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Establishment of translocated populations of smallmouth yellowfish, *Labeobarbus aeneus* (Pisces: Cyprinidae), in lentic and lotic habitats in the Great Fish River system, South Africa

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This study presents an assessment of the establishment success of smallmouth yellowfish, *Labeobarbus aeneus* (Burchell 1822), in the Great Fish River (GFRI), where they were introduced by the Orange–Fish River interbasin water transfer scheme and in the Glen Melville Reservoir (GMR), where the species was subsequently introduced from the GFRI. Edge Analysis of asteriscii validated an annual deposition rate of one growth increment per year and sampled fish were aged at between 0 and 10 years old. Combined sex length-at-age (L_t) was described by $L_t = 650(1 - e^{-0.066(t + 4.22)})$ mm FL for GMR and $L_t = 498(1 - e^{-0.23(t + 0.373)})$ mm FL for GFRI. Natural mortality rate was estimated at 0.56/yr in GFRI and 0.96/yr in GMR. Condition factor was significantly higher in the GFRI than in GMR. In comparison with other populations, the GFRI population had reproductive and growth traits that were similar to those in its natural riverine range. Reproductive assessment showed ripe male and female fish in October to December in the GFRI, while in the GMR, ripe male fish but few ripe female fish were recorded. This was attributed to the lack of spawning cues in the reservoir. As a result, *L. aeneus* were considered established in the GFRI, but were not established and likely dependent on introductions in the GMR.

Key words: Eastern Cape, growth, maturity, reproduction, age, mortality, condition factor, interbasin water transfer.

INTRODUCTION

As a result of numerous introductions and translocations of fishes, South Africa has recently been identified as a fish invasion hotspot (Leprieur *et al.* 2008). In freshwater ecosystems invasion by alien species is considered a leading mechanism driving environmental change (Clavero & Garcia-Berthou 2005; Garcia-Berthou *et al.* 2005). In South Africa, documented effects of fish invasions include the extirpation of indigenous fishes through predation (Cambray 2003), changes in invertebrate community structure (Lowe *et al.* 2008) and hybridization (Canonico *et al.* 2005). As a result, the management of alien species is a high national priority (National Environmental Management: Biodiversity Act 2004). Such management requires an understanding of the biology, ecology and establishment success of fishes outside their native range.

Labeobarbus aeneus (Burchell, 1822), is a medium-sized (max. weight 7 kg, Skelton 1993) cyprinid fish, endemic to the west-flowing drainage of the

Orange-Vaal River system in southern Africa (Jubb & Farquharson 1965). It is a popular angling species and as a result of past stocking programmes, together with inter-basin water transfer schemes, its distribution range has expanded significantly. Locality records for invasive populations include the east-flowing Gouritz, Great Fish, Sundays, Kariega, Kei, and Limpopo River systems (Fig. 1). Despite these introductions, limited published information is available on *L. aeneus*' establishment success in these systems.

In 1975, the Orange–Fish River inter-basin water transfer (IBWT) scheme was completed (Cambray & Jubb 1977). This IBWT connects the Gariiep Dam on the Orange River system with the headwaters of the Great Fish River (GFRI) through an 82.45 km-long tunnel (Fig. 1A; Cambray & Jubb 1977). This IBWT transfers c. 350×10^6 m³ water/yr and breaches the natural boundary between the two river systems, facilitating the transfer of Orange River biota to the GFRI. The first record of *L. aeneus* in the GFRI was from Grassridge Dam in 1976 (Cambray & Jubb 1977). In addition, three other

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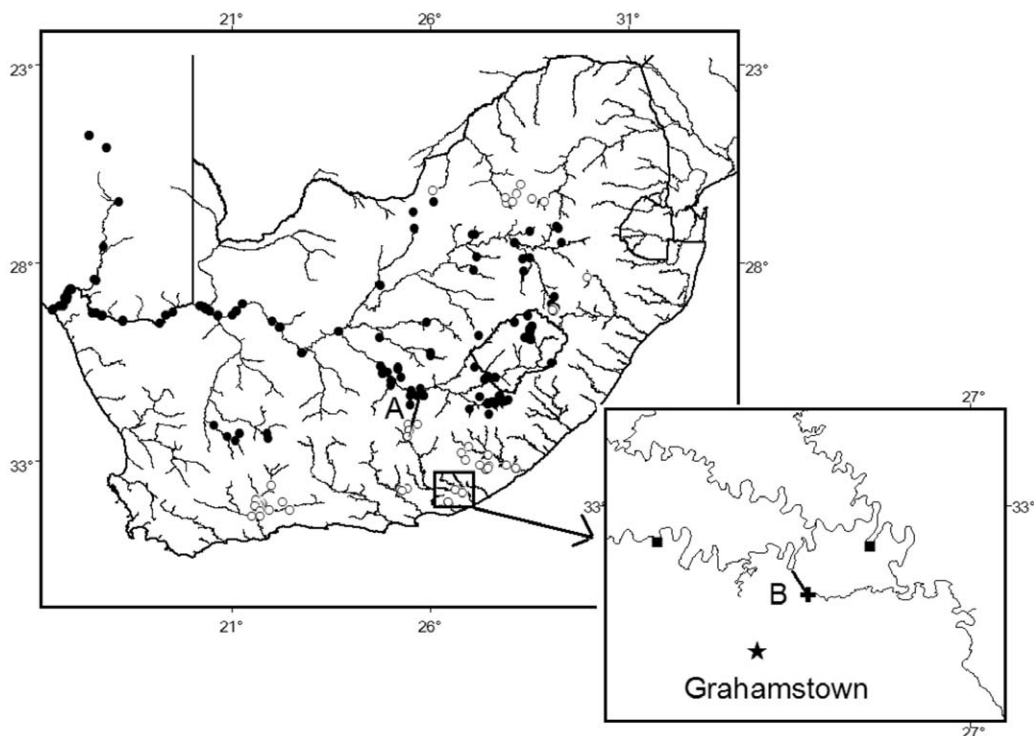


Fig. 1. Map of South Africa showing the locations from museum-lodged voucher specimens of *Labeobarbus aeneus*, together with an inset map of the Great Fish River waterbasin. The natural distribution of *L. aeneus* is in the Orange River waterbasin (●) together with introductions into other waterbasins (○). The inset map shows the location of the Glen Melville Reservoir (★), the two sampling sites on the Great Fish River (■) and Grahamstown (★). The underground water transfer tunnels (—) are labelled: (A) Orange River to Great Fish River, and (B) Great Fish River to Glen Melville Reservoir.

