Life history and population dynamics of invasive common carp, *Cyprinus carpio*, within a large turbid African impoundment

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Abstract. As one of the most widely established freshwater fishes globally, the invasive success of common carp, *Cyprinus carpio*, is beyond dispute. Although detailed knowledge on its biology would assist in its management, relatively few life history studies have investigated *C. carpio* outside of its natural range. The present study analyses the life history and population structure of exotic *C. carpio* in a 364 km^2 African impoundment. We used whole astericus otoliths to show that *C. carpio* attained ages of up to 7 years and grew more rapidly than has been recorded for any population from Europe or Australia. Macroscopic staging of gonads indicated protracted spawning, with highest reproductive activity observed during late spring and early summer. Total mortality, natural mortality and fishing mortality rates were estimated at 0.72, 0.60 and 0.12 year^{-1} respectively. Life history comparisons across the species' global distribution showed large variations in growth and longevity, whereas early maturation (2–3 years) appeared to be a rather conservative trait. The combination of early maturity, fast growth and relatively high natural mortality rates suggests a rapid population growth potential associated with high resilience to management interventions once *C. carpio* has been introduced.

Additional keywords: age, angling competition, growth, maturity, mortality rate, non-native, otolith, spawning season.

Introduction

Common carp (*Cyprinus carpio*) is one of the world's most widely introduced and established freshwater fishes (Casal 2006). The species is considered to be one of the eight most invasive freshwater fishes (Lowe *et al.* 2000) and worldwide, it accounts for most of the records of successful establishments and adverse ecological effects (Casal 2006; Kulhanek *et al.* 2011). This invasive success suggests that feral *C. carpio* is equipped with a set of adaptable life history attributes that allow it to successfully colonise a wide range of habitats (Koehn 2004; Zambrano *et al.* 2006; Britton *et al.* 2007).

Where feral *C. carpio* occurs in high densities, it is often perceived as an invasive pest species (Sivakumaran *et al.* 2003; Brown and Walker 2004; Koehn 2004) because it can have severe impacts on habitat heterogeneity and biodiversity by increasing water turbidity through its bottom feeding behaviour, increasing nutrient availability, decreasing benthic and macrophyte density and diversity, altering zooplankton assemblages and decreasing endemic fish abundance (Zambrano *et al.* 2001; Khan 2003; Kulhanek *et al.* 2011). Within south-east Australia, for example, *C. carpio* comprises the largest proportion of the ichthyobiomass in the continent's largest river system – the Murray–Darling Basin (Gehrke *et al.* 1995). As a

consequence, serious concerns about its threat to endemic freshwater species (Koehn 2004) have prompted several of the most recent investigations into its life history (e.g. Sivakumaran *et al.* 2003; Smith and Walker 2004; Brown *et al.* 2005). Other potential threats posed also include competition with indigenous species and the spread of diseases and parasites (Dudgeon *et al.* 2006). In South Africa, for example, Asian tapeworm *Bothriocephalus acheilognathi* is now widely distributed in seven river systems and has infected eight novel cyprinid hosts due to the translocation of infected by *C. carpio* from a centralised aquaculture facility (Stadtlander *et al.* 2011).

The invasive potential of *C. carpio* is beyond dispute as it can dominate the ichthyofauna of invaded systems to the extent that it is now the target species in several fisheries (Cochrane 1987; Moreau and De Silva 1990; Oyugi *et al.* 2011) or, in other instances, that costly management interventions are considered to control its abundance or prevent further spread (Brown and Walker 2004; Koehn 2004; Weber and Brown 2009). Understanding *C. carpio*'s life history and population dynamics would assist in its fisheries management or possibly eradication (Brown and Walker 2004; Brown *et al.* 2005; Oyugi *et al.* 2011).

Despite its global importance, relatively few life history studies have investigated *C. carpio* outside its natural range.

Within Australia, the Murray–Darling population has been comprehensively assessed with validated otolith-derived estimates of age, growth, age-at-maturity and mortality rates (Vilizzi and Walker 1999; Brown *et al.* 2004; Brown *et al.* 2005) and in Lake Naivasha, Kenya, scale-based estimates of age, growth and maturity were determined (Oyugi *et al.* 2011). The aim of the present study was to contribute to the knowledge of the biology of *C. carpio* within a warm-temperate invaded system outside its natural range together with providing a review of published life history parameters from localities throughout its global distribution.

Materials and methods

Study area

Lake Gariep (30°38′S; 25°46′E; 1250 m above mean sea level) is on the upper Orange River, South Africa (Fig. 1). The impoundment has a surface area of ~364 km², a mean depth of 16.3 m and a maximum depth of 50 m at full water level (Hamman 1981).

The region's climate is semiarid. Rainfall is seasonal with most of the ~400 mm annual precipitation falling in spring and 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 an oligo-mesotrophic impoundment that is highly turbid due to high levels of silt from the Orange River

(Keulder 1979). Annual average surface water temperature during this period was 15.9°C. The mean surface water temperature is 21.4°C (range 16.6–26°C) in summer and 10.2°C (8.7–11.3°C) in winter.

Sampling

Most of the samples were donated by anglers during four bank angling competitions held in November 2006, January 2007, April 2007 and October 2007 (Fig. 1). During these events, participant numbers ranged from 10 anglers during a 1-day trial competition to 120 anglers who fished over 3 consecutive days. During competitions, teams (consisting of two anglers) fished a randomly assigned 25 m fixed section along the shoreline within a larger demarcated fishing area. Each angler fished with two rods for the same strictly controlled 8 h competition period. After the official competition weigh-in was completed, specimens were collected by the research team for biological analysis from randomly selected weigh-in stations.

