, however, not included in subsequent analyses due to their low contribution to the overall catches. *Labeo capensis* dominated the gillnet catches by number (60.7%) and mass (41.7%) and was caught in 98% of gillnets (n = 130). This resulted in the highest percentage contribution to the total IRI (60.6%), indicating that this species dominates the gillnet-available ichthyofauna of Lake Gariep. By contrast, the four other commonly caught species common carp (*Cyprinus carpio* L.), sharptooth catfish (*Clarias gariepinus*) (Burchel 1822), largemouth yellowfish (*Labeobarbus kimberleyensis*) (Gilchrist & Thompson 1913) and moggel (*Labeo umbratus*) (Smith 1841) only contributed 5%, 3%, 1% and <1% by numbers, respectively.

Age and growth

Of all otolith pairs investigated, 34 or 6.2% were rejected as unreadable. The APE index was 4.94% and the mean CV was 6.95%. The maximum number of accepted opaque zone counts (age) was nine for males and twelve for females. Length-at-age was described adequately using the von Bertalanffy growth model and no violation of the assumed homoscedasticity of residuals was apparent (Fig. 2).

Growth differed significantly between males and females ($P < 0.05$), with females attaining a larger maximum size than males. The data from unsexed juveniles were then pooled with male, female and combined data from both sexes (Table 1).

Linear regression *t*-tests of the natural logarithm-transformed length–weight relationships for *L. capensis* showed no significant differences between males and females (intercepts: $P = 0.24$,

slopes: $P = 0.27$). The data were therefore pooled and the length–weight described as w(g) = $0.0000024 \times L_F$ (mm)$^{3.132}$ ($n = 743$, $r^2 = 0.97$).

Reproductive biology

The length-at-(50%) maturity (Lm_{50}) was calculated at 298 mm L_F ($\delta_L = 12$/mm L_F) for males and at 323 mm L_F ($\delta_L = 19$/mm L_F) for females. The estimated asymptotic maturity (m_∞) was 0.65 for males and 1.00 for females. Male maturation proceeded faster ($\delta_t = 0.68$/yr) than maturation of the females ($\delta_t = 0.93$/yr) ($P < 0.05$). Age-at-(50%)-maturity was calculated as 5.3 years and 6.2 years, for males and females, respectively.

The proportion of reproductively active stages in adult *L. capensis* (>320 mm L_F) indicated that reproductive activity extended from spring until late summer (October–March) (Fig. 3). However, the pattern of gonadal recrudescence revealed considerable variability within and between spawning seasons, and no consistent correlation was apparent when gonadal development was assessed against changes in the lake's water level and temperature.

This variability was exemplified by the large decrease in the proportion of fish with reproductively active gonads by January 2007 (10.5%) and a subsequent increase to a maximum (89%) by March 2007, while water levels constantly receded over the same period. During the subsequent months (April–August 2007), reproductive activity was consistently low, with more than 72% of gonads categorized as resting. Between April and June 2007, the few reproductively active *L. capensis* were dominated by spent individuals, whereas by August 2007, all reproductively active gonads (14%) were categorized as developing. By October 2007, spawning activity had increased again, and of the 40.5% reproductively active gonads, 18.9% and 21.6% were categorized as ripe and developing, respectively. The proportion of reproductively mature specimens was further increased by January 2008 (45.2%), and the first spent individuals became apparent (8.4%). In contrast to the previous year, however, spawning activity had decreased again by March 2008 (25%).