Orange River species, *Labeo capensis* (A. Smith, 1841), *Clarias gariepinus* (Burchell, 1822) and *Austroglanis sclateri* (Boulenger, 1901), were also introduced into the GFRI (Cambray & Jubb 1977; Laurenson & Hocutt 1985).

Based on 1983–1984 data, Laurenson *et al.* (1989) observed that viable spawning populations of *L. aeneus* had not established in the GFRI and hypothesized that populations were being maintained by the continued transfer of eggs, larvae and occasional adults through the IBWT (Laurenson & Hocutt 1985). They did, however, note that the species was increasing its distribution range and subsequent formal distribution records (Scott *et al.* 2006) and informal reports by anglers have demonstrated that the species is now present throughout the length of the GFRI.

The current study presents an assessment of the establishment success of *L. aeneus* by investigating growth, condition, maturity, reproductive seasonality and population structure, in a lentic and a lotic environment in the GFRI system.

METHODS

Study area

Fish were sampled from two sites on the GFRI (33°05'18"S, 26°46'50"E and 33°04'52"S, 26°18'48"E) and the Glen Melville Reservoir (GMR; 3°11'42"S, 26°38'46"E).

The GFRI has a flow regime that was altered by the IBWT from irregular seasonal flow to a perennially flowing river with decreased seasonal flow variation (O'Keefe & De Moor 2006). The river is turbid (Secchi depth <10 cm) and varies in water chemistry depending on water releases through the IBWT. During the study period, the water temperature varied between 12°C in winter and 22°C in summer.

The GMR is a 6.5×10^6 m³ (gross supply level) potable water supply reservoir with a surface area of 76 ha. This reservoir was completed in 1992 and the water level is artificially regulated by water transfer from the GFRI (Fig. 1B). This regulation is a rapid filling of the reservoir over a 3–4-day

Table 1. Macroscopic criteria for assessing gonadal recrudescence in *Labeobarbus aeneus*, from the Great Fish River and the Glen Melville Reservoir, Eastern Cape, South Africa (modified from Weyl & Booth 1999).

Stage	Macroscopic appearance
Juvenile	Gonads discernible as thin white bands. Sex not distinguishable.
Resting	Testes appear as a thin white band while ovary is pale white-red in appearance and granular when cut open.
Developing	Testes thicker and milky coloured. Ovary larger, red with a rough appearance externally. Individual ova are visible.
Ripe	Testis white and sperm can be extruded from a cut testis, or later (ripe running) by applying pressure to the abdomen. Ovary red to yellow, individual ova clearly visible and can be separated from the ovary when opened. Later (ripe running) by applying pressure on the abdomen of the fish.
Spent	Ovary and testes flaccid, sac like and appear bruised. Some remaining ova may be visible in the ovary.

period in March and August, via a tunnel from the GFRI, and a subsequent draw-down to $\leq 10\%$ of its supply level between filling events. The small catchment (53 km²) and low mean annual rainfall (520 mm per annum) result in a negligible contribution of runoff to the reservoirs water budget (DWA 1993). During the study period, water temperature in the GMR ranged from 12°C in winter to 27°C in summer and the water was relatively turbid, with an average Secchi depth of ≤ 20 cm.

The ichthyofauna of the GFRI prior to, and shortly after the completion of, the IWBT is summarized by Laurenson & Hocutt (1985). Prior to the IBWT the native freshwater ichthyofauna comprised an anabantid *Sandelia bainsii* Castelnau, 1961, the cyprinids *Barbus anoplus* Weber, 1897, *Barbus pallidus* A. Smith, 1841 and *Labeo umbratus* (A. Smith, 1841) and four anguillid eels. In the lower reaches of the river, this freshwater ichthyofauna was complemented by estuarine and marine fishes, including members of the families Clupeidae, Gobiidae, Monodactylidae, Mugilidae, Haemulidae and Sparidae. Five alien fishes *Lepomis macrochirus* Rafinesque, 1891, *Micropterus salmoides* (Lacepède, 1802), *Oncorhynchus mykiss* (Walbaum, 1792), *Cyprinus carpio* Linnaeus, 1758 and *Tilapia sparrmanii* A. Smith, 1840 were also present in the system. As *B. anoplus*, *L. umbratus* and *C. carpio* occurred in both systems prior to the IBWT, these species may also be transferred (Laurenson & Hocutt 1985), but an assessment of this would require genetic assessment.

Fish sampling

Fish were sampled on 11 sampling days in the GFRI and 20 sampling days on GMR from Novem-

ber 2005 to September 2006. Sampling gear used differed between sampling areas. Gillnets, fyke nets, angling and electrofishing were used in GMR and in the GFRI fish were sampled using fyke nets, angling and electrofishing. To avoid gill net selectivity constraints from determining population structure a wide range of mesh sizes was employed. The gill net fleet consisted of 10 m long \times 1.5 m deep panels of monofilament gill nets with stretched mesh sizes of 25, 38, 51, 64, 76, 102 and 127 mm and were surface set during the day (10:00–16:00) or overnight (17:00–08:00) in GMR. Fyke nets were double-ended with an 8 m guiding net and a first-ring diameter of 55 cm with a 10 mm mesh size at the cod end. Fyke nets were set overnight (17:00–08:00) on one night per sampling month. Species composition estimates are based on samples collected between November 2005 and March 2006. During this period, all species collected using experimental gear were identified and counted. After March 2006, sampling was directed towards *L. aeneus* and angling and electrofishing was used to supplement samples from GMR.