Fork length was measured to the nearest millimetre (L_F mm). Subsamples of measured specimens were selected at random, weighed to the nearest gram and sexed and the developmental stage of gonads macroscopically determined according to the criteria summarised in Table 1. Astericus otoliths were removed, dried and stored in Eppendorf tubes for later age determination.

Due to the standardised sampling design and large sample sizes, the data collected during angling competitions were
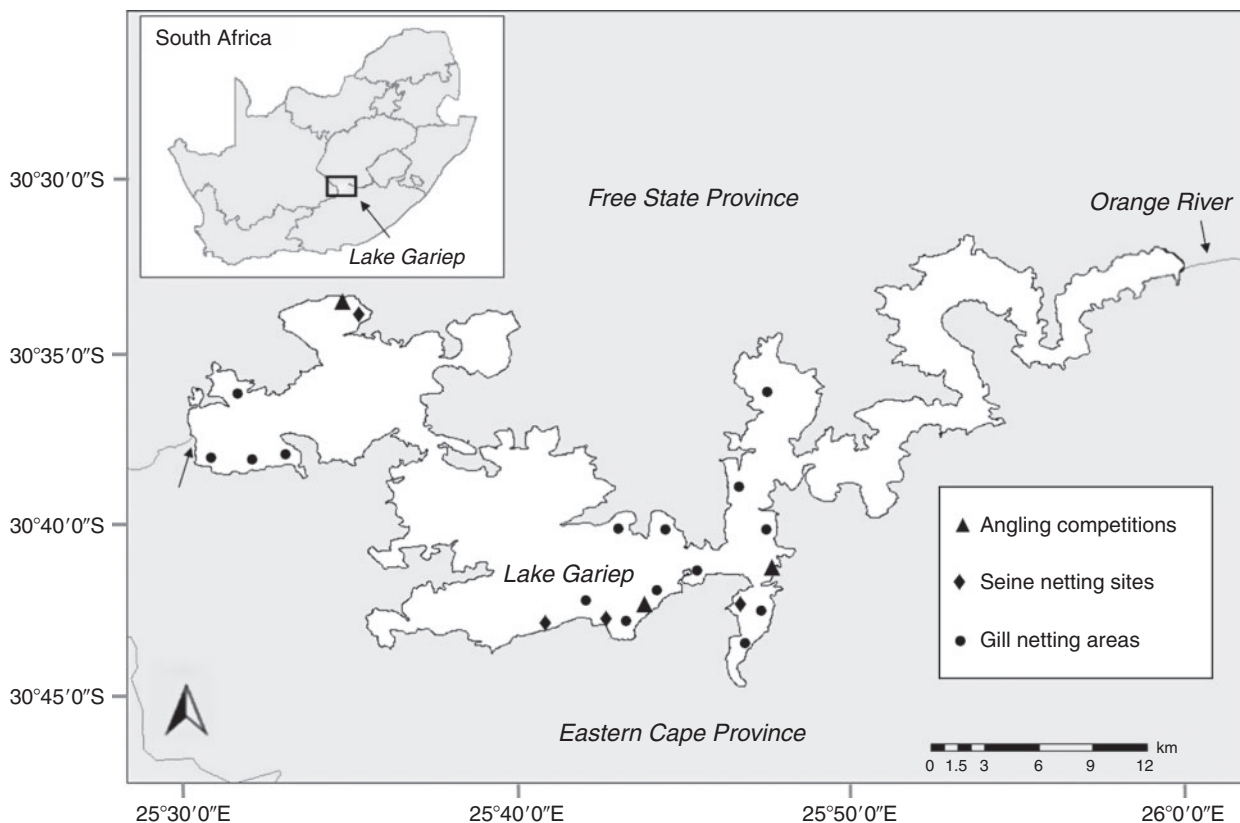

Fig. 1.   Map of Lake Gariep showing locations of sampled angling competitions, gill netting sites and areas used for seine netting experiments.

considered as being suitable to determine growth, size- and age-at maturation and size structure of the *C. carpio* population. For the evaluation of temporal changes in gonadal development and to obtain additional length-at-age information, these samples were supplemented by specimens collected during bi-monthly gill net surveys (March 2007–March 2008) conducted with a fleet of five 45 m multifilament nets (5 × 9 m panels of 47, 65, 77, 105 and 152 mm stretched mesh size) and during seine netting experiments (April 2007, January 2008 and May 2008) (Fig. 1).

Overall, more than 2500 specimens were measured, of which 1500 were sexed and staged and otolith pairs were removed from more than 800 specimens. Angling competitions contributed significantly to the dataset (i.e. 86% of all *C. carpio* measured; 75% of all sexed and staged individuals and 81% of otoliths).

