



Research Article

The tropical South American cichlid, *Geophagus brasiliensis* in Mediterranean climatic south-western Australia

Stephen J. Beatty*, David L. Morgan, James Keleher, Mark G. Allen and Gavin A. Sarre

Freshwater Fish Group and Fish Health Unit, Murdoch University, South St, Murdoch, Western Australia, Australia 6150

E-mail: s.beatty@murdoch.edu.au (SJB), d.morgan@murdoch.edu.au (DLM), j.keleher@murdoch.edu.au (JK),

m.allen@murdoch.edu.au (MGA), gsarrrre@ozemail.com.au (GAS)

*Corresponding author

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Abstract

The highly endemic (82%) freshwater fishes of south-western Australia are imperiled due to severe habitat and water quality declines and impacts of introduced species. As a case study of the recent tropical aquarium fish introductions, the biology and ecology of the pearl cichlid *Geophagus brasiliensis* was determined in the Swan River catchment south-western Australia. Unlike endemic freshwater fish species of this Mediterranean climatic region, *Geophagus brasiliensis* underwent a protracted spawning period during the warmer period from December to May. It appeared that recruitment only occurred in lentic habitats; however the species also persists in downstream lotic habitats. Growth rate and maximum size (245 mm TL) of the species exceed all but one of the region's native freshwater fishes. Whilst minimum water temperature may help limit its establishment in many aquatic ecosystems, its salinity tolerance and omnivorous diet would facilitate its colonisation in this region, including freshwaters and estuaries. Past and future habitat and climatic change is predicted to continue to favour species from sub-tropical and tropical regions.

Key words: freshwater fishes; invasive species; saline bridges; ecological impacts

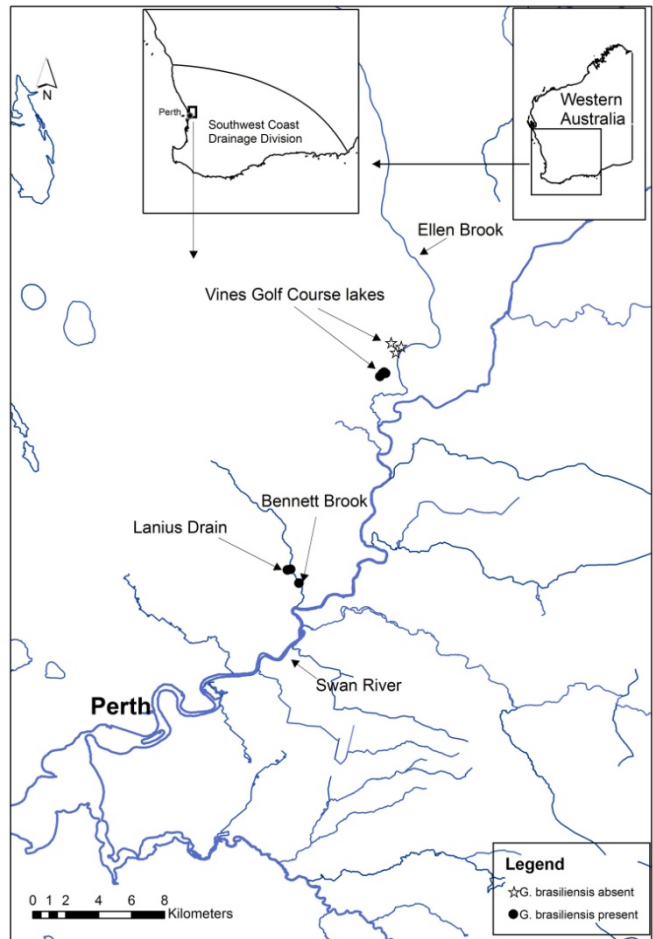
Introduction

Recognised as a global biodiversity hotspot (Myers et al. 2000), Australia's South West Coastal Drainage Division has a depauperate yet highly endemic freshwater fish fauna (Allen et al. 2002; Morgan et al. 1998, 2011a). The region boasts the highest proportion of endemic species on the continent, with nine of the 11 freshwater fish species being endemic; yet they have undergone major range reductions through habitat and water quality decline (e.g. Morgan et al. 2003; Beatty et al. 2011) and many are threatened by introduced freshwater fishes (Allen et al. 2002; Morgan et al. 2004; Beatty and Morgan 2013). Quantifying the impacts of introduced fishes on aquatic ecosystems relative to other environmental stressors caused by anthropogenic pressures can be difficult (Kennard et al. 2005). However, there are a number of at least partially demonstrated impacts of several introduced freshwater fishes on native fishes and crayfishes of this region including direct predation and agonistic interactions (e.g.

Gill et al. 1999; Morgan et al. 2002, 2004; Tay et al. 2007). Of great concern is that there has been a 44% increase in the number of introduced freshwater fishes during the past decade (to a total of 13 species) and the majority originated from sub-tropical or tropical regions; despite south-western Australia having a Mediterranean climate (Beatty and Morgan 2013).

Native to the coastal drainages of eastern and southern Brazil and Uruguay, the pearl cichlid (also known as the pearl eartheater) *Geophagus brasiliensis* (Quoy & Gaimard, 1824) is a popular aquarium species and has been introduced into natural systems of the USA, Taiwan, Philippines and Australia (Axelrod 1993; Fuller et al. 1999; Liang et al. 2006; Fishbase 2012). Sightings of *G. brasiliensis* in a wild aquatic system in Western Australia were first reported to the authors from Bennett Brook (a major tributary of the Swan River, Figure 1) in February 2006. The species was not recorded in a previous survey of the catchment in 1998 (Bamford et al. 1998). In 2011, *G. brasiliensis* was also reported in irrigations lakes on the

Figure 1. Sites sampled and capture and non-capture sites for *Geophagus brasiliensis* in Bennett and Ellen Brooks, south-western Australia (see also Appendix 1).



Vines Golf Course (Ellen Brook), another major tributary of the Swan River (C. Bird, Department of Fisheries, Government Western Australia, pers. comm.).

The potential invasiveness and ecological impact of *G. brasiliensis* and more generally other introduced species in south-western Australia may be facilitated by an opportunistic diet (Lazzaro 1991), prolonged or flexible reproductive strategy (Mazzoni and Iglesias-Rios 2002), ability to exist in both lentic and lotic habitats (Mazzoni and Iglesias-Rios 2002), and high tolerance of environmental variables such as salinity (de Graaf and Coutes 2010; Beatty and Morgan 2013). Along with habitat and water quality decline due to agricultural and urban development, south-western Australia has undergone major rainfall, surface flow and groundwater reductions since the 1970's with global climatic models predicting this to

continue (Suppiah et al. 2007; Whetton et al. 2005; CSIRO 2009a, b; Barron et al. 2012; Silberstein et al. 2012). Temperature increases are also projected for the region creating milder winters (Suppiah et al. 2007; Department of Water Government of Western Australia 2010). These past and projected changes have been predicted to exacerbate other stressors on native freshwater fishes of this region and also favour introduced freshwater fishes (Morrongiello et al. 2011). Specifically, the recent trend of sub-tropical and tropical introductions may be further aided by future temperature increases.

The current study aimed to determine the distribution, reproductive biology, age and growth, and seasonal dietary composition of *G. brasiliensis*. It is hypothesised that life-history, physiological and ecological traits of *G. brasiliensis* have facilitated its establishment in this region.