Biological analysis

Upon capture, *L. aeneus* were weighed to the nearest 0.1 g, measured to the nearest millimetre fork length (FL), sexed and the developmental stage of the gonads macroscopically staged according to the criteria summarized in Table 1. The gonads and viscera were then removed from the fish. The gonads and the eviscerated fish were weighed (nearest 0.1 g) and the asteriscus otoliths were removed and stored dry for later analysis.

To allow for comparisons of nutritional status between size classes and populations, condition factor (CF),

CF = $\frac{\text{eviscerated fish mass (g)}}{\text{length (mm)}^3} \times 100$, was calculated.

Age and growth

Fish were aged using the asteriscus otoliths, as these were the largest otoliths and easiest to interpret. Both asteriscus otoliths were removed and stored dry in gelatine capsules.

Otoliths were viewed whole, submerged in methyl-salicylate under transmitted light at varying magnifications ($\times 10$ – 40). Growth zones were visible as alternating translucent and opaque zones (Fig. 2). The periodicity of increment formation was assessed by Edge Analysis (EA), where the optical composition of the margin of the otolith (opaque or translucent) was expressed as a function of time, using otoliths collected from November 2005 to September 2006.

Growth zones were counted on whole otoliths collected between November 2005 and February 2006. Growth increments were counted twice on otoliths that were randomized, such that each reading was undertaken without prior knowledge of fish FL, sampling month or sex and without knowledge of the counts from previous readings. If the counts from the two readings were the same the count was accepted. If the readings differed, a third count was made. If this resulted in two identical counts, then this was accepted as the final estimate. If the three readings differed by two (e.g. 2, 3, 4) then the median estimate was accepted if the readings differed by more than two (e.g. 1, 2, 4), then the otolith was rejected from the dataset.

Under the assumption of the deposition of one growth increment per year, length-at-age, L_t , was described by the von Bertalanffy growth function (VGBF) of the form:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_∞ is the predicted asymptotic length, K is the Brody growth coefficient and t_0 is the age at 'zero' length. Parameter estimates were obtained by minimizing the negative log-likelihood of the normal distribution. Asymptotic estimates of parameter variability were calculated from the inverse Hessian matrix.

For each of the two sampling sites, sex-specific and combined sex models were fitted. In the sex-specific datasets, age data for unsexed juveniles were included in the data from unsexed fish. Therefore, for the combined sex models, only one set of unsexed juvenile data was included in the analyses. Likelihood ratio tests (LRTs) were used to test the null hypotheses that: 1) growth parameters were equal between the GFRI and GMR popu-

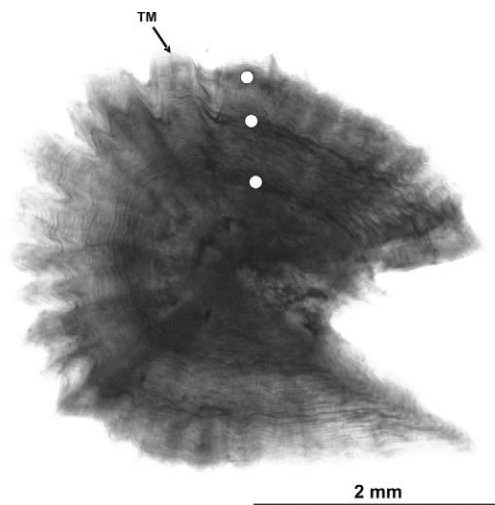


Fig 2. A photomicrograph of an asteriscus otolith, under transmitted light, of a 3-year-old, 265 mm fork length female *Labeobarbus aeneus* from the Glen Melville Reservoir, Great Fish River system, South Africa. Opaque zones are marked (O) and the otolith, collected in February 2006, has a translucent margin (TM).

lations; 2) growth parameters were equal between sexes for each population; and 3) that growth parameters were equal between sexes across both GFRI and GMR populations.

Mortality

A first approximation of the instantaneous rate of total mortality (Z) was estimated by catch-curve analysis (Ricker 1975). Pooled length frequency data were converted to age-frequency data by means of an age-length key. The negative of the slope of the linear regression through the descending data points of the natural logarithm of frequency at age against age, provides a first approximation of Z . As there is no directed fishery for *L. aeneus* on GMR or in the GFRI, Z was assumed equal to natural mortality (M).

Reproductive biology

To determine the length at 50% maturity, the proportion of sexually mature individuals (ripe and spent) by 10 mm FL class, collected during the spawning season, was fitted with a logistic curve of the form:

$$\psi(l) = (1 + e^{-(l-\phi)/\sigma})^{-1},$$

where $\psi(l)$ is the proportion of mature fish of length l , ϕ is the length-at-50%-maturity and σ the inverse steepness of the maturity function. As all fish in the sample were aged using otoliths, age at

Table 2. Catch composition by number in experimental gear fished in the Glen Melville Reservoir (GMR) and the Great Fish River (GFRI), South Africa, from November 2005 to March 2006. Percentage contributions are shown in brackets.