Age and growth

To determine length-at-age, 782 whole astericus otoliths were examined by submerging them in methyl salicylate and viewing them under transmitted light using varying magnifications (×10–40) according to the procedures outlined by Winker *et al.* (2010). Mark–recapture of adult *C. carpio* chemically tagged using oxytetracycline hydrochloride, along with edge analysis and corroboration by a length-based age structured model provided evidence that two growth zones are deposited each year, one in early summer and one during winter (Winker *et al.* 2010). To minimise potential ageing biases caused by variability in the timing of biannual growth zone depositions, spawning periodicity or differences in gear selectivity, only the two largest otolith samples, collected during angling competitions in November 2006 ($n = 325$) and January 2007 ($n = 241$), were used for modelling length-at-age. As age-0 fish were absent from these samples, otolith samples from young-of-the-year fish (YOY) were also added. The YOY fish were collected from small-meshed seine net catches in January 2008 ($n = 8$), March 2008 ($n = 12$) and May 2008 ($n = 4$). To avoid false year–class identification, monthly age estimates were back-calculated by assuming that all fish were born in November (the peak spawning period) and that one (post spawning) opaque zone formation occurred between November and January and a second (winter) between June and August (Winker *et al.* 2010). For those specimens caught between January and May, the number of months between November and date of capture was therefore added together.

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

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

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 minimising the negated normal log-likelihood function. Likelihood ratio tests were used to test the null hypothesis that growth was equal between sexes. Parameter variability was estimated using the conditioned parametric bootstrap re-sampling technique described by Efron (1981). 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

The sex and the developmental stage of gonads were determined macroscopically according to the criteria in Table 1. Length-at-(50%)-sexual maturity (Lm_{50}) was determined based on 436 male and 467 female fish collected during peak reproduction periods. The proportion of reproductively active fish (developing, ripe or spent) was calculated by grouping specimens into 10 mm size classes and fitting a two-parameter logistic model:

$$P(L) = \left(1 + \exp\left(-\frac{(L - Lm_{50})}{\delta_L} \right) \right)^{-1}, \quad (2)$$

where $P(L)$ is the proportion of mature fish at length L and δ_L the width of the ogive. Maximum likelihood estimates of these parameters were obtained by minimising the negated binomial log-likelihood function. Age-at-maturity was described as the fraction of mature fish per age class using age estimates from otoliths.

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. Only those sampling months where the sample size exceeded 10 adult fish were considered in the analysis.

Population structure

The length–frequency data collected during angling competitions were considered as being most suitable to represent the size structure of the *C. carpio* population. The corresponding age structures of these samples were estimated by transforming the length frequencies into age frequencies using an age-length-key

Table 1.   Macroscopic criteria used to determine gonadal development stages in *Cyprinus carpio* from Lake Gariep, South Africa (modified from Smith and Walker 2004; Weyl and Booth 1999)

Stage	Macroscopic appearance
Juvenile	Not possible to visibly distinguish the sex. Gonads appear as translucent thin strips
Immature	Sex distinguishable. Ovary visible as translucent strip. Testes form thin, but opaque white strips
Resting	Ovary increased in size and translucent. Testis visible as a white and straight strip
Developing	Enlarged ovary becomes opaque and is orange–red. Oocytes are visible. Testis increased in size and becomes lobular in shape
Ripe	Ovaries turgid with oocytes filling the entire abdominal cavity. Oocytes are olive-green in colour. Blood capillaries are abundant. Testes creamy white, enlarged and fill more than a third of the body cavity. Sperm can be extruded from testes
Spent	Ovary and testis flaccid and reddish in appearance. Ovary occasionally with a few vitellogenic oocytes present

based on length-at-age data of 737 individuals. Age-0 fish were not included in the analysis as these were absent from angler catches. The catchability of larger *C. carpio* may be strongly influenced by a size-dependent shift in seasonal habitat use (García-Berthou 2001; Penne and Pierce 2008). Therefore, size and age distributions from angling competitions were graphically assessed and related to season and spawning activity to choose the age distributions that most closely resemble the population structure.

Mortality

Estimates of the instantaneous total mortality (Z) were obtained from normalised age frequencies by means of a catch curve analysis (Ricker 1975) and the maximum likelihood method described by Chapman and Robson (1960). As the *C. carpio* population in Lake Gariep can be assumed to be only lightly exploited ($\sim 2\,\mathrm{kg\,ha^{-1}\,year^{-1}}$; Ellender *et al.* 2010*b*), the empirical equation described by Hoenig (1983) was considered as suitable to obtain a first estimate of the instantaneous rate of
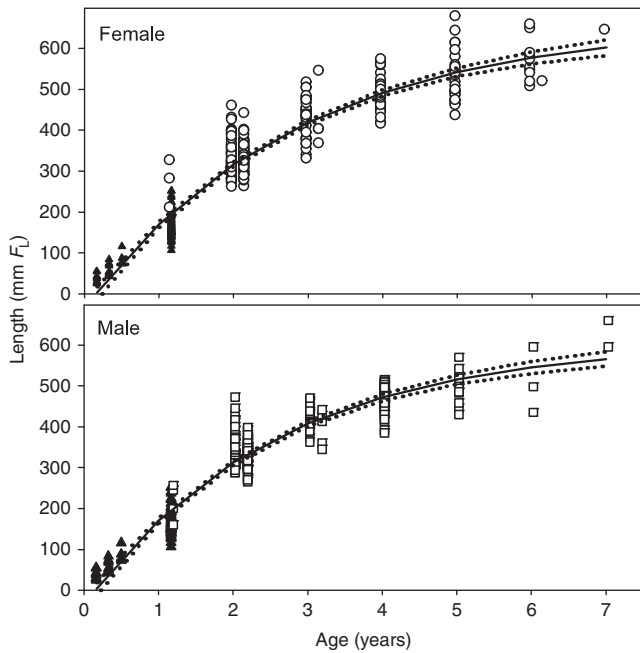
natural mortality (M). Fishing mortality (F) was then calculated by subtraction, as

$$F = Z - M. \tag{3}$$

A non-parametric bootstrap procedure (Efron and Tibshirani 1986) was applied to estimate standard errors (s.e.), coefficients of variation (CV) and confidence intervals for Z. For this purpose, random datasets were generated by re-sampling the length measurements and length-at-age data with replacement using a dynamic length–frequency table and a dynamic age-length-key respectively. The Ricker (1975) and the Chapman and Robson (1960) model was executed 1000 times and the percentile method (Buckland 1984) was used to estimate 95% confidence intervals from resulting bootstrap vectors.

