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Life-history characteristics of an age-validated established invasive African sharptooth catfish, *Clarias gariepinus*, population in a warm–temperate African impoundment

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It has been suggested that the invasive, omnivorous *Clarias garipienus* is capable of rapid invasions and long-term persistence in recently inhabited freshwater systems. To test this hypothesis, the life history of the established, extralimital Darlington Dam (33°10′31″S, 25°09′13″E) population was investigated. By counting post-fluorescent mark increments on otoliths from 21 chemically tagged wild fish recaptured 244–537 days later, the deposition of growth zones, comprising alternating opaque and translucent bands, was validated as annual. Examination of sectioned otoliths from 175 fish revealed that the oldest fish, two males of 840 and 1074 mm total length (TL), were 25 years old – 10 years older than previously described for any *C. gariepinus* population. The oldest female was 885 mm TL and 21 years old. Length-at-age was subsequently described using the von Bertalanffy growth model. Combined-sex growth was best described as $L_t = 931.7\,(1 - \exp(-0.15(t + 2.43)))$ mm TL. Total mortality (Z) was calculated using catch curve analysis and the Chapman & Robson estimator to be 0.35/yr. The presence of specimens 15 years and older indicates that these fish established quickly and supports the finding that mortality rates are low, which, in turn, suggests likely long-term population persistence.

Key words: annulus validation, von Bertalanffy, mortality, longevity.

INTRODUCTION

African sharptooth catfish *Clarias gariepinus* (Burchell, 1822) is a widely distributed fish that has now invaded water bodies in South America, Eastern Europe, Asia and South Africa (Cambray 2003). In South Africa it is native as far south as the Orange-Vaal river system, but inter-basin water transfer schemes (IBWTs), illegal stocking by anglers and from aquaculture has resulted in the establishment of extralimital populations in almost all river systems (van Rensburg *et al*. 2011). Within the Eastern Cape Province, *C. gariepinus* has invaded the Great Fish and Sundays rivers through IBWTs, that connect the Orange River to the Great Fish River and then to the Sundays River system which flows directly into Darlington Dam (Kadye & Booth 2013a) (Fig. 1). Soon after the completion of the IBWTs sharptooth catfish were recorded in Grassridge Dam in 1976 (Laurenson & Hocutt 1985), and later from Darlington Dam in 1981 (Scott *et al*. 2006). Although Cambray & Jubb (1977) are of the opinion that the species was translocated prior to the IBWT connection, there is now a permanent corridor between the Orange River and its receiving river systems that can facilitate the continued introduction of non-native Orange River fishes and other aquatic biota.

There is concern that highly mobile, large and omnivorous fishes, such as *C. gariepinus*, can negatively impact native fish communities (Kadye & Booth 2012a,b, 2013a,b). Understanding the biology of *C. gariepinus* in invaded environments is therefore important for determining its potential impacts and future invasions. While our understanding of its potential impacts is improving (Kadye & Booth 2012a,b, 2013a,b) there have been few life history studies within its extralimital distribution range. The objective of this study was to evaluate the long-term establishment success of

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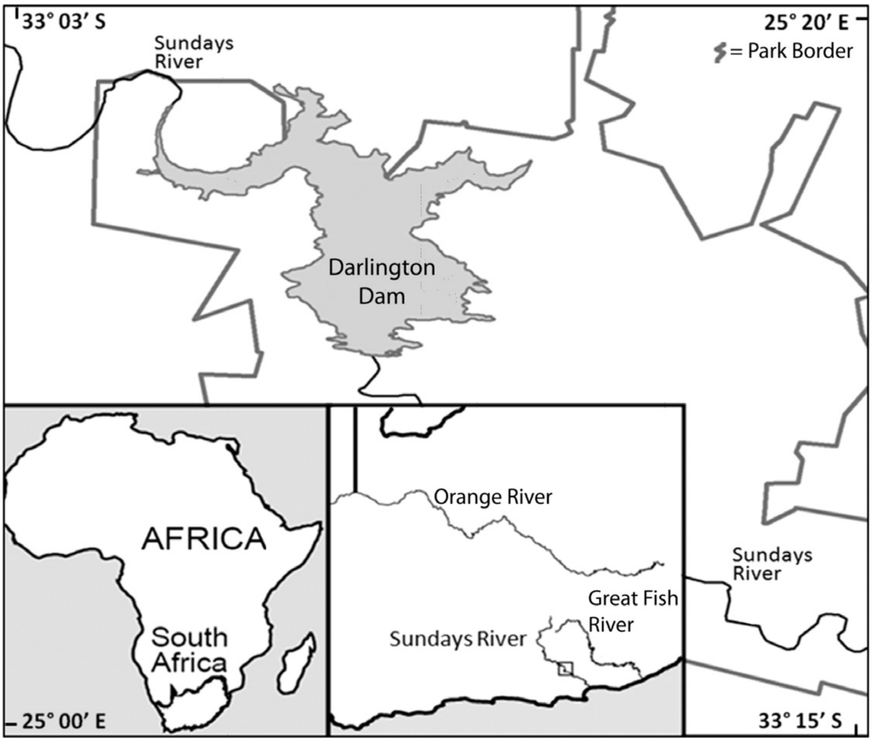

