



## Review

## Introduced freshwater fishes in a global endemic hotspot and implications of habitat and climatic change

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### Abstract

Introductions of alien freshwater fish species into the Mediterranean-climatic South-west Coast Drainage Division of Australia have impacted a highly endemic ( $\approx 82\%$ ) yet depauperate (11 species) native freshwater fish fauna. This study updates the current known introduced freshwater fishes in Western Australia, assesses the historic rate of introductions and how habitat, water quality and climatic changes have facilitated those introductions. South-western Australia has undergone a  $\approx 63\%$  increase in alien freshwater fish introductions since 1970 (44% increase over the past decade) to 13 species; overtaking the number of native fishes. Aquarium species represent 80% of the latest introductions (46% of total number) and the majority (54%) of introduced fishes in the region are of sub-tropical or tropical origin. As found elsewhere, species with broad environmental tolerances and generalist diets are likely to continue to be the main colonizers in this region. We propose that past and future climatic and habitat changes in the Mediterranean-climatic south-west region will facilitate continued invasion of tropical and sub-tropical aquarium fishes and that strategic monitoring, control and public education programs are required to halt future introductions.

**Key words:** alien fishes; aquarium species; life-history traits; Mediterranean climate; flow reduction; temperature increase

### Introduction

Globally, the rate of non-native freshwater fish introductions has doubled in the past 30 years driven primarily by aquaculture and attempts to improve wild stocks (Gozlan 2008; Gozlan et al. 2010). It is predicted that introduced fishes will continue to result in homogenisation of freshwater fish faunas and there is therefore an urgent need for increased risk-based management of alien fishes (Britton et al. 2011). Aquaculture and wild stock enhancements are key vectors driving freshwater fish introductions (Gozlan et al. 2010); however, another key vector has been aquarium releases (e.g. Lintermans 2004; Smith et al. 2008).

Marr et al. (2010) demonstrated that 76 species of freshwater fishes had been introduced to the five Mediterranean climate regions with four orders having been introduced to all of those regions (i.e. Cypriniformes (16 species),

Cyprinodontiformes (10 species), Perciformes (26 species), and Salmoniformes (nine species)). There has therefore been an 8% overall increase in the similarities of the freshwater fish fauna of Mediterranean-climatic regions due to those non-native introductions (Marr et al. 2010). Homogenisation of the Australian freshwater fish fauna due to species introductions has also been specifically demonstrated (Olden et al. 2008). For example, the introduction of the common carp *Cyprinus carpio* Linnaeus, 1758 and eastern gambusia *Gambusia holbrooki* (Girard, 1859) to the Lake Eyre and the South-west Coast Drainage Divisions has resulted in a present-day similarity of 7.3%, when historically they shared no species.

The non-randomness of aquatic introductions (Strayer 2010) should allow some degree of predictability and therefore strategic approach to control and prevention of introductions provided that there is sufficient understanding of the

patterns of introductions on a regional scale (see Lapointe et al. 2012). Establishment success of introduced freshwater fish into new countries has been shown to be related to the degree to which the climate in that new country matched the climate elsewhere within their geographic range (Bomford et al. 2010). In terms of freshwater fish introductions into five Mediterranean climatic regions, orders with high numbers of tropical species have been underrepresented; that is believed to be due to their inability to tolerate wide temperature ranges and other harsh abiotic conditions (Marr et al. 2010).

Owing to spatial variation in ecosystem invisibility of freshwater fishes, it is important to examine patterns of invasions within specific bioregions (Lapointe et al. 2012). South-western Australia (Figure 1) is a Mediterranean-climatic region that is recognised as one of the world's biodiversity hotspots due to its high rates of endemism (Myers et al. 2000). Nine of the 11 species of freshwater fish are endemic to the region as are all 11 species of freshwater crayfish (Allen et al. 2002; Morgan et al. 2011a). Introduced freshwater fishes in the region have been shown to predate on native fauna, compete for food and habitat and show agonistic behaviour towards native fishes and are likely to have resulted in major changes to the structure and function of many aquatic ecosystems (Morgan et al. 2002, 2004; Morgan and Beatty 2007). Although the relative impacts of habitat degradation versus introduced species on the decline in ecosystem health and native fish populations specifically has not yet been investigated in Western Australia, it is likely that introduced species have exacerbated the impacts of major habitat and water quality decline such as secondary salinisation (Morgan et al. 2003; Beatty et al. 2011), construction of instream barriers (e.g. Morgan and Beatty 2006), and reductions in surface flows and groundwater levels (Morrongiello et al. 2011).