Intra-specific life history comparison

Available age-derived life history parameters for *C. carpio* populations across a wide range of different locations were collated from published literature. For ease of comparison between this study and growth studies conducted on other populations of *C. carpio*, the growth performance index (Φ') was calculated:

$$\Phi' = \log K + 2 \log L_\infty, \tag{4}$$

where Φ' is measured in cm (Pauly and Munro 1984) and used. 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. All length estimates given in total length (L_T mm) and standard length (L_S mm) were first converted to fork length (F_L mm) by using the length–length relationships

$$T_L = 18.22 + 1.064 L_F, \tag{5}$$

and

$$L_S = 35.24 + 1.117 L_S, \tag{6}$$

($n = 436$) (Treer *et al.* 2003).

Results

Age and growth

Length-at-age was described adequately using the von Bertalanffy growth model (Fig. 2). A likelihood ratio test showed that growth differed significantly between males and females ($\chi_3^2 = 10.33$, $P < 0.001$), with females attaining a larger maximum size than males. The data from unsexed juveniles ($n = 81$) were then pooled with male ($n = 222$), female ($n = 257$) and combined data from both sexes. The fitted parameters for the von Bertalanffy growth function are summarised in Table 2.

Fig. 2. Length-at-age data for *Cyprinus carpio* using whole otoliths ($n = 474$) sampled in Lake Gariep, South Africa. Growth was best described by the von Bertalanffy growth model assuming a normal error distribution. Growth curve fits illustrated for females (○; $n = 257$) and juveniles (▲; $n = 87$) for males (□; $n = 222$) and juveniles. Thin dotted lines indicate upper and lower 95% confidence intervals.

Table 2.   Parameter estimates and 95% confidence intervals (in parentheses) of length-at-age data using the von Bertalanffy growth model with a normal error structure for *Cyprinus carpio* sampled at Lake Gariep, South Africa

Parameter	Juveniles + males ($n = 310$)		Juveniles + females ($n = 345$)		Combined ($n = 566$)	
L_∞ (mm F_L)	607.3	(580.3, 640.7)	662.3	(627.0, 701.2)	625.8	(604.6, 652.1)
K (year^{-1})	0.39	(0.35, 0.43)	0.35	(0.32, 0.39)	0.39	(0.35, 0.41)
t_0 (years)	0.16	(0.08, 0.22)	0.16	(−0.02, 0.02)	0.16	(−0.07, 0.22)

A maximum age of 7 years was attained by both sexes. The weight-length relationship was described as weight (g) = $0.000053 \times F_L$ (mm)$^{2.829}$ ($n = 275$; $R^2 = 0.97$).

Reproduction

Length-at-(50%)-maturity was estimated at 295.9 mm F_L ($\delta_L = 37.7$ mm) for males and 334.8 mm F_L ($\delta_L = 45.6$ mm) for females. The smallest mature male and female in the sample was 258 mm F_L and 276 mm F_L respectively. The proportion of mature males ($n = 136$) and females ($n = 187$) per age class was based on the age estimates available from otolith samples obtained from the peak spawning period in November 2006

(Fig. 3). The results showed that the onset of maturity proceeded relatively quickly. While none of the age-1 fish were mature, 75% of the age-2 males and 58% of the age-2 females were categorised as reproductively active (Table 3). By age-3, over 80% of the females and close to 100% of the males attained sexual maturity (Table 3). The adult population was only slightly female-dominated with a ratio of 1.1 females : 1 male (length bins 330 – 680 mm F_L) and did not differ significantly from unity ($\chi^2_1 = 0.52$, $P = 0.470$).

The interpretation of spawning dynamics on a seasonal level was restricted by the inherent difficulty of consistently obtaining sufficiently large adult *C. carpio* samples during routine gill net
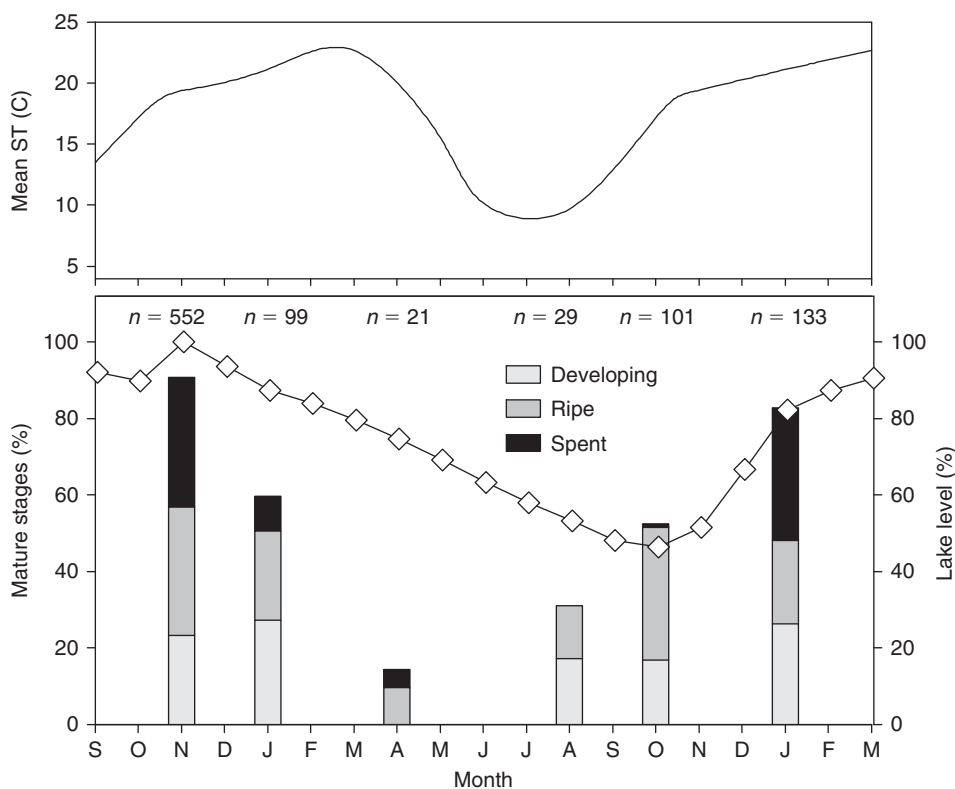