Fig. 1. Map showing the location of Darlington Dam situated within the Addo Elephant National Park, South Africa.

C. gariepinus in one of the first invaded impoundments in the Eastern Cape, South Africa, by determining its longevity, rates of growth and mortality, and comparing these to other native and extralimital populations. As these life history characteristics depend on the accurate determination of age (Campana 2001), the current assessment included a comprehensive validation experiment based on the mark–release–recapture of chemically tagged wild fish.

MATERIALS & METHODS

Study site

Darlington Dam (33°10′31″S, 25°09′13″E) is a 3453 ha impoundment situated in the Eastern Cape, South Africa (Fig. 1). It is shallow (maximum depth ~5 m), turbid (Secchi depth = 16 ± 5 cm), moderately conductive (638 ±70 μS/cm) and does not stratify. Water temperatures ranged from 10.5°C in mid-winter (August) to 24.5°C in mid-summer (February). Between 2000 and 2009 the mean water level of the dam was 37% of full capacity as regulated by the Sundays River Irrigation Authority (Department of Water Affairs unpubl. data). Submerged habitat in the dam is homogeneous and dominated by mud and shale. The fish community consists of 11 species of which only four are native. The native eel, *Anguilla mossambica,* and the non-native *C. gariepinus* are the only large predatory fishes (Kadye & Booth 2013b).

Sampling protocol

Sampling was conducted bi-monthly between June 2007 and August 2009 using gill nets, long lines and angler donations. Gill nets measured 45 m in length and comprised five panels (44, 60, 75, 100 and 144 mm stretched mesh sizes), each 9 m long and 3 m deep. Each long line comprised 100 m of floating line, 20 m of lead line and snoods of approximately 1 m at 4–5 m intervals each fitted with a baited 6/0 circle hook. Gill nets and long lines were set following a randomly stratified sampling protocol that was designed to cover both bays and open water sites to ensure a comprehensive, balanced sampling of all areas. Soak time for all gear ranged from 5–12 hours.

Age and growth

The study comprised an age validation and a fish ageing component. In order to validate the period-

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icity of otolith growth zone formation, a mark–recapture experiment of chemically tagged wild fish (MRCT), using methods described in Weyl & Booth (2008), was undertaken. Between August 2008 and February 2009, 1094 fish caught by long line and angling, were measured (to the nearest 10 mm TL), macroscopically sexed, injected with 60 mg/kg oxytetracycline (OTC) hydrochloride (HiTet 120; Bayer, Leverkusen, Germany), tagged using Hallprint® plastic dart tags (Victor Harbour, South Australia, Model PDL) and released. If tagged fish were recaptured during the experiment they were sacrificed acccording to SAIAB standard procedures, measured to the nearest mm total length (TL), sexed and the sagittal otoliths removed and stored dry for later age determination. Otoliths from all OTC-injected fish were stored in the dark to prevent denaturation. For ageing, sagittal otoliths were sampled from 175 fish during the study period. Prior to otolith removal these fish were sacrificed, measured and sexed as described for those retained in the validation experiment.

For the age analysis, otoliths were embedded in clear casting resin, sectioned transversely through the nucleus to a thickness of 0.2–0.4 mm and mounted on glass microscope slides with DPX mountant using the procedures described by Weyl & Booth (2008). Each section was examined under transmitted white light using a compound light microscope at variable magnification (×10–40). Growth zones, comprising one pair of alternating opaque and translucent zones, were counted by three independent technical assistants without prior knowledge of the length or sex of the specimen. Counts were only accepted if the estimated age differed by two or less between each reader. OTC-injected otoliths were also examined under reflected fluorescent light (460–550 nm) and the number of growth increments distal to the OTC mark counted for each otolith.