Materials and methods

Sampling protocol

In order to determine the biology and ecology of *G. brasiliensis* in the Bennett Brook system, a perennial tributary of the Swan-Avon River catchment, monthly sampling occurred at two sites in Lanius Drain and one in the lower reaches of Bennett Brook between January and December 2010 (Figure 1). This sampling involved the use of single-pass back-pack electrofishing (*Smith Root Model LR20*) at three areas within the Bennett Brook catchment: two within Lanius Drain (where the species was previously reported in large numbers), and one within Bennett Brook downstream of the confluence with Lanius Drain. In each section of stream, three sites were sampled. All fishes and crayfishes captured were identified to species (Morgan et al. 2011) and all native fishes and crayfishes returned immediately to the site of capture. All *G. brasiliensis* were retained and immediately placed in an ice slurry for later processing in the laboratory. Physicochemical parameters (temperature (°C), pH, dissolved oxygen (% and ppm), NaCl concentration (ppt), total dissolved solids (ppt) and conductivity ($\mu\text{S cm}^{-1}$)) were measured using a hand held multimeter (Oakton™ PCD650) at three locations at each site and a mean and standard error (SE) determined.

In order to determine the wider distribution of *G. brasiliensis* in the Swan River catchment, sampling occurred in the lower section of Helena River (≈ 500 m upstream of the Swan River confluence) in February 2010. Other distributional information was also reviewed from a recent survey (Beatty et al. 2010) in the Ellen Brook and Brockman River (a total of 16 sites in November 2009 and February 2010). Additionally, sampling for *G. brasiliensis* was undertaken in April and May 2010 at a total of 12 sites in the nearshore shallow waters of the upper Swan River Estuary adjacent to the Bennett Brook and Helena River confluences. Each of these latter sites were sampled using a 21.5 m seine net, which consisted of a 1.5 m wide bunt of 3 mm mesh and two 10 m long wings (each comprising 4 m of 3 mm mesh and 6 m of 9 mm mesh). The latter net swept an area of 116 m² and was laid parallel to the bank and then hauled onto the shore. All fish captured were then identified to species and counted. All native fish were then

returned to the water alive. In the case that any alien fish species were encountered, an ice slurry was on hand for euthanising.

To determine the distribution, population structure and inferred viability of the recently reported *G. brasiliensis* population from the Vines Golf Course irrigation lakes (Ellen Brook catchment), seven lakes were sampled for fishes in December 2011 using single pass boat electrofishing (Smith Root Model VVP). Owing to time restrictions on the golf course, single pass boat electrofishing was conducted to qualitatively survey for freshwater fish as it allows the coverage of greater areas than multiple pass with fewer resources in terms of time and effort (Meador et al. 2003; Meador 2005).

Spatial and temporal patterns in abundance

The mean densities of all freshwater fishes and crayfishes recorded at each site sampled in Lanius Drain and Bennett Brook proper were determined on each sampling occasions using the equation $D = N/A$, where D = density of the species, N = number captured and A = area sampled (m²). The spatial and temporal pattern in the distribution and density of *G. brasiliensis* in the Bennett Brook system was examined by plotting its mean density (± 1 SE) at each site in each month.

All *G. brasiliensis* retained from all sites on all occasions were measured to the nearest 1 mm total length (TL). To determine whether there was a spatial difference in population structure within the Bennett Brook system and between it and the lake population, length-frequency histograms were plotted separately based on site of capture, i.e. Lanius Drain upstream site, the Lanius Drain downstream site, Bennett Brook downstream site, and the Vines irrigation lake population.

Reproductive biology

Subsamples of <75 *G. brasiliensis* were dissected each month for analysis of reproductive development from the Bennett Brook system (including Lanius Drain). The sex of each fish was determined by removal and examination of the gonad under a dissecting microscope. Each gonad was initially macroscopically assigned to one of six developmental stages: I/II (virgin or maturing), III (developing), IV (developed), V (gravid), VI (spawning), and VII (spent). A random sample of a range of female gonads stages were fixed in Bouin's solution, dehydrated in

alcohol, and sectioned (at 6 μm) after being embedded in paraffin wax (Morgan et al. 1995). These sections were examined microscopically to verify the macroscopically assigned stages. Gonad stages were then plotted over months for females and males to examine trends in reproductive development. For determination of spawning period, the monthly gonadosomatic index (GSI) was calculated for immature (stages I/II) and mature (stages III–VII) females and males using the formula $\text{GSI} = (W_1/W_2) \times 100$, where W_1 = wet weight of the gonad, and W_2 = wet weight of the fish.

TL at first maturity was determined for female and male *G. brasiliensis* in the Bennett Brook system. This was achieved by assigning maturity status, i.e. mature stages III–VII or immature stages I–II, to fishes captured between January and April (i.e., within the peak spawning period, see results). Logistic regression analysis, using bootstrapping of 1000 random samples, was undertaken on the percentage of mature females and males in 5 mm TL increments. The logistic equation is:

$$P_L = 1/[1 + e^{-\ln 19(L-L50)/(L95-L50)}]$$

where P_L is the proportion of *G. brasiliensis* with mature gonads between January and April at TL interval L , and $L50$ and $L95$ are the TLs at which 50% and 95% of the population mature. Analyses were conducted using the Solver tool in Excel software program.

Growth

Fish used in the growth analysis were measured to the nearest 1 mm TL and standard length (SL) and weighed to the nearest 0.01 g. The relationship between the SL and TL for each sex was determined using linear regression and, in order to determine whether differences existed between sexes for those relationships, likelihood ratio tests were undertaken (Cerrato 1990). For age and growth determination, the otoliths of a subsample of up to 122 fish per month were removed, immersed in glycerol and viewed through a dissecting microscope using reflected light. A seasonal climate in south-western Australia results in the otoliths of most freshwater fishes (both native and introduced) having clearly discernible annuli (translucent zones) laid down each year (e.g. Morgan et al. 2002). Although a protracted spawning period was recorded throughout the sampling period, the birth date was assumed to be January 1st;

based on the prevalence of spent mature fish from this month onwards (see results) and TL of each fish was plotted against its age and a growth curve fitted using a von Bertalanffy growth equation: $L_t = L_\infty[1 - E^{-K(t-t_0)}]$, where L_t is the TL at age t (years), L_∞ is the asymptotic TL of the population, K is the growth coefficient and t_0 is the hypothetical age at which the fish would have zero TL.

Dietary analysis

Stomachs were removed from 30 individuals each season and their contents examined under a dissecting microscope. Items were identified to the highest possible taxa and allocated to one of 14 prey categories. Diets were analysed using the frequency of occurrence and percentage overall volumetric contribution to the diets of each category. The frequency of occurrence is the proportion of stomachs that contained the prey item and the volumetric contribution is the proportion that each prey contributes to the overall stomach content of all fish or those in specified categories (Hynes 1950; Hyslop 1980). In order to determine whether there were seasonal or ontogenetic changes in dietary composition, these analyses occurred separately for season and for four size classes (<60, 60–100, 100–150, and >150 mm TL).

In order to determine the level of similarities among different size classes and seasons, the volumetric data were square-root transformed and a Bray Curtis similarity matrix constructed in the PRIMER v6 statistical package (Clarke and Gorley 2006). The significance of differences in the dietary composition between the four size classes and four seasons was examined via constructing a ranked similarity matrix from the original similarity matrix and undertaking a two-way crossed analysis of similarity (ANOSIM) (Clarke and Gorley 2006).