Species	GMR			GFRI
	Gill nets	Fyke nets	Both gear	Fyke nets
<i>Anguilla</i> spp. ¹	0	8 (3%)	8 (1%)	84 (17%)
<i>Labeo umbratus</i> ²	233 (37%)	163 (69%)	396 (46%)	5 (1%)
<i>Labeobarbus aeneus</i> ³	334 (53%)	15 (6%)	349 (40%)	327 (67%)
<i>Clarias gariepinus</i> ³	9 (2%)	21 (9%)	30 (4%)	67 (14%)
<i>Cyprinus carpio</i> ⁴	51(8%)	28 (12%)	79 (9%)	7 (1%)
Total	627	235	862	490

¹Species indigenous to GFRI; ²species indigenous to the GFRI but also to the Orange River (ORI); ³species translocated from the ORI; ⁴alien species introduced to GFRI and ORI prior to the inter-basin water transfer.

50% maturity was estimated by fitting the same ogive to data where fish were grouped by observed age class instead of length. Parameters were estimated by non-linear minimization of a negated Binomial log-likelihood function.

To assess for the timing and duration of the spawning season gonad stage and gonad mass of fish larger than the length at 50% maturity was used. A gonadosomatic index (GSI) was calculated for fish larger than the length at 50% maturity, using the equation:

$$\text{GSI} = \frac{\text{Gonad mass (g)}}{\text{Eviscerated fish mass (g)}} \times 100.$$

The monthly progression of the proportion of ripe and spent fish in the population and GSI plotted against sampling month was then used to indicate spawning period.

RESULTS

Catch composition

Labeobarbus aeneus was among the most abundant species by number in both the GFRI and GMR (Table 2). In GMR, *L. aeneus* did not dominate inshore fyke net catches (6%) but dominated offshore gill net (53%) catches. Other species sampled included *Labeo umbratus* and alien *C. gariepinus* and *C. carpio*.

Condition factor

Condition factor (CF) was independent of length in GMR (regression analysis, $P > 0.05$, Fig. 3), but in the GFRI, CF was significantly lower in fish smaller than 200 mm FL (Fig. 3). There were no interactions between sex, locality, season and mean CF (multi factorial ANOVA, $P > 0.05$), although CF was significantly correlated to locality and sex. CF differed between juveniles (fish

smaller than 200 mm FL), and males and females larger than 200 mm FL in the GFRI (ANOVA, $P < 0.05$), but was similar for all groups in GMR (ANOVA, $P > 0.05$). Juvenile CF was similar in the GFRI and GMR, while that of both male and female fish >200 mm FL was significantly higher in the GFRI than in GMR (Fig. 3).

Age and growth

A total of 377 otoliths was sampled from the GFRI and 456 from the GMR populations. The monthly proportion of otoliths with an opaque edge was unimodal in both the GFRI and GMR (Fig. 4). This deposition rate was consistent with that validated in the Vanderkloof Reservoir (29°59'29.22"S, 24°43'55.81"E; Tómasson 1983). As a result, the interpreted growth zones could be considered as annuli and suitable structures to estimate age.

The index of average percentage error between otolith readings was calculated as 7.03%. Combined sex age-length keys are provided in Table 3. Male, female and combined sex von Bertalanffy growth functions for the GMR and GFRI populations are presented in Table 4. Combined sex length at age and fitted VGBF's are illustrated in Fig. 5. Growth rate did not differ between sexes in the GMR population (LRT, $P > 0.05$). Combined sex growth rate was faster in the GMRI population than in the GMR population (LRT, $P < 0.05$).

Population structure

A summary of the length and age distributions by sampling area, together with the estimated total mortality rate, is presented in Fig. 6. Seventy-three and 95 individuals were juvenile fish of indeterminate sex in the GFRI and GMR samples,

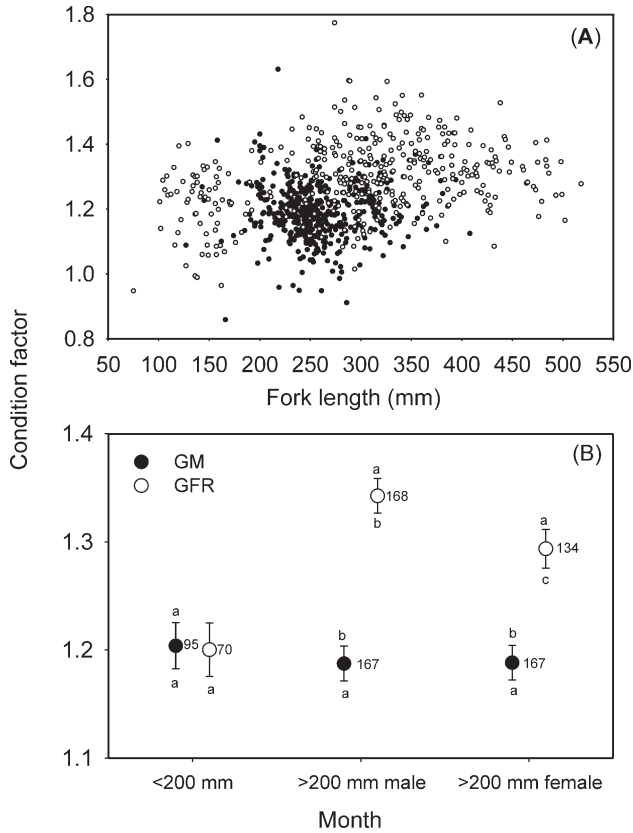


Fig. 3. The relationship between condition factor and length (A) and mean \pm 95% CI condition factor for fish >200 mm FL and <200 mm FL (B) sampled from the Glen Melville Reservoir (GMR) and the Great Fish River (GFR) in the Eastern Cape, South Africa, between November 2005 to September 2006. Different letters above error bars denote significant difference between GM and GFR samples per size class; different letters below error bars denote significant differences between size classes from the same location. Numbers denote sample size.