Fig. 3. Proportion of reproductively active adult *Cyprinus carpio* (combined bar height) from Lake Gariep and the lake's water levels expressed as percent of the full capacity ($\diamond$, solid line) for the period September 2006 to March 2008. The proportion of adult reproductive stages is illustrated within each bar. The upper graph illustrates general trends in mean surface water temperature in °C (ST) based on measurements taken during bi-monthly gill net surveys (May 2007–March 2008), which were then interpolated across the study period.

Table 3. Observed proportion of mature *Cyprinus carpio* per age class calculated from otolith subsamples collected at Lake Gariep during a peak spawning period (November 2006)

Sex		Age class (years)						
		1	2	3	4	5	6	7
Female	Fraction mature	0.00	0.58	0.83	0.95	0.96	1.00	1.00
	Sample size (n)	8	69	35	39	25	10	1
Male	Fraction mature	0.00	0.75	0.96	1.00	1.00	1.00	1.00
	Sample size (n)	5	56	23	34	13	3	2

surveys. Nevertheless, a seasonal trend could be derived from the six sampling events investigated (Fig. 3). November 2006 marked a peak spawning event with more than 90% of the adult population ($>335\,mm$ F_L) categorised as reproductively active and more than 60% staged as either ripe or spent (Fig. 3). Spawning activity had decreased slightly in January 2007 and the proportion of spent specimens was small (9%). However, 23% of the adult population was still in ripe condition and an increase in the developing stage (38%) indicated the potential for subsequent spawning events. By April 2007, the proportion of reproductively active individuals reached a minimum, with no gonads found to be in a developing stage and more than 85% of gonads categorised as resting. Gonadal development had increased by August 2007 (17%), when the first ripe gonads (12%) were also observed. By October 2007, this trend was amplified with 35% of gonads found in a ripe stage. By January 2007, more than 80% of the gonads examined were categorised as reproductively active, indicating a peak spawning period. Water level fluctuations and gonadal development showed similar trends with a small lag between changes in the proportion of gonad stages and water levels (Fig. 3). Highest spawning activity was noted at high water levels and at temperatures in excess of 17°C. Spawning activity decreased as water levels receded during late summer and early autumn (Fig. 3).

Population structure and mortality rates

The largest proportion of fish $>400\,mm$ F_L and older than 2 years (3+ group) was caught during shore angling competitions in November 2006 (Fig. 4*a*) that coincided with peak spawning (Fig. 3). Smaller size classes were virtually absent from this sample and recruited into angling competition catches only during subsequent events in January and April 2007, whereas the age-3+ group became rare during these periods (Fig. 4*f, g*). By October 2007, the proportion of the age-3+ group had increased again (Fig. 4*h*), accompanied by a relative increase in spawning activity (Fig. 3). Length and age frequencies still appeared to be truncated with respect to larger and older fish when compared with November 2006, when spawning activity reached a relative maximum (Fig. 3). As a result, it was assumed that the large November sample ($n = 695$) best resembled the population structure of age-2+ fish, whereas samples obtained during other periods appeared to be negatively biased towards larger specimens and would therefore have resulted in unrealistically truncated age distributions that would positively bias the high total mortality estimates ($Z = 0.84$–2.48) (Fig. 4 *f, h*).

The resultant total mortality rates and 95% confidence intervals were estimated as $Z = 0.72$ (0.67, 0.77) by the Chapman and Robson (1960) estimator and $Z = 0.74$ (0.63, 0.10) using catch curve analysis. Although the catch curve analysis provided a relatively good fit of the linear regression ($R^2 = 0.97$), the non-parametric bootstrapping procedure showed that the Chapman and Robson (1960) estimate was less variable with a CV of 4.0% compared with 12.7% from catch curve analysis and was, therefore, considered the more precise estimate. Natural mortality was estimated at $M = 0.60$ year^{-1} based on a maximum observed age of 7 years. Fishing mortality was relatively low and estimated at $F = 0.12$ year^{-1}.