Population structure

Most of the 2234 *L. capensis* were caught in the 77 mm (n = 892) and 65 mm (n = 813) mesh sizes. The 153 mm mesh size caught less than 0.001% of the total sample (n = 9), and was therefore excluded from the selectivity model. It should be
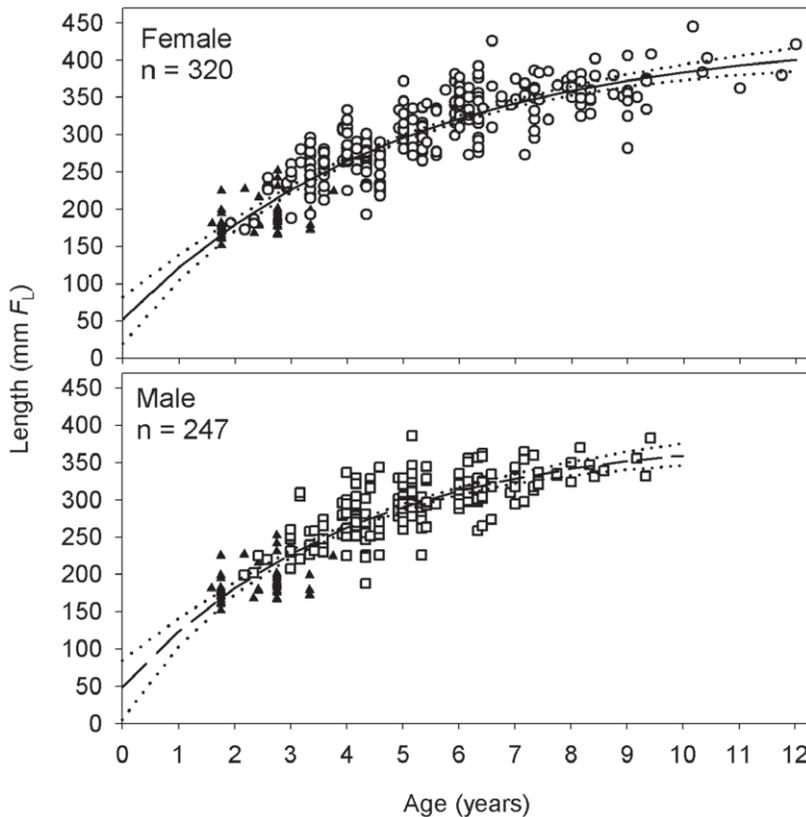
Fig. 2. Length-at-age data for *Labeo capensis* sampled at Lake Gariep, South Africa, using whole otoliths ($n = 525$). The von Bertalanffy growth curve fit for females (○; $n = 263$) and juveniles (▲; $n = 72$) is indicated by a solid line and that for males (□; $n = 190$) and juveniles (▲; $n = 72$) by a dashed line. Dotted lines represent the upper and lower 95% confidence intervals of each estimated growth curve.

noted that the excluded individuals caught in the 153 mm mesh size also increased the robustness of the model by reducing the degrees of freedom from 133 to 99 without significantly influencing the model fit ($\chi^2 = 0.02$, d.f. $= 34$, $P = 1.00$) that also explained 95% of the variation ($r^2 = 0.95$) in the data. The scaling parameters, k_1 and k_2, that are used to determine the maximum length at capture and the standard deviation for each selectivity curve were estimated at 3.81 and 0.16, respectively.

The observed proportion of females and males in each 10 mm L_F size class is illustrated in Fig. 4a. The adult population (>320 mm L_F) was female-dominated with an adult sex ratio of 2.5 females: 1 male that differed significantly from unity ($\chi^2 = 106.8$, d.f. $= 4$, $P < 0.05$). The sex ratio in smaller size classes (≤ 320 mm L_F) was 1 female:1 male and was not significantly different from unity ($\chi^2 = 16.0$, d.f. $= 14$, $P = 0.31$). Assuming an equal sex ratio in the smaller size classes, the observed and predicted size structures showed that the uncorrected gillnet length frequency data largely over-

Table 1. Parameter estimates [95% CI] of length-at-age data using the von Bertalanffy growth function with a normal error distribution for *Labeo capensis,* sampled at Lake Gariep, South Africa