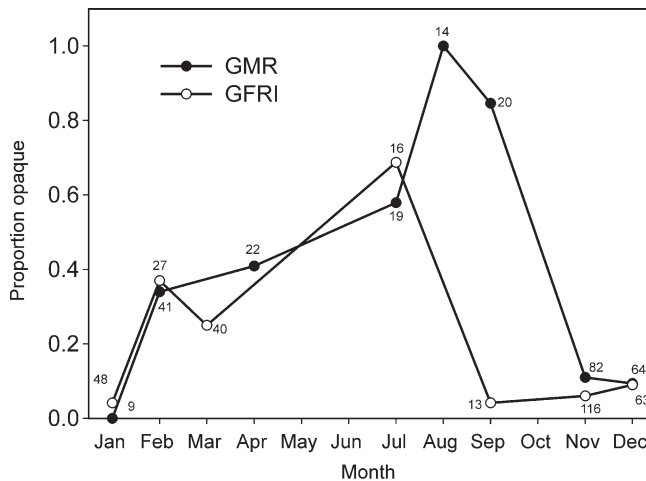


Fig. 4. Edge analysis showing the proportion of *Labeobarbus aeneus* asterisci with an opaque margin sampled between November 2005 and September 2006 from the Great Fish River (GFR) and the Glen Melville Reservoir (GMR), Eastern Cape, South Africa. Numbers next to data points denote sample size.

Table 3. Length at age key for *Labeobarbus aeneus* sampled from the Great Fish River and the Glen Melville Reservoir, South Africa. Fish were aged by counting growth zones on astericus otoliths.

Length class (mm)	Great Fish River										Glen Melville Reservoir							
	0	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	8
101–110			3															
111–120	1	2																
121–130		4										1						
131–140		5																
141–150		5	2										2					
151–160		1											1					
161–170			2										2					
171–180														2				
181–190			2									1	1					
191–200		1										1	8	3				
201–210		1											5	4	1			
211–220			1										2	3	1			
221–230			1	2									8	7	3			
231–240			2	1									4	13	13			
241–250			6	1	1								10	12	10			
251–260			3	5	3								4	16	3			
261–270			2	4	2								5	10	8	2		
271–280			1	5	6								1	8	10	1		
281–290			2	4	4	2							1	7	4	1		
291–300			1	1	5	1								1	7	3		
301–310				4	6	5								6	7	6	1	
311–320				3	5	4								2	5	6	1	
321–330				3	3	3	2							2	3	3	2	
331–340				4	1	3								1		1	1	1
341–350				3	2	5	1	1							1		1	
351–360				1	4	1	2									1		
361–370					2	4	3								1	2		
371–380					1	1		2	1							2		
381–390					2	3	1										1	
391–400				1		3	3											
401–410						3		2		2								
411–420					1		1	1										
421–430					1	2	4	1										
431–440							2	1	1	2								
441–450							1	1		1								
451–460									1									
461–470							1		1		1							
471–480							2											
481–490								1	1									
491–500							2	1										
511–520									1									

respectively. The sex ratio of the adult fish did not differ from unity in either the GFRI (168 ♀:134 ♂) or GMR (171 ♀:170 ♂) populations, nor did the sex ratio differ between GMR and GFRI populations ($\chi^2 = 1.93$, d.f. = 1, $P > 0.05$).

The length frequency distributions differed significantly between sampling sites (Kolmo-

gorov-Smirnov 2-sample test: $P < 0.05$). The population sampled from GFRI comprised larger fish than the GMR population. GFRI fish were also older (mode 4 years, range 0–10 years) than in the GMR population (mode = 3 years, range 1–8 years). The first estimate of natural mortality rate was 0.56/yr for the GFRI and 0.96/yr for GMR.

Table 4. Parameter estimates (and asymptotic coefficients of variation in brackets) for the von Bertalanffy growth model fitted to male, female and combined sex *Labeobarbus aeneus* data. Data were collected in the Glen Melville Reservoir and the Great Fish River, Eastern Cape, South Africa, between November 2005 and March 2006.

Parameter	Glen Melville Reservoir		
	Males (<i>n</i> = 206)	Females (<i>n</i> = 233)	Combined (<i>n</i> = 345)
L_{∞}	406.71 (16.98%)	13259.0 (99.41%)	649.73 (73.89%)
K	0.193 (46.42%)	0.001 (188.93%)	0.066 (123.16%)
t_0	-1.954 (44.89%)	-6.85 (11.61%)	-4.225 (48.56%)

Parameter	Great Fish River		
	Males (<i>n</i> = 165)	Females (<i>n</i> = 185)	Combined (<i>n</i> = 291)
L_{∞}	374.33 (5.33%)	515.58 (5.01%)	497.91 (5.11%)
K	0.403 (16.71%)	0.235 (12.63%)	0.23 (13.06%)
t_0	-0.064 (246.25%)	-0.145 (97.89%)	-0.373 (44.96%)

Reproductive biology

For the GFRI population, the length and age-at-50% maturity (ϕ) was calculated at 333 mm FL and 4+ years for females and 247 mm FL and 3+ years for males (Fig. 7). In GMR, very few ripe and spent fish were observed in the population over the spawning season. For the available data, length and age at 50% maturity was calculated at 327 mm FL and 7+ years for females and 297 mm FL and 6+ years for males (Fig. 7).

Monthly GSI and maturity stage of mature male and female fish ($\geq \phi$) in the GMR and

GFRI are illustrated in Fig. 8. In the GFRI, ripe fish were observed in samples from September to April. The proportion of ripe fish peaked in November, with the samples being dominated by spent fish in February and March. In the GMR, few ripe and spent fish of either sex were observed. The only ripe female was sampled in November. For males, ripe individuals were sampled over the same period from both sampling sites. Too few females larger than maturity were sampled from GMR for meaningful assessment of spawning season.