Otoliths were read by two experienced (O.L.F.W. and A.J.B.) and one inexperienced (R.W.) reader. As a result of a systematic overestimation of age by R.W. (chi-square-test of symmetry: $\chi^2 = 57.6$, 40 d.f., $P < 0.05$) relative to the two other readers, fish age was only accepted from concordant estimates from the two experienced readers. Using these final age estimates, growth was modelled by fitting a von Bertalanffy growth function (VBGF) to the sex-specific length-at-age data. The VBGF is expressed as: $L_t = L_\infty(1 - \exp(-k(t - t_0)))$, where L_t is the length at age t, L_∞ is the predicted asymptotic length, k is the Brody growth coefficient, and t_0 is the age at zero length. The model was fitted by minimizing a negated normal log-likelihood function. A likelihood ratio test was used to test the null hypothesis that there were no differences in growth parameters between sexes. Parameter variability was calculated using a parametric bootstrapping procedure with 250 iterations (Efron 1982) with standard errors and 95% confidence intervals determined using the percentile method (Buckland 1984).

Mortality

To avoid any bias associated with between-gear variation in selectivity only long line data were used to estimate population size- and age-structure. Instantaneous total mortality rate (Z) was estimated as the inverse-variance weighted average of a catch-curve analysis (Ricker 1975) and the Chapman & Robson (1960) estimator. Both analyses used age-frequency data obtained from converting the sex-aggregated length-frequency data from a total of 1009 specimens to age-frequencies with an age-length key constructed based on the 175 aged fish.

RESULTS

During the validation experiment a total of 21 recaptured fish were sacrificed. Growth increments were clearly visible as alternating opaque and transluscent zones (Fig. 2). In all but one of the 21 chemically tagged fish recaptured after being at liberty between 244 and 537 days there was a relationship between time at liberty, season at liberty, and the number of growth increments distal to the fluorescing OTC band (Table 1). Otoliths from fish that were at liberty during summer and sampled by the end of summer clearly exhibited the deposition of a translucent growth zone, while those fish that were sampled after winter and overwintered at liberty showed depositions of an opaque growth zone. Deposition of otolith growth zones was therefore directly related to season in that the deposition of one complete growth zone pair was considered to be an annulus.

The largest fish aged was 1240 mm TL, a 13-year-old female. The oldest fish were two males of 840 mm and 1074 mm TL that were both 25 years old. The oldest female was 885 mm TL and 21 years old. Sex-specific growth patterns were statistically different ($\chi^2 = 20.85$, 3 d.f., $P < 0.05$). Male, female and combined sex (including three sexually indeterminate juveniles) VBGFs are summarized and illustrated in Table 2 and Fig. 3, respectively.

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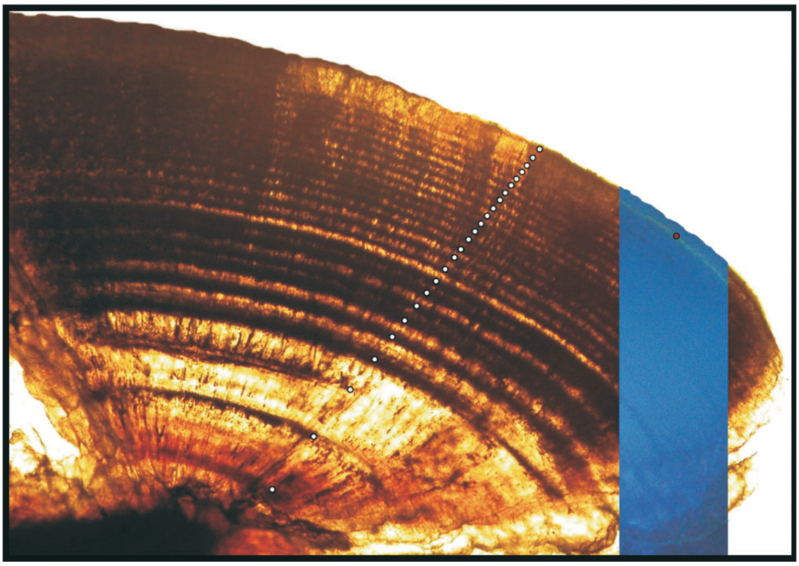

Fig. 2. Composite photomicrograph of a sectioned *Clarias gariepinus* (840 mm TL) sagittal otolith injected with oxytetracycline 344 days prior to recapture in Darlington Dam, South Africa, viewed at ×20 magnification. The base image is of the otolith as viewed using transmitted light while the insert is of an overlaid portion viewed with reflected fluorescent light showing the position of the fluorescent mark. The small circle (red dot in online version) indicates the incorporation zone of the fluorescent marker while each of the 25 white dots denotes an annulus. There is one translucent and one opaque zone exterior to the fluorescent mark.