Parameter	Juv. + males ($n = 310$)		Juv. + females ($n = 345$)		Combined ($n = 566$)	
L_∞ (mm L_F)	387.7	[358.8, 435.7]	433.8	[402.9, 477.9]	417.1	[394.4, 450.6]
K (/y)	0.25	[0.18, 0.32]	0.20	[0.15, 0.26]	0.21	[0.17, 0.26]
t_0 (yrs)	−0.54	[−1.21,−0.05]	−0.64	[−1.21, −0.20]	−0.70	[−1.24, −0.27]
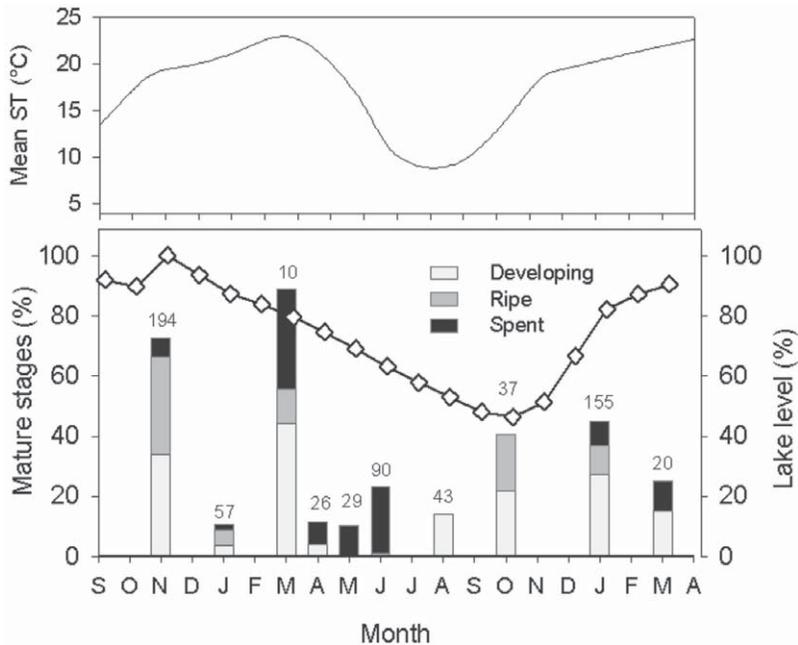
Fig. 3. Proportion of reproductively active adult (>female Lm_{50}) *Labeo capensis* (combined bar height) from Lake Gariep and lake levels expressed as percentage of the full capacity ($\diamond$, solid line) for the period from September 2006 to March 2008. The proportion of adult reproductive stages is illustrated within each bar. Numbers above bars denote the sample size. The upper graph illustrates general trends in mean surface water temperature in °C (ST) based on measurements taken during bi-monthly gillnet surveys (May 2007 – March 2008), which were then interpolated across the study.

estimated the abundance of fish in the size range from 240 to 300 mm L_F and underestimated, in particular, the female-dominated size classes from 340 to 370 mm L_F (Fig. 4b).

Catch curves were fitted over the same range of age classes for males and females (4–9 years), and a linear regression t-test revealed that the slopes, representing the total mortality (Z), differed significantly between sexes ($P < 0.05$). Female age classes from age-10 to age-12 were also excluded from the catch curve analysis because the sample size in these age groups comprised fewer than three fish.

Total mortality estimates ($Z = M$) derived from catch curve analyses and using the maximum likelihood estimator by Chapman & Robson (1960) are summarized in Table 2. The total mortality estimates from the Chapman & Robson (1960) estimator were less variable and considered to be more robust than those from the catch curve analyses. Due to the similarity in the total mortality estimates for males, the statistically more robust Chapman & Robson (1960) estimate of $Z = 0.65$ [95% CI = 0.58–0.72]/yr for males was accepted for further analyses. By contrast, catch curve analyses resulted in a smaller mortality estimate for the

Table 2. Estimates of the instantaneous rates of total mortality ($Z = M$) for the *Labeo capensis* population at Lake Gariep, South Africa.