Results

Physicochemical variables in Bennett Brook

During the current study, temperature ranged from 13.8°C to 29.3°C with a mean of 23.2°C (± 1.59) and 19.8°C (± 1.44) in the Lanius Drain and Bennett Brook sites, respectively. The water temperature was invariably more than 2°C warmer (and up to 4.3°C in January) within the drain site *cf* with the downstream site in Bennett Brook. Conductivity ranged from 566.4 $\mu\text{S}\cdot\text{cm}^{-1}$

Table 1. Mean densities (\pm SE) of freshwater fish, estuarine fish, and freshwater decapods at the sites sampled between January and December 2010 in Lanius Drain and Bennett Brook, Western Australia. Species codes: Gb = *Geophagus brasiliensis*, Go = *Galaxias occidentalis*, Nv = *Nannoperca vittata*, Bp = *Bostockia porosa*, Gh = *Gambusia holbrooki*, Ca = *Carassius auratus*, Po = *Pseudogobius olorum*, Cc = *Cherax cainii*, Cq = *Cherax quinquencarinatus*, Cd = *Cherax destructor*, Pa = *Palaemonetes australis*. N.B. * alien species.

Site	Freshwater fishes				Estuarine fishes			Freshwater decapods			
	Gb*	Go	Nv	Bp	Gh*	Ca*	Po	Cc	Cq	Cd*	Pa
Lanius Drain (upstream)	0.26 (0.08)	0.13 (0.08)	0	0	0.87 (0.36)	0	0	1.8×10^{-4} (1.8×10^{-4})	3.1×10^{-3} (1.7×10^{-3})	0.10 (0.05)	0
Lanius Drain (downstream)	0.51 (0.16)	0.10 (0.06)	0.04 (0.01)	0.02 (0.00)	2.52 (0.65)	1.3×10^{-3} (8.3×10^{-4})	0.02 (0.01)	1.2×10^{-3} (9.2×10^{-4})	0.02 (0.00)	0.01 (0.00)	0.04 (0.03)
Bennett Brook	0.06 (0.02)	0.36 (0.12)	0.12 (0.06)	2.3×10^{-3} (1.7×10^{-3})	4.68 (1.12)	2.8×10^{-3} (2.6×10^{-3})	0.04 (0.02)	0	0.21 (0.18)	2.3×10^{-3} (2.4×10^{-3})	4.59 (2.49)
Total (% of total fish)	2505 (8.10)	1800 (5.82)	412 (1.33)	51 (0.16)	26007 (84.10)	11 (0.04)	137 (0.44)	4	885	443	13150

Table 2. Percentage contribution (% Vol.) and percentage occurrence (% Occ.) of the different food items in the stomachs of *G. brasiliensis* in the Bennett Brook system in 2010. N.B. – indicates absent prey types.

Prey Type	Summer		Autumn		Winter		Spring	
	% Vol. (\pm 1SE)	% Occ.	% Vol. (\pm 1SE)	% Occ.	% Vol. (\pm 1SE)	% Occ.	% Vol. (\pm 1SE)	% Occ.
Teleost	–	–	0.67 (0.66)	3.33	1.07 (0.62)	13.33	0.63 (0.43)	16.67
Arachnida	0.33 (0.39)	6.67	–	–	0.73 (0.43)	26.67	3.5 (0.71)	56.67
Insecta (terrestrial)	6.5 (1.38)	20	–	–	13.1 (1.83)	30	0.33 (0.39)	6.67
Trichoptera	0.7 (0.5)	20	1.0 (0.81)	3.33	3.17 (1.40)	6.67	–	–
Odonata larva	0.17 (0.33)	3.33	6.0 (1.33)	16.67	–	–	–	–
Chironomidae larva	2.33 (0.84)	23.33	22.27 (1.76)	70	2.63 (1.05)	23.33	38.83 (1.73)	86.67
Culicidae	–	–	2.0 (1.11)	3.33	2.33 (0.96)	13.33	–	–
Coleoptera larva	3.83 (0.96)	26.67	4.33 (1.11)	16.67	3.57 (1.33)	13.33	3.13 (1.24)	16.67
Coleoptera adult	3.83 (0.87)	33.33	5.67 (1.37)	13.33	5.0 (1.51)	6.67	–	–
Parastacidae	3.0 (1.40)	3.33	7.0 (1.63)	10	–	–	–	–
Ostracoda	1.3 (0.48)	36.67	2.8 (0.76)	36.67	6.33 (1.15)	56.67	7.93 (0.93)	83.33
Cladocera	0.77 (0.43)	23.33	7.67 (1.60)	13.33	0.4 (0.41)	6.67	0.07 (0.21)	3.33
Ancylidae	–	–	7.33 (1.48)	16.67	6.07 (1.46)	23.33	0.53 (0.43)	13.33
Vegetation/detritus	77.27 (1.71)	100	33.27 (1.97)	76.67	55.6 (2.01)	100	45.03 (1.72)	100

Table 3. R values for two-way crossed analysis of similarities (ANOSIM) of dietary composition (calculated from % points) of the different dietary data of *G. brasiliensis* from different seasons in Bennett Brook. * indicates that R value is significant at $P < 0.05$.

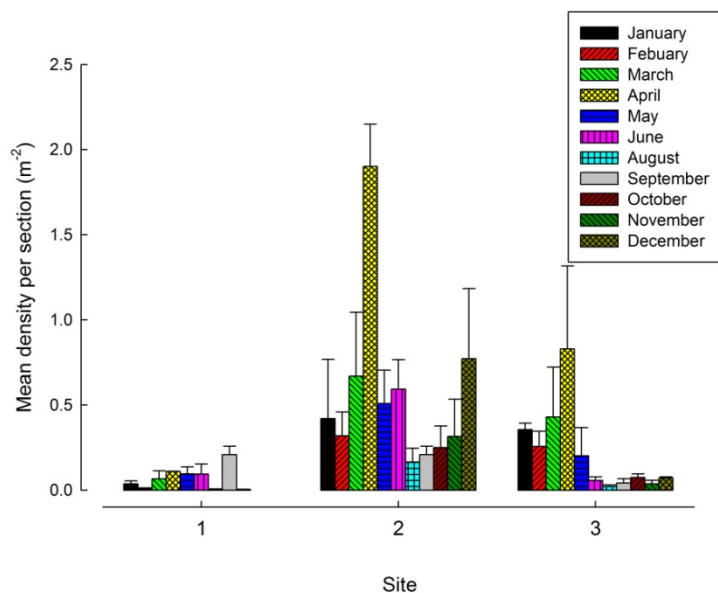
Season	Summer	Autumn	Winter
Autumn	0.281*	–	–
Winter	0.055*	0.175*	–
Spring	0.442*	0.119*	0.245*

in November (Lanius Drain) to $787.1 \mu\text{S}\cdot\text{cm}^{-1}$ in January (Bennett Brook) with a mean of $678.0 \mu\text{S}\cdot\text{cm}^{-1}$ (± 24.64) and $679.2 \mu\text{S}\cdot\text{cm}^{-1}$ (± 17.46) in the Lanius Drain and Bennett Brook sites, respectively. Dissolved oxygen ranged from 49.9% in March (Bennett Brook) to 132.4% in December (Lanius Drain) and was invariably greater in Lanius Drain (mean = $98.3\% \pm 5.00$) than Bennett Brook (mean = $59.9\% \pm 2.93$).