Table 1. Summary of injection with oxytetracycline (OTC), recapture date, days at liberty, total length (TL), incorporation position of OTC (on translucent/opaque growth zone), number of increments post-OTC (1 = translucent and opaque zone pair; 0.5 = single translucent or opaque zone), and total number of growth increments for 21 recaptured *Clarias gariepinus* from Darlington Dam, South Africa.

Date of marking	Date recaptured	Time at liberty		Recapture TL (mm)	Incorportation point	Post-OTC growth increments	Total growth increments
		Days	Years				
24 Feb 2008	25 Oct 2008	244	0.67	903	Translucent	0.5	19
24 Feb 2008	25 Oct 2008	244	0.67	685	Translucent	0.5	21
24 Feb 2008	25 Oct 2008	244	0.67	943	Translucent	0.5	20
24 Feb 2008	25 Oct 2008	244	0.67	996	Translucent	0.5	19
24 Feb 2008	25 Oct 2008	244	0.67	829	Translucent	0.5	23
24 Feb 2008	25 Oct 2008	244	0.67	897	Translucent	0.5	13
24 Feb 2008	25 Oct 2008	244	0.67	872	Translucent	0.5	20
24 Feb 2008	25 Oct 2008	244	0.67	946	Translucent	1	18
16 Nov 2007	25 Oct 2008	344	0.94	847	Opaque	1	21
16 Nov 2007	25 Oct 2008	344	0.94	980	Opaque	1	17
16 Nov 2007	25 Oct 2008	344	0.94	665	Opaque	1	16
16 Nov 2007	25 Oct 2008	344	0.94	1050	Opaque	1	23
16 Nov 2007	25 Oct 2008	344	0.94	840	Opaque	1	25
24 Feb 2008	1 Mar 2009	371	1.02	872	Translucent	1	21
24 Feb 2008	1 Mar 2009	371	1.02	996	Translucent	1	16
24 Feb 2008	1 Mar 2009	371	1.02	857	Translucent	1	17
24 Feb 2008	1 Mar 2009	371	1.02	915	Translucent	1	21
8 Oct 2007	25 Oct 2008	383	1.05	885	Opaque	1	19
27 Nov 2007	1 Mar 2009	460	1.26	880	Opaque	1.5	16
27 Nov 2007	1 Mar 2009	460	1.26	865	Opaque	1.5	16
24 Feb 2008	14 Aug 2009	537	1.47	960	Translucent	1.5	17

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Table 2. Von Bertalanffy growth model parameters estimates and 95% confidence intervals for *Clarias gariepinus* sampled from Darlington Dam, South Africa.

	n	L_∞(mm)	*k*	t_0
Male	97	999.57 [927.86, 1132.10]	0.13 [0.08, 0.18]	-2.72 [-4.39,-1.62]
Female	78	867.93 [820.2, 986.56]	0.17 [0.11, 0.24]	-2.08 [-3.8,-1.35]
Combined	175	931.71 [884.37, 989.03]	0.15 [0.11, 0.2]	-2.43 [-3.47,-1.38]

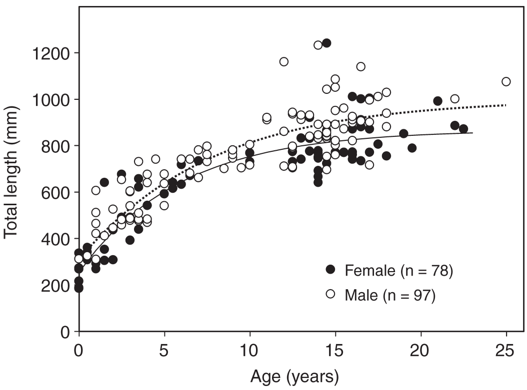

Fig. 3. Observed and von Bertalanffy growth model predicted lengths-at-age for male and female *Clarias gariepinus* sampled from Darlington Dam, South Africa. Solid line = female, dotted line = male.

The Darlington Dam *C. gariepinus* population was found to be unimodally distributed with multiple cohorts ranging between 12 and 17 years of age (Fig. 4). Total mortality was estimated as 0.32/yr using catch curve analysis and 0.38/yr using the Chapman and Robson (1960) estimator resulting in a mean of 0.35/yr.