Method	Sex	Estimate	CV (%)	95% CI
Chapman & Robson (1960)	*F*	0.52	3.9	[0.48, 0.56]
	M	0.65	5.3	[0.58, 0.72]
Catch curve analysis	*F*	0.40	12.7	[0.32, 0.52]
	M	0.66	13.9	[0.52, 0.90]
Mean	F	0.46	7.2	[0.40, 0.54]
	M	0.66	8.7	[0.56, 0.79]
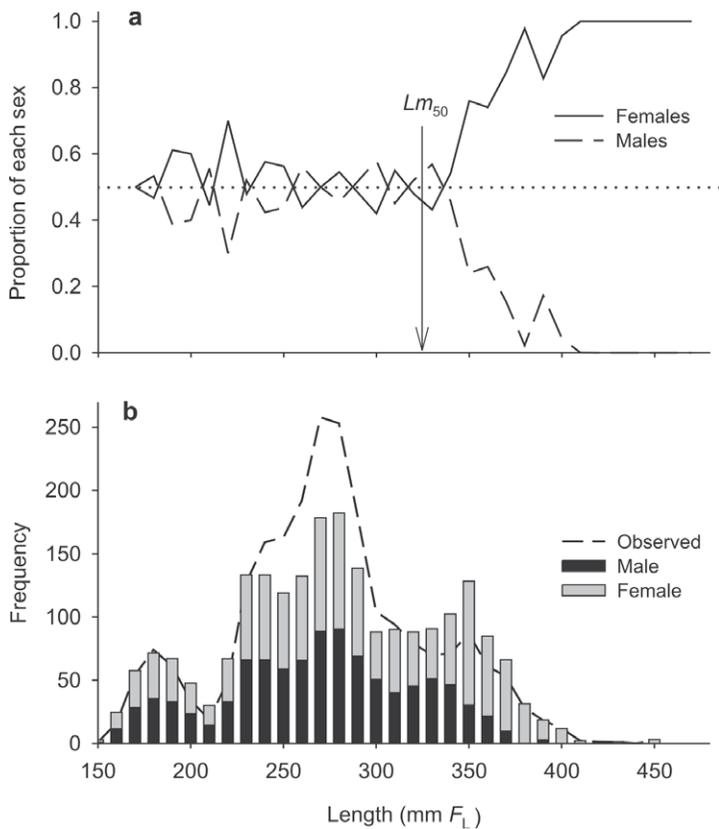
Fig. 4. **a**, Observed proportion of male (– –) and female (—) *Labeo capensis* in each 10 mm L_F size class with the arrow denoting the length-at-(50%)-maturity (Lm_{50}) estimated for females and the horizontal line (·····) a 1:1 sex ratio; **b**, observed and gillnet selectivity corrected female and male length-frequencies for *L. capensis* sampled during bi-monthly gillnet surveys (2007–2008) at Lake Gariep.

females ($Z = 0.40$/yr) than the Chapman & Robson (1960) estimator ($Z = 0.52$/yr), and in order to account for this increased uncertainty, the mean of both methods, $Z = 0.46$/yr [95% CI = 0.40–0.54/yr] was considered to be more appropriate for female *L. capensis.*

Reproductive contribution

Assuming an instantaneous natural mortality rate and longevity of 0.46/yr and 12 years for females, and 0.66/yr and 9 years for males, it was noted that the total female reproductive contribution, expressed as spawner biomass per recruit, was double that of males despite males maturing a year earlier than females.