Life history comparison

The comparison among *C. carpio* populations indicated that feral *C. carpio* populations introduced to Australia, the USA and Africa generally had a faster growth performance (Φ') than their European conspecifics, with the considerably slow growing Barmah Forest *C. carpio* population in Australia being the only exception (Table 4). Age-at-maturity was similar among feral and koi populations and typically attained during the second year of life. By contrast, age-at-maturity in females from the only available record for the wild form of *C. carpio* was considerably delayed. Differences in age-at-maturity between sexes appeared to be less pronounced in feral and koi *C. carpio* when compared with the wild form. Maximum age estimates showed large variations among populations ranging from 28 years for the Barmah Forest, Australia, to as short as 3 and 4 years in the equatorial Lake Navaisha, Kenya. The Lake Gariep population was relatively short lived (7 years), comparable to the South African population in Hartbeespoort Dam and the Mediterranean Guadalquivir River population in Spain.

Discussion

Fast growth, earlier maturity, short generation times and, thus, a high intrinsic rate of population increase concomitant with a high rate of natural mortality are considered typical traits that maximise the colonising capability of fishes in general (e.g. Winemiller and Rose 1992) and of *C. carpio* in particular (Koehn 2004; Weber and Brown 2009). Compared with other feral *C. carpio* populations, the Lake Gariep population exhibited similar early maturation in combination with a relative fast growth performance and short generation turn over. This emphasises the potential of *C. carpio* to rapidly colonise and dominate currently uninvaded freshwater systems.

Growth

The comparison of growth performances among *C. carpio* populations is, to some extent, limited by the uncertainty about the annual frequency of growth zone deposition for the majority of *C. carpio* populations worldwide. The Lake Gariep population, for example, showed strong evidence for a biannual growth zone deposition rate (Winker *et al.* 2010), whereas a commonly assumed annual growth zone deposition rate would have resulted in a severe underestimation of the growth performance as well as different age-at-maturity, longevity and mortality estimates. Although *C. carpio* is one of the better studied cyprinids, detailed life history studies based on formal validation of growth zone deposition rate and accuracy of ageing are rare and to date, asteriscus otoliths represent the only hard structure that has been directly validated using fluorochrome marking (Brown *et al.* 2004; Winker *et al.* 2010). In general, comparisons of ageing structures for *C. carpio* indicated that age and growth estimates based on dorsal spines and asteriscus otoliths can be considered more reliable than those based on scales (Vilizzi and Walker 1999; Jackson and Quist 2007; Phelps *et al.* 2007).

Overall, invasive feral *C. carpio* populations in Australia, the USA and South Africa tended to grow faster than reported for European populations. In this regard, milder temperature regimes have been suggested to play an important role for
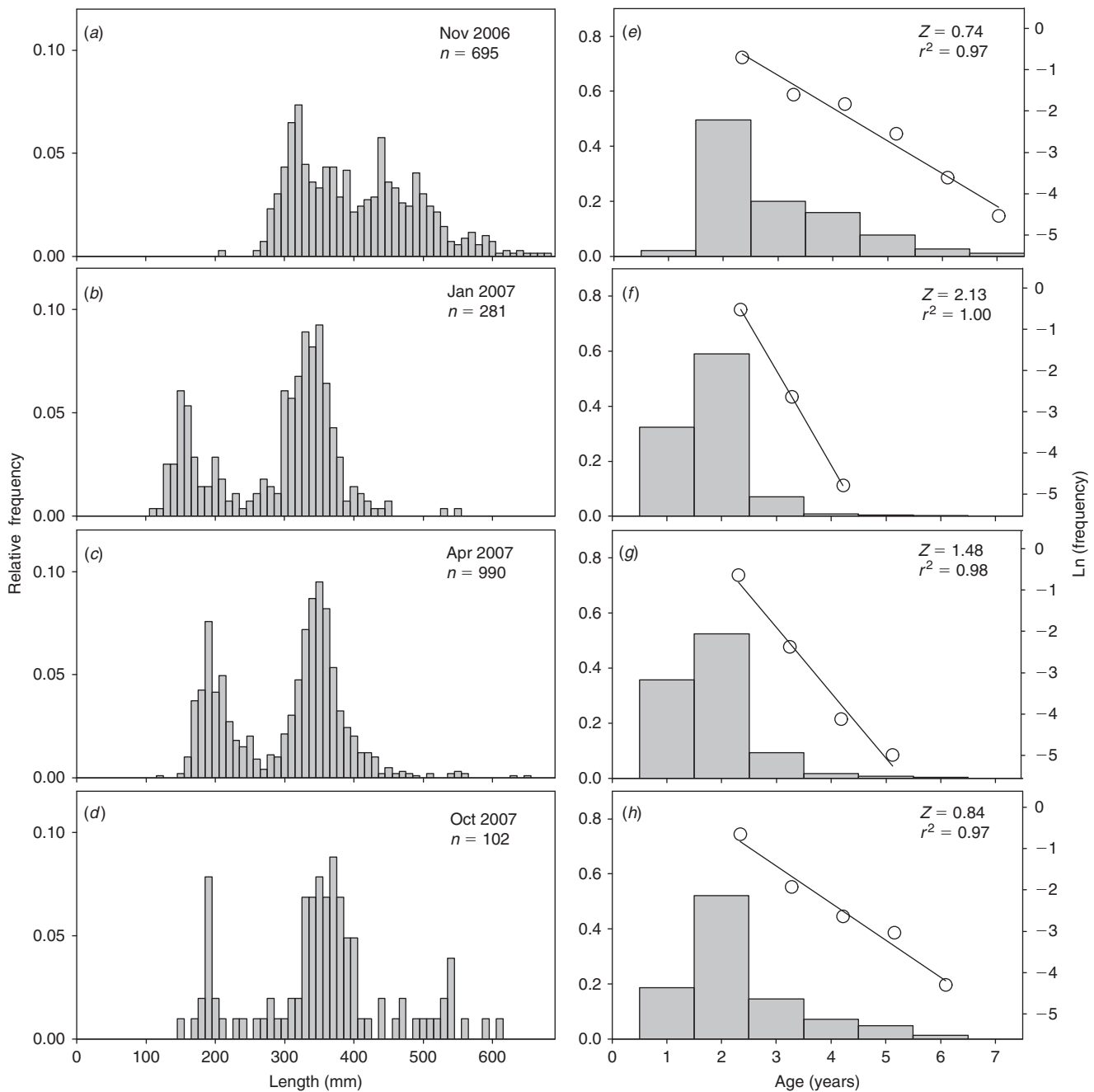
Fig. 4. Relative length–frequency distributions (*a–d*) and corresponding transformed age-frequencies with catch curves (*e–h*) of *Cyprinus carpio* derived from data collected during four angling completion surveys (2006–2007) at Lake Gariep, South Africa.