Spatial and temporal fish community structure

A total of 30923 fish from seven species were recorded from Lanius Drain and Bennett Brook between January and December 2010 (Table 1). Of these, 2505 (8.1% of all fishes) were *G. brasiliensis*. Other species included three south-western Australian endemic species the western pygmy perch *Nannoperca vittata* (1.3%

Figure 2. Mean (± 1 SE) densities of the *Geophagus brasiliensis* at the sites sampled in Bennett Brook (1) and Lanius Drain (2 - downstream, 3 - upstream) between January and December 2010.



of all fishes), nightfish *Bostockia porosa* (0.2%), and western minnow *Galaxias occidentalis* (5.8%) (Table 1). Also captured was the native estuarine Swan River goby *Pseudogobius olorum* (0.4%), the introduced *G. holbrooki* (84.1%), and *C. auratus* (<0.1%) (Table 1). The density of *G. brasiliensis* ranged from zero captures in November and December 2010 at the Bennett Brook downstream site to 1.90 (± 0.25) fish.m⁻² at the Lanius Drain downstream site in April 2010 (Figure 2, Appendix 1). Densities were generally greatest during summer and autumn particularly in March and April (Figure 2). Densities were greatest in all months at the Lanius Drain downstream site with the site in Bennett Brook having overall the lowest density of *G. brasiliensis* aside from winter when it exceeded that recorded at the Lanius Drain upstream site (Figure 2).

The downstream site in Bennett Brook housed the same seven fish species as the downstream site on Lanius Drain, however, the former site contained far fewer *G. brasiliensis* (i.e. overall average densities 0.06 (± 0.02) fish.m⁻² cf 0.51 (± 0.16) fish.m⁻² at those sites, respectively) (Table 1). The native freshwater species *N. vittata* and *B. porosa*, the native estuarine *P. olorum* and introduced *C. auratus* were found at the downstream site in Lanius Drain and Bennett Brook, however they were not recorded from the upstream site in Lanius Drain (Table 1). The Bennett Brook site also had much greater overall density of the introduced *G. holbrooki* than the

downstream Lanius Drain site (i.e. 4.68 (± 1.12) fish.m⁻² cf 2.52 (± 0.65) fish.m⁻², respectively), and also much greater density of the native *G. occidentalis* (0.36 (± 0.12) fish.m⁻² cf 0.10 (± 0.06) fish.m⁻², respectively). The native *N. vittata* was also most abundant at the Bennett Brook site compared to the downstream site in Lanius Drain (0.12 (± 0.06) fish.m⁻² cf 0.04 (± 0.01) fish.m⁻², respectively). The native freshwater crayfishes *Cherax cainii* and *Cherax quinquecarinatus* were recorded in low densities in both the Lanius Drain sites with the latter also recorded in the Bennett Brook site (Table 1). The introduced freshwater crayfish *Cherax destructor* was recorded from all sites but was greatest in abundance at the upstream site in Lanius Drain (Table 1).

Sampling in the irrigation lakes of the Vines Golf Course resulted in six fishes and one freshwater crayfish being recorded. *Geophagus brasiliensis* was captured ($n = 164$) from four of the seven lakes surveyed (Figures 1 and 3). Native fishes captured included the estuarine *P. olorum* (two lakes), the endemic freshwater *G. occidentalis* (one lake). The introduced *G. holbrooki* was recorded in all seven lakes sampled. The native freshwater crayfish *C. cainii* was also recorded in two of the lakes. The eastern Australian silver perch *Bidyanus bidyanus* was also recorded from three of the seven lakes surveyed in December 2011 and had a size range ($n = 26$) of 358–461 mm TL (Figure 3). Additionally, the eastern Australian golden

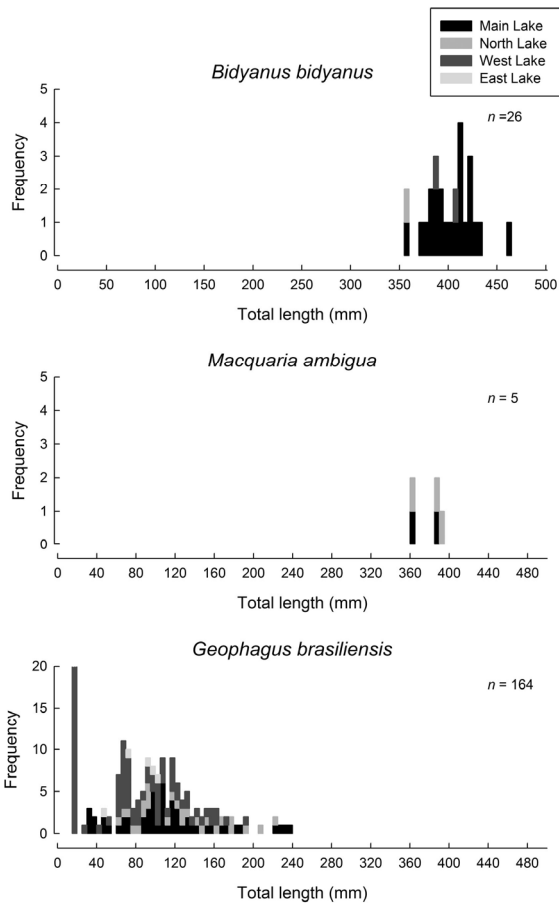


Figure 3. Length-frequency distributions of the introduced a) *Bidyanus bidyanus*, b) *Macquaria ambigua* and c) *Geophagus brasiliensis* in the lakes of the Vines Golf Course in December 2010.

perch *Macquaria ambigua* was also recorded from two lakes and had a size range ($n = 5$) of 360–390 mm TL (Figure 3).

Sampling in the Swan River during April and May 2010 did not record *G. brasiliensis*. However, during a recent fish kill event (June 2012), ≈ 60 *G. brasiliensis* were recorded in the Swan River upstream from the confluence of Bennett Brook and small number of the species had previously been reported from that area (K. Trayler, Swan River Trust, pers. comm.).