Intraspecific life history comparison

A summary of this study and previous age and growth studies on *L. capensis* together with lengths- and ages-at-maturity estimates is presented in Table 3. On closer inspection of the computed Φ' values, the low values for the 1978/79 year class in Vanderkloof Dam ($\Phi' = 2.30$, 2.34) appeared to be outliers as they differed significantly from the rest of the data (t-value = 5.96, $P < 0.05$) and resulted in unrealistically old age-at-maturity estimates (Table 3). If they were omitted, the remaining Φ'-values showed a relatively narrow range ($\Phi' = 2.56$–2.77) for both impoundment and riverine populations in the Orange River system. In most populations, maturation is attained at an age older than half of the maximum observed age (Table 3). On average, *L. capensis* first reproduced at 62% and 52% of their maximum theoretical sizes and ages, respectively.

DISCUSSION

Four decades post-impoundment, *L. capensis* have persisted to remain a dominant component within the larger ichthyofauna of Lake Gariep despite

Table 3. Ageing methods, von Bertalanffy growth parameters, growth performance $\Phi' = 2\log(L_\infty/10)+\log(K)$ (Pauly & Munro 1984), length-at-(50%)-maturity (Lm_{50}), age-at-(50%)-maturity, maximum observed age (t_{max}) of *Labeo capensis* from different localities within the Orange/Vaal River system. All lengths are reported in mm F_L.

Locality	Sex	Method	L_∞	K	t_0	Φ'	Lm_{50}	tm_{50}	t_{max}	tm_{50}/t_{max}	Period	Source
Lake Gariep	Male	Otoliths	388	0.25	−0.54	2.58	298	5.3	9	0.59	2007–08	This study
	Female	Otoliths	434	0.20	−0.64	2.58	322	6.1	12	0.51	2007–08	
Lake Gariep	Male	Scales	562	0.15	0.35	2.68	280	4.9	8	0.62	1972–77	Hamann (1981)
	Female	Scales	647	0.12	0.01	2.70	360	6.8	10	0.68	1972–77	
Vanderkloof Dam	Male	Otoliths	506	0.19	0.48	2.69	330	6.0	13	0.46	1977/78	Tomasson (1983)
	Female	Otoliths	609	0.16	0.03	2.77	380	6.1	16	0.38	1977/78	
	Male	Otoliths	533	0.07	0.10	2.30	330	13.9	13	–	1978/79	
	Female	Otoliths	742	0.04	0.20	2.34	380	18.1	16	–	1978/79	
	Male	Otoliths	593	0.11	0.20	2.59	330	7.6	13	0.58	1979/80	
	Female	Otoliths	688	0.09	0.39	2.63	380	9.3	16	0.58	1979/80	
	Male	Otoliths	490	0.15	0.38	2.56	330	7.8	13	0.60	1980/81	
	Female	Otoliths	557	0.13	0.43	2.61	380	9.2	16	0.58	1980/81	
Caledon River	Male	Scales	–	–	–	–	200	3.4	8	0.43	1970–71	Baird (1976)
	Female	Scales	–	–	–	–	230	4.1	8	0.51	1970–71	
Vaal River	Male	Scales	–	–	–	–	260	3.7	8	0.46	1969–71	Mulder (1973)
	Female	Scales	–	–	–	–	310	4.7	9	0.52	1969–71	
	Combined	Scales	491	0.23	0.38	2.74	310	–	9	–	1969–71	
Hardap Dam	Male	Scales	–	–	–	–	253	4	7	0.57	1988–92	Van Zyl *et al.* (1995)
	Female	Scales	–	–	–	–	260	4	7	0.57	1988–92	