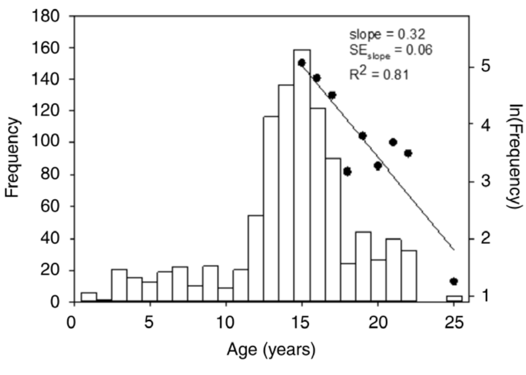

Fig. 4. Age frequency distribution and catch curve (regression line fitted to the natural logarithm-transformed age-frequencies, Slope ± S.E. = 0.32 ± 0.06, r^2 = 0.81) for *Clarias gariepinus* sampled in Darlington Dam, South Africa.

DISCUSSION

Clarias gariepinus is a successful invader and extralimital populations have established in several impoundments in the warm temperate Eastern Cape (Potts *et al.* 2008; Weyl & Booth 2008; Richardson *et al*. 2009). Within Darlington Dam, the presence of multiple cohorts provides evidence for a fully established extralimital population. Obtaining validated estimates of age is a critical first step towards understanding the biology of this species within its invaded environment. The MRCT results confirmed that growth zone deposition rate in otoliths from this locality is annual. This was in agreement with one other validation study (Weyl & Booth 2008). Age estimates and the VBGF fitted to age-at-length data showed that while growth was similar to other populations of this species in temperate environments (Richardson *et al*. 2009; Potts *et al*. 2008), Darlington Dam fish were long-lived compared to previously aged populations of this species (Table 3). As the oldest aged *C. gariepinus* to date was aged at 15 years (Weyl & Booth 2008), the observed maximum age of 25 years from Darlington Dam is a new longevity record for this species globally.

In comparison with other populations it appears that fish from the more temperate Eastern Cape are longer lived than those from more subtropical and tropical environments (Table 3). It must, however, be noted that possible resorption of calcium from cellular structures such as spines and vertebrae could have negatively biased previous longevity estimates (Quick & Bruton 1984). Comparisons between populations that were aged using otoliths indicate that differences in longevity between the Darlington and other Eastern Cape populations (Potts *et al*. 2008, Richardson *et al*. 2009) may be due to different introduction histories. The birth date of the 25-year-old fish sampled from Darlington Dam during 2008 for example was in 1985, only four years after this species was first recorded from the system. Similarly, Weyl & Booth (2008), sampled 15-year-old fish from the Glen Melville reservoir in

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Table 3. Summary of life history parameters of *Clarias gariepinus* from several localities in southern Africa. T_{max}: maximum observed age; L_{max} (mm TL): maximum observed length; L_∞, k and t_0: von Bertalanffy growth parameters; $\omega = kL_\infty$: growth performance (Gallucci & Quin 1979); Z: total mortality rates.

Ageing structure	Sex	T_{max}	L_{max}	L_∞	k	t_0	ω	Z	Latitude	Longitude	Locality
Pectoral spines	Combined	10	–	–	–	–	–	–	24°41′43″S 24°01′58″S	30°10′16″E 31°29′09″E	Elands & Olifants Rivers[1]
Vertebrae	Male Female	– –	– –	1394 789	0.08 0.17	– –	112 134	– –	16°19′57″S	35°05′00″E	Elephant Marsh[2]
Vertebrae	Combined	9	1480	1560	0.06	–0.91	94	–	24°28′00″S	17°48′00″E	Hardap Dam, Namibia[3,4]
Vertebrae	Combined	10	1020	1280	0.07	–1.85	89	0.54 0.68	20°20′00″S	31°05′00″E	Lake Kyle, Zimbabwe[3,4]
Vertebrae	Combined	9	860	1240	0.06	–1.55	74	0.59	17°00′00″S	27°50′00″E	Lake Kariba, Zimbabwe[3,4]
Vertebrae	Combined	7	990	1510	0.07	–0.88	105	0.71	17°54′00″S	30°48′00″E	McIlwaine, Zimbabwe[3,4]
Vertebrae	Combined	7	620	1470	0.06	–2.03	88	–	26°09′08″S	28°21′15″E	Rynfield Dam[4]
Vertebrae	Combined	8	–	–	–	–	–	–	25°59′10″S	27°50′40″E	Crocodile River[4]
Vertebrae	Combined	8	1250	2770	0.05	–0.45	138	–	30°38′13″S	25°49′05″E	Lake Gariep[4]
Pectoral spines	Combined	8	–	–	–	–	–	–	30°15′00″S	25°45′00″E	VanderKloof Dam[5]
Otoliths	Combined	15	–	–	–	–	–	–	33°11′42″S	26°38′45″E	Glen Melville Dam[6]
Otoliths	Combined	10	1221	930.2	0.19	0.28	176	–	32°33′59″S	26°46′08″E	Kat River Dam[7]
Otoliths	Combined	15	1230	1406.6	0.17	–0.16	238	–	32°57′32″S	27°30′05″E	Laing Dam[7]
Otoliths	Combined	12	*	1179	0.2	–0.37	236	0.26	31°50′57″S	27°10′00″E	Xonxa Dam[8]
Otoliths	Male Female Combined	25	1430	999.6 867.9 931.7	0.13 0.17 0.15	–2.72 –2.72 –2.43	133 146 141	0.32 0.38	33° 10′ 31″S	25° 09′13″E	Darlington Dam[9]