Growth and population structure of *Geophagus brasiliensis*

The relationships between TL and SL of female and male *Geophagus brasiliensis* were $TL = 1.276(SL) + 2.037$ ($r^2 = 0.987$, $P = 0.000$), and $TL = 1.289(SL) + 1.103$ ($r^2 = 0.993$, $P = 0.000$),

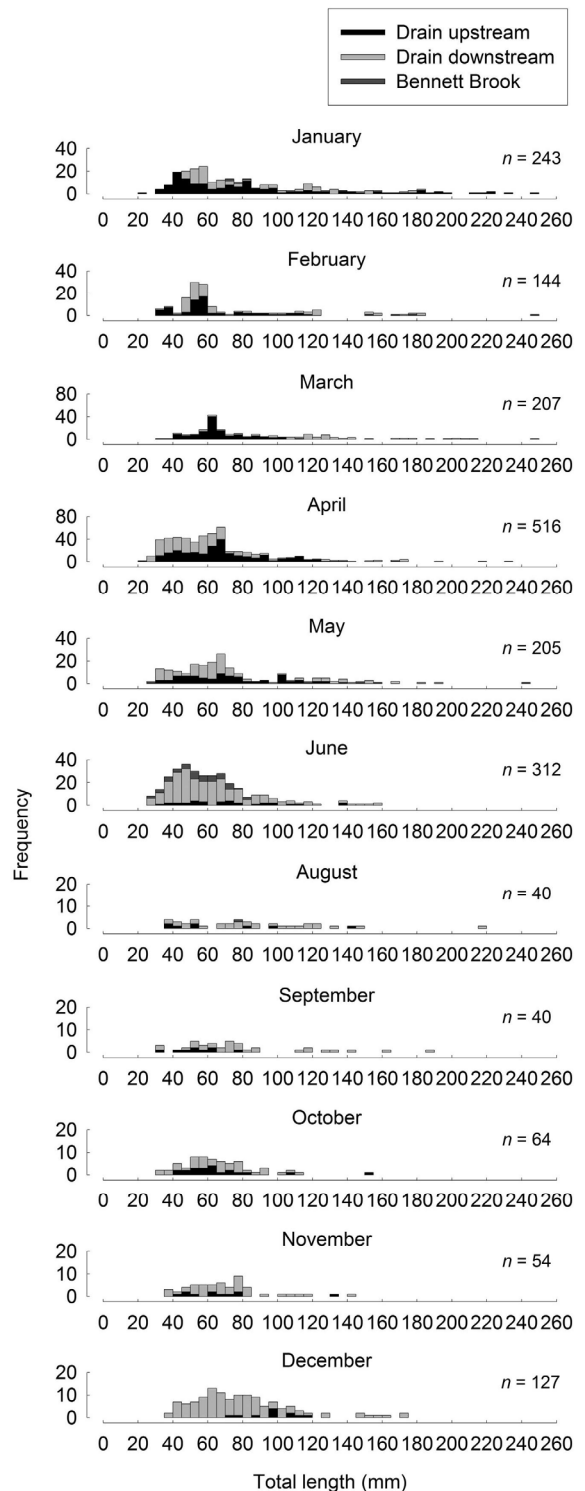


Figure 4. Length-frequency distribution of *Geophagus brasiliensis* at the sites sampled in Bennett Brook and Lanjus Drain between January and December 2010.

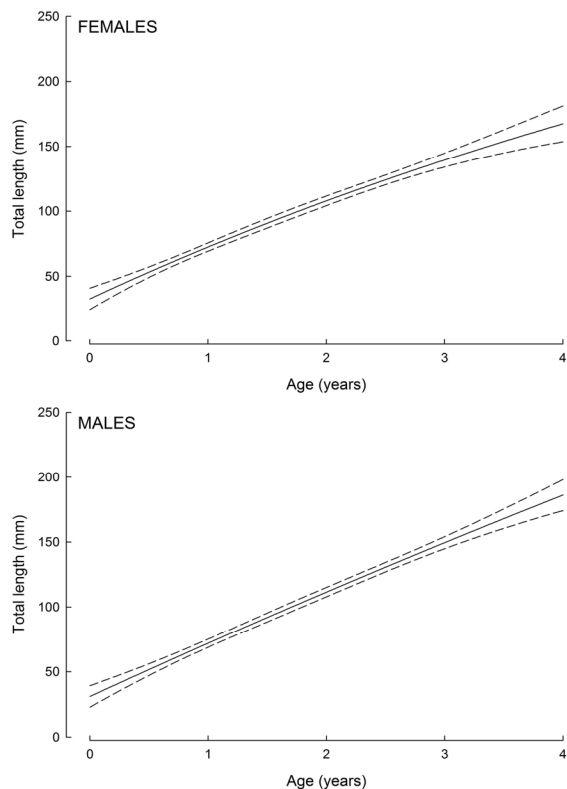


Figure 5. von Bertalanffy growth curves for female and male *Geophagus brasiliensis* in the Bennett Brook system.

respectively and these relationships were significantly different (likelihood ratio test, $P < 0.05$). As there was no significant difference between sexes in the relationship between wet weight and TL, the sexes were pooled and the relationship was $W = 7.539 \times 10^{-6}(TL^{3.167})$ ($r^2 = 0.992$, $P = 0.000$). The size range of *G. brasiliensis* in the lakes of the Vines Golf Course ranged from 15–235 mm TL (Figure 3). At least two distinct modes in the length-frequency distribution were present 15–20 and 65–70 mm TL with others at larger sizes less discernible (Figure 4). Similar to the population in the lakes of the Vines Golf Course, the length-frequency distribution of *G. brasiliensis* within the Bennett Brook system had a wide size range (20–245 mm TL) that represented a number of age cohorts (see below). Fish of lengths between 40–70 mm dominated the population in most months with juveniles (<40 mm TL, see age results below) also present in all months (Figure 4). However, very few juveniles <30 mm TL were recorded (23 individuals or 1.4% of total captures) and no

juveniles or larvae <20 mm TL were recorded on any occasion (Figure 4). The greatest abundances of new recruits (20–40 mm TL) were detected in April, May and June (Figure 4).

Of the 762 *G. brasiliensis* that were aged during this study, approximately 36.7, 29.7, 22.7 and 10.9 % belonged to the 0+, 1+, 2+ and 3+ age classes, respectively. The von Bertalanffy growth curve parameters demonstrated a considerably higher growth coefficient (K) for females than males, i.e. 0.117 *cf* 0.038, respectively. Growth of females approached an asymptote (L_∞) earlier than the males, i.e. 392.7 *cf* 1121.9 mm TL, respectively (Figure 5). Males were found to grow marginally faster than females, and attained, on average, TLs of 72.0, 111.5, 149.4 and 186.0 mm TL at the end of their 1st, 2nd, 3rd and 4th years of life, respectively. Females, on average, attained lengths of 72.5, 108.0, 139.5 and 167.5 mm TL at ages one, two, three and four, respectively.

Reproductive biology

Of *G. brasiliensis* that could be sexed, a sex ratio of 0.91F:1M was recorded. The temporal pattern in gonadal stages suggested that reproductively active (gravid V, spawning stage VI and/or spent stage VII) fish were present throughout the sampling period with the greatest activity occurring between January to May and least activity being recorded in spring (i.e. September to November) (Figure 6). Females of spawning stage VI were present from December to May with additional spawning condition fish being recorded in August (Figure 6).

The temporal pattern of GSI of mature females also suggested the species underwent a protracted spawning period as no clear precipitous decline in female GSI was observed (Figure 7). A gradual decline was observed between February and June largely coinciding with the period of greatest proportional presence of reproductively active (stage V–VII) female gonads (Figure 6). The GSI of mature males was greatest between December to June with a modest peak occurring in May (Figure 7).

The lengths at which 50% and 95% of females and males matured in the Bennett Brook system were found to be 91.4 and 111.4 mm TL for females, and 81.9 and 118.3 mm TL for males, respectively. Based on the age and growth relationship, the majority of the female and male population matured in their second year of life.