having retained a life history strategy that is considered to be well adapted to seasonal riverine environments but usually confers a high vulnerability to either damming or overfishing (Winemiller 2005; Olden *et al.* 2006). The findings support those by Skelton *et al.* (1991) who noted that the genus has inflexible life history characteristics. According to the trilateral continuum proposed by Winemiller (1989) and Winemiller & Rose (1992), *Labeo capensis* is most likely a periodic strategist, which typically refers to a group of fishes that inhabit seasonal environments and where adults delay their maturation to a large size to synchronously spawn large clutches of eggs when conditions are favourable. Although some aspects such as fecundity and spawning behaviour were not investigated here, there seems to be sufficient evidence from the literature to support this characterization (Mulder 1973; Gaigher *et al.* 1980; Tómasson *et al.* 1984). Periodic strategists are considered to be the least adapted to habitats that have become temporally stable and that are subject to low resource availability due to decreased inundation of floodplains from damming (Olden *et al.* 2006). In addition, fishes with a long lifespan, delayed maturation and low adult mortality are typically vulnerable to overfishing (Adams 1980; Winemiller 2005; Froese *et al.* 2008). The persistence of *L. capensis* in Lake Gariep may therefore be linked to a combination of negligible fishing pressure and strong seasonal fluctuations in water levels, turbidity and floodplain availability that proximate environmental conditions suitable for successfully maintaining a periodic life-history strategy.

In Lake Gariep, fish were relatively slow-growing, long-lived and had a delayed maturity with males maturing after five years and females after six years after they attained 75% of their maximum theoretical size. Both sexes grew at a similar rate until the onset of maturation, after which males showed a relative decline in growth rate and significantly higher mortality rates, explaining the larger maximum length and age attained by females. The lower adult mortality in female *L. capensis* was also reflected in the highly skewed female-dominated sex ratio of adult fish, a trend that has also been found in other populations of *L. capensis* (Mulder 1973; Baird 1976; Gaigher *et al.* 1980; Tómasson *et al.* 1984). As female body mass and fecundity increase exponentially with size (Gaigher *et al.* 1980; Tómasson *et al.* 1984), the advantage of this strategy has been suggested to increase the total egg production capacity (Nikolskii

1969; Gaigher *et al.* 1980) illustrated by the differential reproductive contribution by females at a lower natural mortality rate and longevity.

While the higher mortality rates predicted for males might be partly explained by their earlier maturation (Charnov *et al.* 2001; Shuter *et al.* 2005), there are also indications that sex-specific differences in mortality rates are directly related to the spawning behaviour of this species. Tweddle & Davies (1997) suggested that ripe-running males remain congregated at the spawning ground to breed with individual females, which move up from deeper water, release their eggs and return to the open water again. Thus spawning males are likely to exhibit the more exhaustive spawning behaviour and are exposed longer to predation and injuries at the, usually, shallow spawning sites.

The choice of spawning sites may depend on the availability of suitable habitat. Spawning seems to occur preferably between newly inundated vegetation in flooded riparian areas as well as in impoundments (Mulder 1973; Gaigher *et al.* 1980; Tómasson *et al.* 1984), but spawning behaviour has also been observed over shallow riffles in the highly regulated lower Orange River (Cambray 1985). Synchronized longitudinal mass spawning migrations, as has been described for many other congeners (Skelton *et al.* 1991; Weyl & Hecht 1999; Rutaisire & Booth 2005), have never been reported for *L. capensis* (Mulder 1973; Baird 1976; Tómasson *et al.* 1984; van Zyl *et al.* 1995). Instead, the observed asynchrony in the maturation of adult fish over a prolonged breeding season indicates that *L. capensis* forms a non-homogeneous breeding population throughout the impoundment. During the breeding season spawning events may be a response to cues such as rainfall and associated run-off from temporary tributaries and the availability of temporary floodplain habitat (Cambray *et al.* 1978; Tómasson *et al.* 1984).

Individual females have been reported to spawn all their eggs simultaneously when local conditions for spawning are favourable (Gaigher *et al.* 1980; Tómasson *et al.* 1984; Tweddle & Davies 1997). That was evident by a complete absence of eggs in most of the spent specimens that were examined and spawning can be considered synchronous (Booth & Weyl 2000). The spawning behaviour of *L. capensis* can therefore be seen as an adaptation for maximizing individual batch fecundity during flood periods that normally last for only a few days. Other notable traits, which are

favourable for such a reproductive strategy, are the species' high fecundity (Baird 1976; Gaigher *et al.* 1980; Tómasson *et al.* 1984), as well as the short incubation time of the eggs, which lasts only between one and three days (Mulder 1973; Tómasson *et al.* 1984). Males, by contrast, seem to form larger aggregations at the spawning site (Tweddle & Davies 1997), which may result in increased competition for individual females that come to the spawning site, and release all their eggs at once. This would imply that males follow a batch spawning strategy within a single spawning event such that males are able to maximize their reproductive output by fertilizing ova from more than one female.