increased growth performance (Oyugi *et al.* 2011), which is corroborated by experimental studies that determined maximum growth and food conversion rates at temperatures between 24 and 30°C (Suzuki *et al.* 1977; Goolish and Adelman 1984). However, large variations in growth rates despite comparable climate regimes have been reported among several *C. carpio* populations within South Dakota (Weber *et al.* 2010) and were evident on comparison among the three Australian *C. carpio* populations within the Murray–Darling system

(Table 4), which points towards strong, possibly overriding, influences of other factors on growth rates, such as density-dependent processes and food availability (Lorenzen 1996; Weber *et al.* 2010).

Reproduction

In the Danube, wild *C. carpio* were observed to spawn at 10–14 day intervals, being interrupted when water temperatures

Table 4. Ageing method and measured parameters for *Cyprinus carpio* from different localities

Abbreviations: t_{max}, maximum observed age; L_{max} (mm) FL, maximum observed length; L_∞, K and t_0, von Bertalanffy growth parameters; $\Phi' = 2\text{Log}(L_\infty \text{ mm FL}/10) + \log(K)$, growth performance (Pauly and Munro 1984); L_m (mm) FL, length-at-maturity; T_m, age-at-maturity

Sex	Method	Variant	t_{max}	L_{max}	L_∞	K	t_0	Φ'	L_m	T_m	Region/source
Male	Otoliths[N]	Feral	24	570	489	0.25	−0.52	2.77	307	2–3	Barmah Forest[A], Australia
Female	Otoliths[N]	Feral	28	623	594	0.18	−0.61	2.80	328	2–3	Barmah Forest[A], Australia
Combined	Scales	Feral	13	554	550	0.20	−0.93	2.79	–	2–3	Carmargue[B], France
Combined	Scales	Feral	11	632	752	0.12	−0.81	2.84	–	–	Vrasko Lake[C], Croatia
Female	Scales	Feral	5	494	767	0.15	−0.62	2.94	–	–	Gölhisar Lake[D], Turkey
Male	Scales	Feral	6	460	728	0.17	−0.45	2.96	–	–	Gölhisar Lake[D], Turkey
Combined	Scales	Feral	6	438	796	0.14	0.03	2.96	–	2–3	Guadalquivir River[E], Spain
Combined	Scales	Koi	12	700	675	0.21	0.15	2.98	–	2–3	Waikato region[F], New Zealand
Male	Scales	Wild	15	–	694	0.14	−1.10	2.82	316	3+	Danube[G], Slowakia
Female	Scales	Wild	9	–	615	0.30	0.03	3.06	347	5+	Danube[G], Slowakia
Female	Otoliths[N]	Feral	17	680	538	0.38	−0.39	3.04	273	2–3	Campaspe channels[H], Australia
Male	Otoliths[N]	Feral	17	570	495	0.48	−0.29	3.07	287	2–3	Campaspe channels[H], Australia
Combined	Various[O]	Feral	–	–	679	0.28	0.01	3.12	–	–	41 populations[I], USA
Male	Otoliths[N]	Feral	12	649	600	0.35	0.17	3.10	–	–	lower Murray River[J], Australia
Female	Otoliths[N]	Feral	15	688	639	0.35	0.17	3.16	–	–	lower Murray River[J], Australia
Male	Otoliths[N]	Feral	7	661	607	0.39	0.16	3.16	296	2–3	Lake Gariep[K], South Africa
Female	Otoliths[N]	Feral	7	680	662	0.35	0.16	3.19	335	2–3	Lake Gariep[K], South Africa
Combined	Pectoral fin[N]	Feral	–	1037	786	0.33	–	3.31	–	–	15 populations[L], South Dakota, USA
Male	Vertebrae[N]	Feral	6	729	619	0.56	−0.15	3.33	–	2–3	Hartbeespoort Dam[M], South Africa
Female	Vertebrae[N]	Feral	6	729	639	0.69	0.14	3.45	403	2–3	Hartbeespoort Dam[M], South Africa
Male	Scales[N]	Feral	3	694	618	0.68	–	3.41	340	1	Lake Naivasha[N], Kenya
Female	Scales[N]	Feral	4	694	755	0.75	–	3.63	420	2	Lake Naivasha[N], Kenya