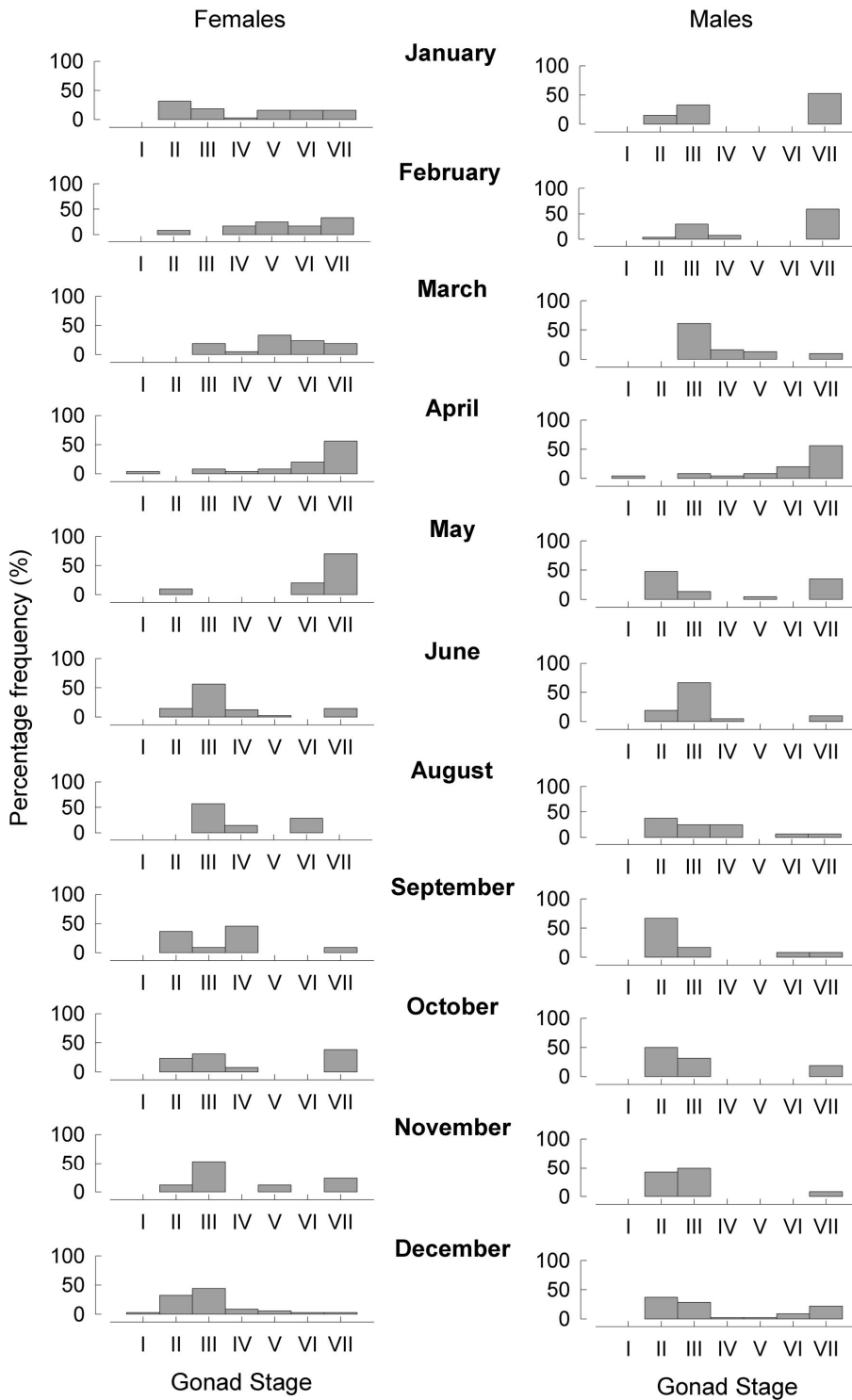


Figure 6. Temporal pattern of gonadal stage frequency for female and male *Geophagus brasiliensis* during the study. N.B. for comparative purposes of spawning activity, fish <50 mm TL (that were invariably stage I) were excluded.

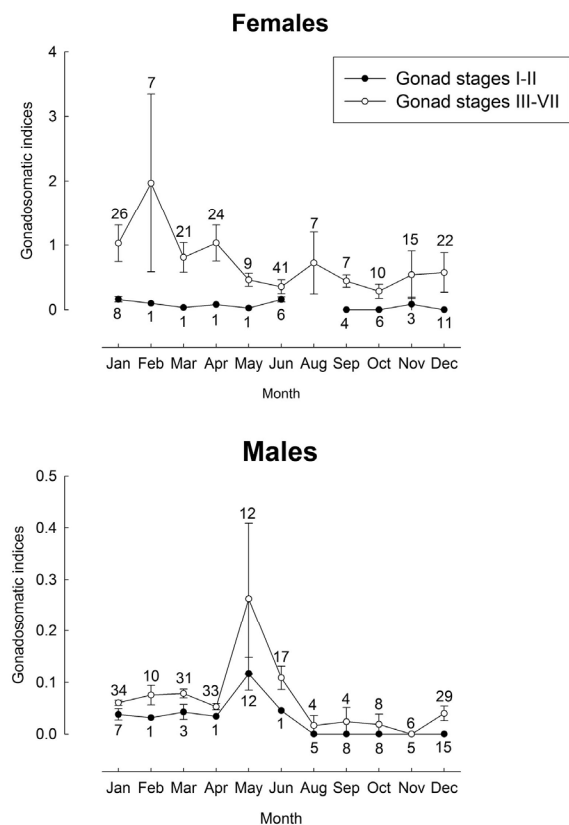


Figure 7. Gonadosomatic indices of female and male *Geophagus brasiliensis* in the Bennett Brook system between January and December 2010.

Dietary analysis

Vegetation and detrital material dominated the diet in terms of frequency of occurrence (e.g. was found in 100% of guts in all seasons apart from autumn) (Table 2). Other common food items in all seasons included ostracods (≈ 37 – 83% occurrence), chironomid larvae (23 – 87%), and coleopteran larvae (13 – 27%). Volumetrically, vegetation and detrital material was most dominant in the diets of fish in summer ($\approx 77\%$ of the overall volume) and least dominant in autumn ($\approx 33\%$ of the overall volume) (Table 2). Chironomid larvae and coleopteran larvae and adults, terrestrial insects, and ostracods were also notable volumetric contributors (Table 2). Parastacids (the native freshwater crayfish *C. quinquecarinatus* and introduced *C. destructor*) were consumed in summer and autumn (albeit in low amounts) and teleosts (*G. brasiliensis*) were also consumed in low amounts in all seasons apart from summer (Table 2).

ANOSIM revealed there was no significant difference in the overall diets between the four size categories. However, there was an overall significant differences in the diets between seasons (Global $R = 0.2$, $P = 0.001$). Pair-wise tests revealed significant differences between all seasons with the most pronounced difference occurring between summer and spring ($R = 0.442$, $P = 0.001$) (Table 3).

Discussion

Biology and distribution of Geophagus brasiliensis

The current study has demonstrated that the *G. brasiliensis* population in the Bennett Brook catchment is a self-maintaining population as evidenced by the seasonal presence of mature and spawning gonads, high overall abundance of the species, and the presence of multiple age classes. Moreover, from the high abundance and clearly discernible multiple length cohorts, the species appears to have also become established in a lentic system in the neighbouring Ellen Brook catchment. Furthermore, based on recent confirmed reports, the species appears to have an ongoing presence in the Swan River itself.