[1]Van der Waal & Schoonbee (1975), [2]Willoughby & Tweddle (1978), [3]Clay (1982), [4]Clay (1984), [5]Quick & Bruton (1984), [6]Weyl & Booth (2008), [7]Potts *et al.* (2008), [8]Richardson *et al.* (2009). [9]This study.

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2007, approximately 15 years after that impoundment was constructed in 1992. These observations support the hypothesis of long-term persistence of *C. gariepinus* following invasion into a novel waterbody. As this species is introduced in the Eastern Cape, more recent introduction histories is the most likely explanation for the relatively younger fish in other Eastern Cape localities (e.g. Potts *et al.* 2008; Richardson *et al.* 2009).

Growth also differed between populations (Table 3). As populations with different growth parameters may have similar growth performances, the statistic $\omega = kL_\infty$ (Gallucci & Quinn 1979) can be used to compare growth between different populations (Weyl *et al.* 2009) (Table 3). Both Laing (Potts *et al.* 2008) and Xonxa (Richardson *et al.* 2009) reservoirs exhibited a higher ω which indicates that these populations had a higher net growth performance (Table 3). In comparison the Kat River population (Potts *et al.* 2008) exhibited a moderate ω while all the others, including the present study, exhibited a lower ω.

Bruton (1976) suggested that populations of *C. gariepinus* feeding primarily on plankton, such as in Lake Kariba and Lake McIlwaine, which are expected to grow to a large size when other variables are considered, grow to a much smaller size than populations with a piscivorous diet, such as at Hardap Dam. Potts *et al.* (2008), when investigating the age and growth of *C. gariepinus* in the oligotrophic Kat River and the eutrophic Laing reservoirs, not only examined environmental variables and growth parameters but included a dietary component. They concluded that, although fish was the preferred food choice of *C. gariepinus* in the reservoirs, the abundance of fish prey was not directly related to growth but rather that the abundance of food sources in general dictated which population exhibited faster growth to a larger size. These studies suggest that growth performance is likely constrained by the availability of food and/or food type.

Longevity is strongly correlated with mortality (Hoenig 1983; Hewitt & Hoenig 2005) with lower mortality rates found in populations with older fish. Clay (1982) was the first to estimate mortality for *C. gariepinus* in southern African water bodies. All the populations investigated by Clay (1982) had higher mortality rates (0.54–0.70/yr) when compared with those from the more temperate Xonxa or Darlington Dams (0.26–0.38/yr) (Table 3). The mortality estimates of this study were, however, similar to the estimates of Richardson *et al.* (2009) for the unexploited Xonxa Dam population (Table 3). Xonxa Dam is approximately 200 km from Darlington Dam and displays similar physical variables to Darlington Dam. An additional cause for the close agreement in mortality estimates between the two localities is that neither population is commercially exploited.

In conclusion, this study has demonstrated that *C. gariepinus* has successfully invaded Darlington Dam and observed longevity suggests that it established soon after the completion of the IBWT. It is, however, uncertain whether this was a result of transport through the IBWT or whether, as suspected by Cambray & Jubb (1977), that it was introduced prior to the IBWT. It is likely that *C. gariepinus* will persist and, because this species is present in the river below the dam (Kadye & Booth 2013a), that Darlington Dam will continue to act as a source for downstream invasion.

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