The comparison of growth and maturity estimates derived from previous studies on *L. capensis* indicated that slow growth and delayed maturity are typical traits for this species. The relatively slow growth becomes particularly pertinent when *L. capensis* Φ'-values are compared to the significantly faster growth performance (Φ' = 3.16–3.19) reported for the non-native common carp *Cyprinus carpio* population in Lake Gariep (*t*-value = 10.25, $P < 0.05$) (Winker *et al.* 2011).

Growth performance estimates obtained in this study appeared to be slightly lower when compared to studies where growth was derived from back-calculated length-at-age data based on scale interpretations (Table 3). Although it is possible that because *L. capensis* is a riverine species and growth conditions may therefore be more favourable under lotic conditions and during the filling phase of reservoirs (Bodaly & Lesack 1984; Tómasson *et al.* 1985), in this case, such interpretation on a relatively fine scale should be treated cautiously. Previous studies that used scales recorded maximum ages of 7–10 years (Table 3), whereas the interpretation of otoliths suggested that a maximum life span of 12 to 16 years can be expected (Tómasson 1983). Little or no growth in scales of older fish often causes age to be underestimated, which seems to be a common trend in studies using scales (Vilizzi & Walker 1999). Underestimation of the age of older fish inevitably results in faster growth rates, larger mean length-at-age and larger theoretical asymptotic length estimates, which would therefore alternatively explain the slightly higher Φ'-values computed for the riverine populations and for Lake Gariep's early impoundment population (Table 3). When considering the overall similarity of Φ'-values and taking into account that scale-based growth esti-mates could be slightly overestimated, there was no indication in the data that *L. capensis* drastically changed its growth performance to adapt to the more lacustrine conditions of Lake Gariep. Similarly, delayed maturity appeared to be a relatively conservative trait among populations with female age-at-(50%)-maturity frequently attained at an age older than half of the observed maximum life span (Table 3).

The observed similarity in growth performance and maturation also supports the general conclusion that the genus typically exhibits little adjustment in their life history traits to artificially created impoundments (Skelton *et al.* 1991). The only documented exception appears to be *L. umbratus* another sympatric congener that is also native to larger systems further south (Skelton 1986). In contrast to *L. capensis, L. umbratus* reveals large variations in the growth and maturity, which indicate a high degree of plasticity as a response to system-specific environmental conditions (Potts *et al.* 2006a) and may also explain why this species can tolerate a wide range of different environmental conditions in small reservoirs (Potts *et al.* 2006a,b)

To conclude, slow growth, delayed maturation in association with an extended life span and high individual batch fecundity are commonly observed traits in fishes that inhabit systems with strong seasonal fluctuations in environmental conditions (Winemiller 1992; Olden *et al.* 2006; Tedesco *et al.* 2008). This life history adaptation allows such populations to persist during extended periods of unsuitable spawning conditions, and take advantage of conditions during favourable years, while simultaneously maximizing individual fitness (Winemiller 1992; Tedesco *et al.* 2008). *Labeo capensis* dominated the ichthyofauna of Lake Gariep several decades after its impoundment, a situation not documented in any other large African impoundment. In Lake Gariep, the absence of fishing and the availability of seasonal floodplains that form when marginal vegetation is inundated by either the unregulated inflow of the Orange River or local erratic rains may therefore have played a vital role for the successful establishment of *L. capensis.*

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