Much greater density of *G. brasiliensis* was recorded in the Lanius Drain sites compared with the most downstream site in Bennett Brook. The sampling at all three sites involved single pass electrofishing and (although not quantified) this was likely to have resulted in the removal of the vast majority of fish on each sampling occasion due to the relatively narrow (<3 m), shallow (<1 m) streamline. However, no clear reduction in the density of *G. brasiliensis* was observed over the sampling period at any site in Lanius Drain or Bennett Brook. Furthermore, upstream recolonisation of the upper Lanius Drain site would be highly unlikely due to a series of ≈ 50 cm instream steps that are present within that site and between it and the sites further downstream. Therefore, given the complete lack of larvae or smaller juvenile individuals (<20 TL) throughout the study (only 1.4% of total captures were <30 mm TL), the consistent presence of the species at least at the upstream site (and probably also the other more downstream sites) in Lanius Drain must have been mostly or entirely due to downstream recruitment from the Altone Park wetlands. The presence of adult fish with gravid, spawning and spent gonad stages in the sites sampled during

the current study would have also been due to their downstream movement from Altone Park wetlands between sampling occasions each month.

The greatest abundances of new recruits (20–40 mm TL) were detected in April, May and June suggesting that downstream immigration of juveniles was occurring from the Altone Park wetlands just prior to or during this period. The species has a reported maximum size of 280 mm TL although are commonly found to be ~90 mm TL in their natural range (Kullander 2003). Therefore, although the maximum size in this study (i.e. 245 mm TL) was slightly less than previously recorded it is consistent with that within its natural range. However, additional sampling conducted by the authors for a separate study in the Bennett Brook catchment recorded numerous individuals >300 mm TL with the largest being 357 mm TL; representing the largest reported size for the species. By their third year of life, the species had attained TLs larger than most of the native freshwater fishes of the region (e.g. Allen et al. 2002; Morgan et al. 1998, 2011).

Attainment of maturity of *G. brasiliensis* in the current study occurred in their second year of life at a L_{50} of ~91 mm TL (~70 mm SL) for females and ~82 mm TL (~63 mm SL) for males. These values fall within the range of the lengths at first maturity determined for the species in Brazil i.e., 59 to 95 mm SL for combined sexes in a river and lagoon population, respectively (Mazzoni and Iglesias-Rios 2002). We are unaware of other studies that have determined age at first maturity for the species in the wild and it has been noted that it is difficult to elucidate those relationships in tropical populations (e.g. Mazzoni and Iglesias-Rios 2002). The unrealistic asymptotic lengths of the von Bertalanffy growth models for both sexes in the current study (Figure 5) may reflect a relative recent introduction of the species to the system as previously occurred with the introduction of Eurasian Perch *Perca fluviatilis* into a reservoir in south-western Australia (Morgan et al. 2002). Alternatively, high mortality rate of larger fish may occur. Either of these scenarios may result in the ‘straightening’ (i.e. a reduced curvature) of the model (as only a small reduction in growth rate was recorded with age) resulting in an asymptote at a very large size.

Geophagus brasiliensis has been demonstrated to be phenotypically flexible in terms of its

reproductive biology and this has been associated with the level of environmental stability (Mazzoni and Iglesias-Rios 2002). The population in the current study is exposed to a Mediterranean climate as compared to subtropical Brazilian populations and they experience considerably different hydrological conditions. The degree of seasonality of reproduction in fishes in temperate environments is also believed to be related to variability in temperature, photoperiod and food availability (McKaye 1984; Payne 1986). Along with revealing a smaller size at the onset of maturity for a Brazilian river population compared to a lagoon population, Mazzoni and Iglesias-Rios (2002) also demonstrated that reproduction occurred throughout the year in the river population but was less protracted (occurring between September and April) in the lagoon population. The greater reproductive investment in the former population was attributed to that environment being more unstable environmentally and therefore the species was maximising the chances of a successful spawning event (Mazzoni and Iglesias-Rios 2002). This contrasts with the findings of the present study where the protracted breeding appears to occur in at least one lentic system with a lack of (at least successful) breeding occurring in the lotic sites. It is not unusual for introduced fishes to display variation in their life history when exposed to different environments and climates as was demonstrated for *P. fluviatilis* in south-western Australia (Morgan et al. 2002). Aside from those associated with climatic differences, there may be numerous other environmental variables (such as river size and food availability) between the systems in the current study and those within South America that may drive differences in breeding strategy of *G. brasiliensis*. Nonetheless, this reproductive variability is typical of an r-strategist that can maximise its chances of population viability by altering its reproductive strategy.

Physicochemical tolerance and potential for spread

There is a single connection point from the Vines Golf Course lake system that discharges seasonally during winter and spring into an ephemeral creek that flows ~500 m into the Ellen Brook. However, it is unclear as to whether this

population is a result of a separate introduction directly into those lakes, or the result of colonisation by the Bennett Brook population that would have had required a ≈ 17.5 river km upstream journey to reach Ellen Brook and then a further ~ 3 km into the ephemeral tributary that flows out of those lakes (Figure 1). The latter is certainly plausible given the salinity tolerance of the species ($<10\%$ mortality over 41 days when gradually acclimatised to 36ppt) would easily enable its survival in that section of the Swan River (De Graaf and Coutts 2010). As mentioned, ≈ 60 *G. brasiliensis* were recorded in the Swan River upstream from the confluence of Bennett Brook during a recent fish kill event (June 2012, K. Trayler, Swan River Trust, pers. comm.) and small numbers of the species had previously been reported from that area. During that fish kill event, the vast majority of deaths consisted of *Acanthopagrus butcheri* ($n \approx 1800$) therefore *G. brasiliensis* only represented a minor component ($\approx 3\%$). This would either be due to them being present in relatively low abundance in the Swan River (which would also explain their lack of detection in the current study and previous estuarine studies in that area), greater tolerance of adverse water quality than *A. butcheri* (particularly low levels of dissolved oxygen), or a combination of both those factors. Although it is possible that those individuals had been flushed downstream from the lentic population in the Ellen Brook, it is more likely that the species now has an ongoing presence in the Swan River; albeit in relatively low abundance and it is as yet unknown whether it successfully spawns in that system.

Brown et al. (2001) found a relatively high and unique (among stenohaline freshwater fishes) hypo-osmoregulatory ability for pikeperch *Sander lucioperca* in the U.K. whereby the species maintained lower plasma chloride concentrations and osmolality than the external media. The latter study noted that that most stenohaline freshwater fishes are thought to survive higher salinities by tolerating high osmolality (Abo Hegab and Hanke 1982; Brown et al. 2001). This resulted in similar salinity tolerance levels (high survival in gradual salinity increases to 29–33 psu) to those of *G. brasiliensis* reported in De Graaf and Coutts (2010). Although the physiological mechanisms that allow *G. brasiliensis* to tolerate high saline conditions have not been specifically examined,

it is possible that they similarly have a relatively high hypo-osmoregulatory ability and it may therefore be possible for the species to move through tidal and nearshore saline marine environments which would enable the species to colonise other river systems of Western Australia via the Indian Ocean. This utilisation of saline environments to facilitate the spread of freshwater fish species has been referred to as using ‘saline bridges’ and was proposed as a possible mechanism to help explain the wide spread of *S. lucioperca* through Europe (Brown et al. 2001). A relatively high tolerance of salinity by *G. brasiliensis* would favour it over most native freshwater fishes whose inland distributions have been greatly reduced due to secondary salinisation (Morgan et al. 1998, 2003; Beatty et al. 2011).