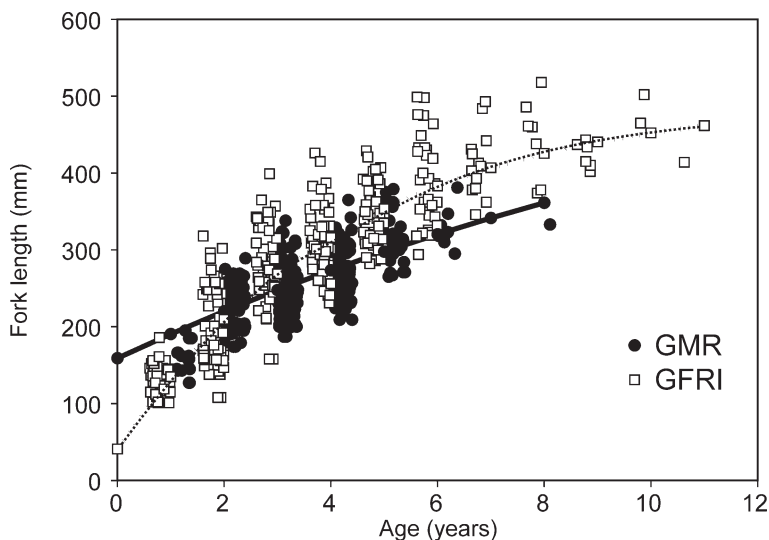


Fig. 5. Observed individual lengths at age and von Bertalanffy growth model predicted fits for *Labeobarbus aeneus* sampled from the Glen Melville Reservoir (GMR) and the Great Fish River (GFRI), Eastern Cape, South Africa, between November 2005 to September 2006.

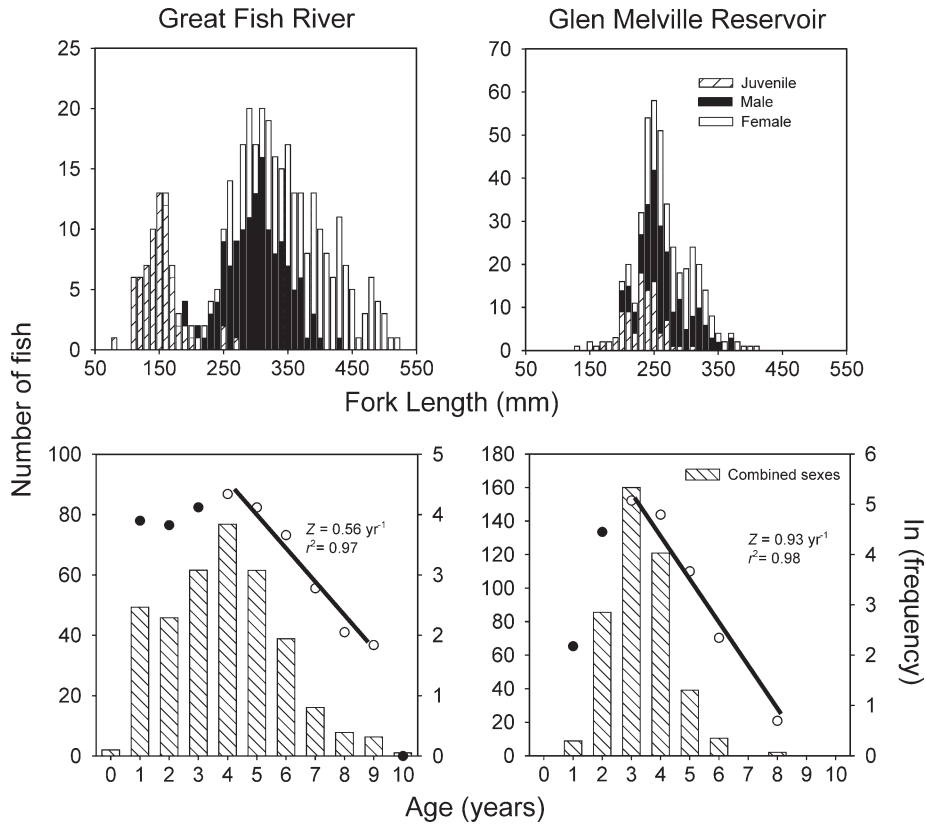


Fig. 6. Length frequency (top) and age frequency (bottom) for *Labeobarbus aeneus* sampled from the Great Fish River and the Glen Melville Reservoir, Eastern Cape, South Africa, from November 2005 to October 2006. Age frequency was estimated by applying an age-length key based on otolith readings to the length frequency data.

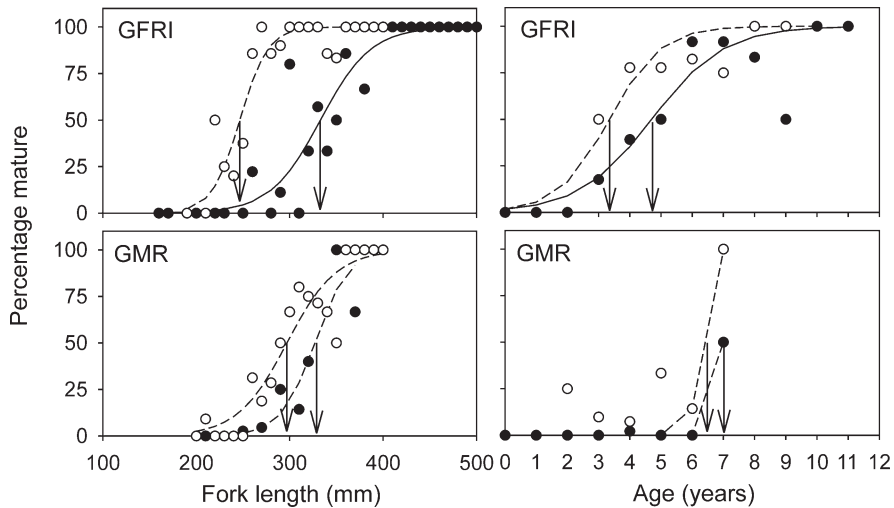


Fig. 7. *Labeobarbus aeneus* female (●) and male (○) length (left) and age (right) at maturity expressed as the percentage of ripe and spent fish in the population during peak spawning season (November–March) in the Great Fish River (GFRI) and the Glen Melville Reservoir (GMR), Eastern Cape, South Africa. Arrows denote length or age at 50% maturity. Sample size (length/age): GFRI females = 144/127; GFRI males = 110/106; GMR females = 140/139; GMR males = 118/118.