[A]Brown *et al.* (2005). [B]Crivelli (1981). [C]Treer *et al.* (2003). [D]Ahmet and Süleyman (2000). [E]Fernàndez-Delgado (1990). [F]Tempero *et al.* (2006). [G]Balon (1995). [H]Brown and Walker (2004). [I]Jackson *et al.* (2008). [J]Vilizzi and Walker (1999). [K]Present study. [L]Weber *et al.* (2010). [M]Cochrane (1985), Oyugi *et al.* (2011). [N]Studies where age and growth is based on validation or corroboration of growth zone deposition rates. [O]Various aging methods.

dropped below 17°C (Balon 1995). Except for the relatively delayed maturation in female wild *C. carpio* (Table 4), comparable spawning behaviour has been documented for feral *C. carpio* populations (Crivelli 1981; Fernàndez-Delgado 1990; Sivakumaran *et al.* 2003; Smith and Walker 2004; Brown *et al.* 2005). The Lake Gariep population followed a similar spawning pattern with spawning activities correlated with water temperatures exceeding 17°C in spring and the availability of recently inundated areas from the spring and early summer rains. The presence of ripe females in all samples ranging from August (late winter) to April (mid-autumn) generally concurs with the observation that the reproductive activity appears to be more protracted in milder climates when compared with temperate northern latitudes (Sivakumaran *et al.* 2003). In extreme cases, spawning may even occur throughout the year, such as reported for the equatorial *C. carpio* population in Lake Naivasha, Kenya (Oyugi *et al.* 2011).

Mortality

Comparative life history studies of fishes have shown that their life history traits are interrelated and constrained among themselves (Pauly 1980; Roff 1984). The timing of maturation, for example, strongly influences growth and mortality (and *vice versa*) because during maturation, energy allocated to reproduction is no longer available for either somatic growth or somatic tissue maintenance (Partridge and Sibly 1991; Charnov *et al.* 2001; Shuter *et al.* 2005). As age-at-maturity was similarly

early among feral and koi populations, it could be hypothesised that the relatively short life span (t_{max}) of the three African populations ($t_{max} = 3$–7 years) is a trade-off between faster growth performances and higher mortality rates, given that mortality and longevity are correlated (Hoenig 1983). In contrast, the oldest aged *C. carpio* was observed in the Barmah Forest *C. carpio* population (Brown *et al.* 2005), which also showed the lowest growth performance.

Reduced longevity can also be caused by heavy fishing pressure. In Hartbeespoort Dam, for example, Cochrane (1987) estimated that recreational anglers harvested 500 tons year^{-1} (250 kg ha^{-1} year^{-1}) of *C. carpio* in 1984, which may have resulted in a severe truncation of the population structure and could explain the low observed maximum age in the population (Table 4). Similarly, Fernàndez-Delgado (1990) did not exclude the effect of fishing mortality as a possible cause for the small number of observed age groups in the Guadalquivir River. By contrast, the impact of fishing mortality is considered minimal for most Australian populations of *C. carpio* (Brown *et al.* 2005), as well as the population in the Camargue, France (Crivelli 1981). The fisheries resource of Lake Gariep is exclusively used by subsistence and recreational anglers (Ellender *et al.* 2009; Ellender *et al.* 2010a) and annual harvest in 2007 was estimated at 71.4 t year^{-1}, of which, *C. carpio* accounted for 78.5% (Ellender *et al.* 2010b). Given the large surface area of the impoundment (~364 km^2), the annual exploitation is low, only approximating 2 kg ha^{-1} year^{-1}.

Therefore, it is reasonable to assume that fishing pressure has a minor effect on the age structure and population dynamics of *C. carpio*, which is also corroborated by the low estimated fishing mortality ($F = 0.12$ year^{-1}). When considering that none of the ~1600 specimens measured during a shore angler roving creel survey (Ellender *et al.* 2010*b*) exceeded the maximum observed length (680 mm F_L) of the present study ($n > 2500$) and that a representative subsample of ~800 specimens were aged, it appears unlikely that a significant proportion of the Lake Gariep population exceeds the maximum observed age of 7 years. Therefore, Hoenig's (1983) empirical equation derived from longevity data of unexploited and lightly exploited populations is considered to provide a relatively accurate indication of the natural mortality rate ($M = 0.6$ year^{-1}) of this population.

Conclusion

To conclude, the results of this study emphasise the difficulty in generalising life history strategies for fishes like *C. carpio* that have colonised a wide range of freshwater systems (Casal 2006; Zambrano *et al.* 2006) and may exhibit extreme phenotypic plasticity within their life history traits (Balon 1995; Matsuzaki *et al.* 2009; Weber and Brown 2009). In this regard, it could be argued that the high degree of phenotypic plasticity is a key adaptive trait of *C. carpio* in that it directly acts on growth and longevity in response to resource availability (Bøhn *et al.* 2004; Fox *et al.* 2007; Weber *et al.* 2010). This is supported by the observation that growth rates and longevity of *C. carpio* revealed large intraspecific variations, even within the same system (Vilizzi and Walker 1999; Brown and Walker 2004; Brown *et al.* 2005) or region (Weber *et al.* 2010). However, age-at-maturity seems to be a rather conservative trait among feral *C. carpio* populations. Maturation at a younger age implies a shorter generation turn over time and therefore a shift towards a more opportunistic life history strategy when compared with its wild form (Winemiller and Rose 1992). In this situation, if there is fast growth, short generation times and high natural mortality rates with an early maturation schedule, then this would provide the optimal conditions for rapid population growth and partially explain the invasive success of feral *C. carpio*.

Acknowledgements

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