Being a tropical species, water temperatures within the native habitats of *G. brasiliensis* range from 11–12°C to 27–28°C at the southern end of its distribution, to 30–37°C in the Amazon River system (Rantin and Petersen 1985). The temperature tolerance of the species was investigated by Rantin and Petersen (1985) and they found its lower lethal temperature limit varied depending on the temperature of acclimatisation and ranged from 8°C (acclimatised at 12.5°C) to 17.8°C (when acclimatised at 32.5°C). Not unexpectedly, its upper thermal tolerance was relatively high ranging from 32.9°C (when acclimatised at 12.5°C) to 38.5°C (when acclimatised at 32.5°C). Therefore, although one would expect it to favour the warmer conditions such as occurs throughout tropical northern Australia, the current study has shown it can tolerate temperature regimes more typical of thermally variable climatic regions; similar to the other tropical and sub-tropical introduced species of this region. *Geophagus brasiliensis* also have a minimum mean dissolved oxygen saturation tolerance of just 10.6% (Webb 2008) and therefore those recorded at all sites (during the day) in the current study would be well above that lower tolerance level.

Potential ecological impact of *Geophagus brasiliensis* in Western Australia

Quantifying ecological impacts of introduced freshwater fish is often difficult due to the complex nature of ecosystems and differentiating their level of impact with those associated with

other stressors and more research is needed globally (e.g. Kennard et al. 2005). For example, *G. holbrooki* in Australia has been demonstrated to be a major determinant of abundance of other fishes and it has also been shown to significantly effect body condition; with other environmental variables playing only a minor role (MacDonald et al. 2012). It is important to note that the potential ecological impacts that *G. brasiliensis* may have on the highly endemic freshwater fishes in south-western Australia discussed below requires a great deal of research to quantify and differentiate from existing anthropogenic stressors.

The benthic dwelling *G. brasiliensis* was found to have a broad omnivorous diet albeit dominated by vegetation and detritus. Similar dietary breadth by the species has been found elsewhere to include detritus, algae, other vegetation, aquatic insects, zooplankton and fish (Arcifa et al. 1988; Romanini 1989; Arcifa and Meschiatti 1993; Marcos et al. 2004). Although ontogenetic dietary shift has been observed for the species (Marcos et al. 2004), as found in the current study, this is not always the case as recorded in a Brazilian reservoir (Arcifa et al. 1988; Arcifa and Meschiatti 1993). The broad omnivorous diets of several introduced species in the region (Beatty and Morgan 2013) contrasts with the entirely carnivorous diets of native freshwater fishes of the region (Morgan et al. 1998) and allow them to occupy a broader range of ecosystems and could also result in them potentially having a considerable impact on the structure and function of the aquatic ecosystems that may be difficult to predict due to the potential de-coupling of trophic cascades.

Geophagus brasiliensis provides some degree of parental care and spawns on the benthos (Castro and Arcifa 1987). However, the level of parental care behaviour is not yet fully described for the species, especially regarding the role played by each sex in the different phases involved in parental care, such as substrate selection, nest preparation, territory defense, nest guard and fry protection (Bastos et al. 2011). Many substrate-guarding cichlids seem pre-adapted to mouth-brooding (Keenleyside 1991). Parental care contributions enhance the survival and reproductive success of the care-givers offspring (Blumer 1982). However in fish, the absence of parental care is common occurring in 78% of all families globally (Gittleman 1981) and in 100% of all the south-western Australian

native freshwater fish species (Morgan et al. 1998; 2011). The level of parental care and agonistic behaviour that *G. brasiliensis* displays should be determined as it would strongly influence the level of impact that species may have in terms of competition for habitat with native fishes and other benthic aquatic species in south-western Australia and elsewhere. The entirely endemic freshwater crayfish fauna of south-western Australia may be particularly impacted by *G. brasiliensis* given they are all benthic species and least one is subject to predation (Table 2).

Within a Brazilian River in its native range, *G. brasiliensis* competes with an introduced tilapia species *Oreochromis niloticus* and the relative abundance of the invasive species was positively associated with degraded (polluted) habitats whereas *G. brasiliensis* abundance was negatively associated with such pollution (Linde et al. 2008). This highlights the propensity of introduced freshwater fishes to thrive in altered habitats, such as novel lentic systems (e.g. Lapointe et al. 2012), in contrast to more unaltered natural habitats within their natural distributions (Marvier et al. 2004). Many aquatic systems in south-western Australia have been degraded through habitat and water quality decline (e.g. salinisation and eutrophication) which would therefore likely favour this and other introduced species (Beatty and Morgan 2013).

Control and eradication options for the two populations of *G. brasiliensis* are currently being examined by the Western Australian Government. Given that there is a single potential escape point in both the Altone Park and the Vines Golf Course lakes populations, fitting screens (such as vertical travelling screens) could be an effective control option. However, partial or complete draining of the systems followed by the application of a piscicide is also currently being assessed. Given complete eradication of freshwater fishes can often be impossible, such strategic control and containment programs can be effective in mitigating their impacts (Britton et al. 2011).

Studies that relate to the distribution and direct impacts of introduced species in south-western Australia include those conducted on *G. holbrooki* (Pen and Potter 1991; Gill et al. 1999), *C. auratus* (Morgan and Beatty 2007), *X. hellerii* (Maddern et al. 2011), *P. fluviatilis* (Morgan et al. 2002), *O. mykiss* (Tay et al.

2007), and reviews of all species (Morgan et al. 2004; Beatty and Morgan 2013). There have also been separate studies that have examined the impacts of habitat alteration and water quality decline on native freshwater fish communities (e.g. Morgan et al. 2003; Morgan and Beatty 2006; Beatty et al. 2011). However, there have yet to be studies that determine the relative impact of habitat and water quality decline versus the presence of introduced species in driving the major range and population declines of the highly endemic native fish fauna of the region. Furthermore, controlled experiments rather than observational studies of wild populations *per se* are required to quantify their ecological impacts in terms of predation, agonistic behavior, and competition for resources.

There are currently 13 known established introduced freshwater fishes in south-western Australia (Beatty and Morgan 2013). Altered thermal and flow regimes, salinisation and climate change are predicted to convey advantages to salt tolerant, omnivorous, tropical and sub-tropical species in the region, such as *G. brasiliensis* (Beatty and Morgan 2013). Physiological thresholds (particularly salinity, temperature, and aerobic scope) and habitat requirements of most established alien fishes in the region need to be quantified in order to help predict population viabilities and potential incursions in aquatic ecosystems under current and future environmental conditions. Public education campaigns are required to help prevent future introductions and increased monitoring effort is required to detect new incursions as early as possible to maximise the chances of their containment or eradication.

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Appendix 1. *Geophagus brasiliensis* capture data (see Figure 1).

Latitude	Longitude	<i>Geophagus brasiliensis</i> sample sites (present = 1, absent = 0)
-31.8741	115.9552	1
-31.8737	115.9569	1
-31.8813	115.9615	1
-31.7666	116.0070	1
-31.7664	116.0088	1
-31.7659	116.0079	1
-31.7681	116.0057	1
-31.7497	116.0118	0
-31.7517	116.0173	0
-31.7548	116.0144	0