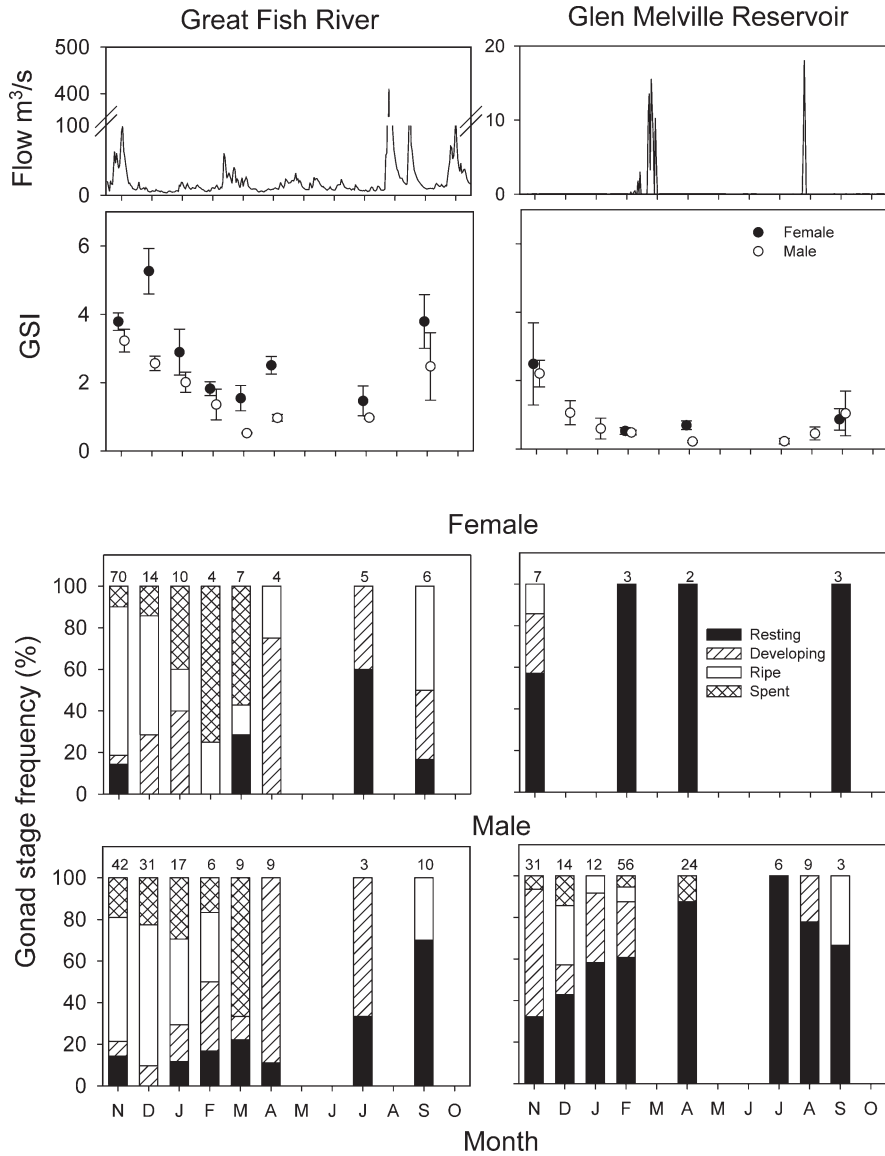


Fig. 8. Water flow, gonadosomatic index (GSI), percentage of gonads from female and *Labeobarbus aeneus* larger than length at 50% maturity, sampled between November 2005 and September 2006 from the Great Fish River (GFR) and the Glen Melville Reservoir (GMR), Eastern Cape, South Africa. River flow data were obtained for Department of Water Affairs and Forestry (DWAFF) gauging weirs on the lower GFR (Q9H018A01) and the tunnel outlet into GMR (Q9H031A01) from DWAFF (2008). Numbers above maturity bars denote sample size for both maturity and GSI data.

DISCUSSION

The lag period between the initial invasion event and the successful establishment of an alien organism population is variable (Peterson *et al.* 2005). Laurenson *et al.* (1989), based on surveys conducted in 1983 and 1984, eight years after the completion of the IBWT, observed that a *L. aeneus* population had not established in the GFR and

that the population was dependent on continued translocation of eggs and juveniles through the tunnel. The results of this study show that by 2005 a breeding population of *L. aeneus* had established in the GFR. Evidence of establishment includes the wide distribution in the GFR, dominance in the experimental catch composition, presence of mature, ripe and spent individuals of both sexes

Table 5. Summary of length and age at maturity and von Bertalanffy growth parameters of South African *Labeobarbus aeneus* populations. L_{mat} = length at maturity; A_{mat} = age at maturity; $\omega = kL_{\infty}$; VBGF = von Bertalanffy growth function; L_{∞} = asymptotic length; K = Brody growth coefficient; t_0 = age at zero length. As populations with different growth parameters may have similar growth performances, the statistic $\omega = kL_{\infty}$ (Gallucci & Quinn 1979), was used compare growth between the GFRI populations and other South African populations. Estimates of k and L_{∞} not cited in older literature, were estimated by fitting a VBGF directly to mean length at age data summarized in Laurenson *et al.* (1989) using non-linear sum-of-squares minimization.

Location	Maturity		VBGF parameters			
	L_{mat}	A_{mat}	ω	L_{∞}	K	t_0
Males						
Boskop Reservoir ¹	67	345	0.195	-0.07		
Gariiep Reservoir ²	210	3	74	676	0.110	-0.09
Glen Melville Reservoir ³	297	6	79	407	0.193	-0.20
Great Fish River ³	247	3	151	374	0.403	-0.06
Vaal River ⁴	280	4	66	1115	0.059	-0.48
Vanderkloof Reservoir ⁵		3	115	603	0.190	0.52
Females						
Boskop Reservoir ¹			48	1560	0.031	-0.53
Gariiep Reservoir ²	310	5	82	684	0.120	-0.20
Glen Melville Reservoir ³	327	7	13	13259	0.001	-6.85
Great Fish River ³	333	4	121	516	0.235	-0.15
Vaal River ⁴	340	5	63	1221	0.051	-0.51
Vanderkloof Reservoir ⁵	300	4	114	710	0.160	0.47
Combined sexes						
Glen Melville Reservoir ³	43	650	0.066	-4.23		
Barberspan Reservoir ⁶	46	1281	0.036	-1.15		
Xonxa Reservoir ⁷	69	276	0.250	-0.63		
Vanderkloof Reservoir ⁵	109	465	0.234	0.369		
Great Fish River ³	115	498	0.230	-0.37		
Vaal River ⁴	115	765	0.150	0.11		

¹Koch 1975; ²Hamman 1974; ³This study; ⁴Mulder 1973; ⁵Tómasson 1983; ⁶Straub 1972; ⁷Richardson *et al.* (in press).

over the breeding period and the presence of 10+ year classes. There were, however, differences between environments, and despite high abundance of fish in the GMR, there were few ripe fish recorded over the spawning season, indicating that the population may not have established in this lotic environment.

The success of a species in a foreign environment is dependent on the suitability of its reproductive style to that environment, its ability to meet nutritional requirements and its adaptation to prevailing abiotic conditions. On comparison with other populations of *L. aeneus* (Table 5) length and age at maturity for the GFRI and GMR are similar to those reported for other populations. The presence of reproductively active fish from November to April was also consistent with summer spawning in other *L. aeneus* populations (Tómasson 1983, Mulder 1973). In rivers, *L. aeneus* spawn on gravel beds in shallow riffles (Jubb 1966) and the onset of the spawning season is believed to be dependent on temperature and/or flow regime (Tómasson *et al.* 1984). Reservoir populations of *L. aeneus* typically spawn in the inflowing rivers (Tómasson *et al.*

1984) and observations of lacustrine spawning in Sterkfontein Dam, South Africa, have been in association with wind-driven currents in shallow rocky bays (Impson 2007).

The river flowing into GMR is episodic, flowing only briefly after heavy thunderstorms or during the artificial flooding of the reservoir over a period of three to four days after the main spawning period of *L. aeneus* (Fig. 8). As a result, stream-flow cues necessary for triggering spawning may be too short in duration, or too late in timing, or absent, in GMR. This may, in part, explain the paucity of ripe and spent fish sampled from this population over the spawning period. The lack of access to suitable riverine spawning habitat, the presence of few mature fish, and the rapid annual draw downs in water level are also likely to limit spawning success of the population in the GMR. It is, therefore, likely that the GMR population of *L. aeneus* is dependent on continued recruitment through the tunnel linking it to the GFRI. As this inflow is episodic, recruitment will depend on the chance of juveniles being flushed into the dam during the three-day filling events. As a result, the population

structure and mortality rates in the GMR cannot be considered representative of a established, steady state, population.

In a study on the success of *M. salmoides* in a subtropical lake, Weyl & Hecht (1999) used growth performance as an indicator for 1) determining the ability of a species to meet nutritional requirements in an invaded environment, and 2) its adaptation to prevailing environmental conditions such as temperature. A comparison of growth performance between various established yellowfish populations is summarized in Table 5. VBGF growth parameters were comparable to other *L. aeneus* populations that had been aged under single-annulus assumptions. In comparison to these previous studies the growth performance of the GFRI population was similar to that reported from its natural range in the Vaal River. While the GMR population exhibited slower growth than the GFRI population, this was within the expected range of other reservoir populations. This difference is likely to be a result of decreased feeding opportunities, which are exemplified by lower CF in the GMR population than in the GFRI population (Fig. 3).

Such differences between lotic and lentic populations were similar to those observed by Tómasson (1983) in the Vanderkloof Reservoir and the inflowing Orange River. He also showed that smaller size classes had better feeding opportunities in Vanderkloof Reservoir. This was because the ability to feed on zooplankton decreased with size, such that larger fish (>200 mm FL) were limited by food availability because of a low abundance of alternative prey. This may be the case in the GMR population, where small fish (<200 mm FL) had similar CF to those in the GFRI, but large fish (>200 mm FL) had significantly lower CFs. As a result feeding conditions in the GMR are probably sub-optimal for *L. aeneus*. A dedicated diet study would, however, be useful to explain these observed differences.

The establishment of *L. aeneus* in the GFRI can be attributed to favourable environmental conditions. Individuals that were introduced through the IBWT were exposed to an environment that provided good feeding opportunities shown by the high CF and growth rate of the GFRI population. The perennial flows of the GFRI, in conjunction with suitable spawning habitat, allowed for successful reproduction once the population had attained critical mass. In the GMR, on the other hand, conditions were not as favourable as shown

by the lower CF and growth rates, as well as by the presence of few reproductively active individuals. The reservoir population is, therefore, not considered established and is likely to be dependent on recruitment from the GFRI.

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