Many rivers in south-western Australia have become secondarily salinised as a result of wide-scale clearing of native vegetation and only 44% of flow in the 30 largest rivers is fresh (Mayer et al. 2005). This has resulted in major range reductions of stenohaline species and concomitant inland colonisation of typically estuarine native species (Morgan et al. 2003; Beatty et al. 2011) and would favour those introduced species more resistant to elevated salinities that could potentially colonise habitats no longer suitable for those species.

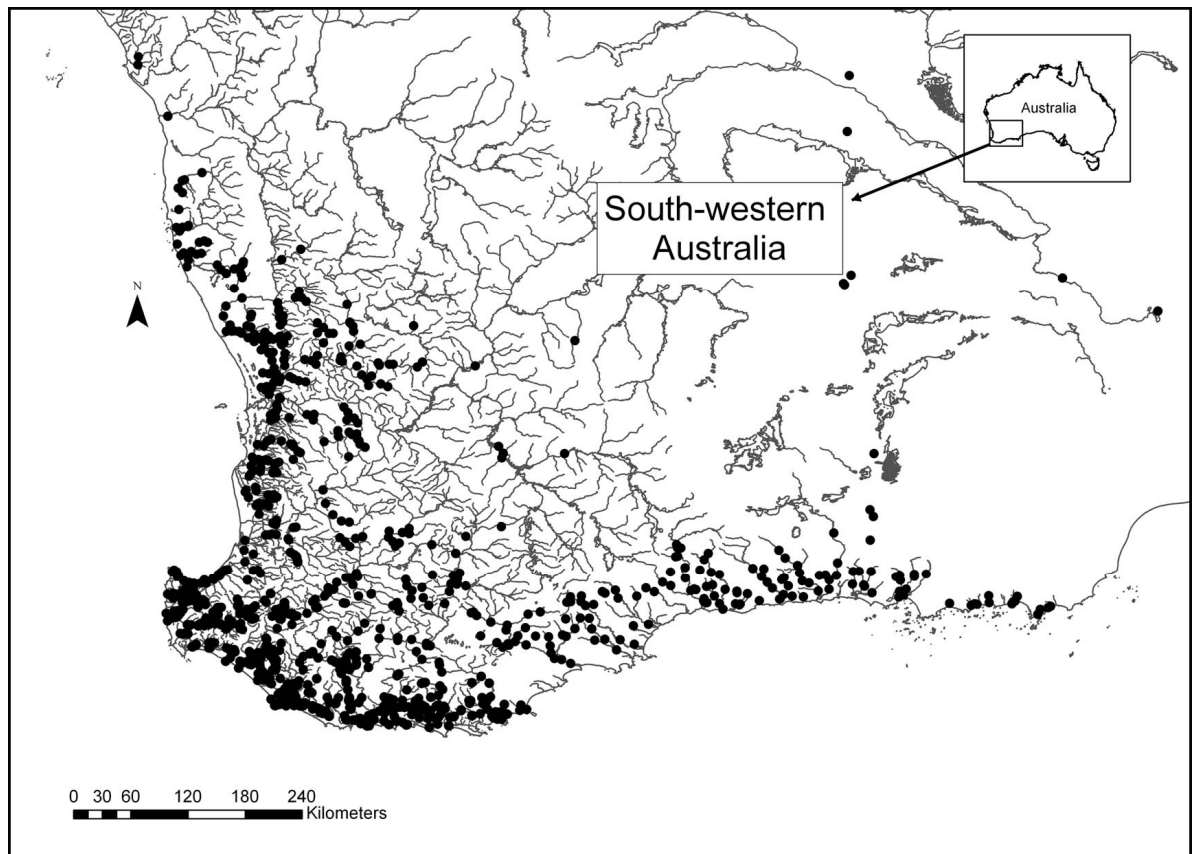
South-western Australia has undergone a 10–15% reduction in mean annual rainfall since the mid 1970's (IOCI 2002), which has resulted in up to a three-fold reduction in stream-flow and a further  $\approx 8\%$  rainfall reduction (median projection) by 2030 (combined with human water extractions) is expected to result in an additional  $\approx 25\%$  reduction in mean annual runoff and broad-scale groundwater reductions (Whetton et al. 2005; Suppiah et al. 2007; CSIRO 2009a,b; Barron et al. 2012; Silberstein et al. 2012). Furthermore, annual mean temperature increases for south-west Australia are projected with greatest proportional increase in winter (8.8–16.0%) (Suppiah et al. 2007; Department of Water Government of Western Australia 2010). As predicted for introduced fishes globally (Rahel and Olden 2009), past and projected climatic shifts in this region may favour introduced species; particularly those of tropical and sub-tropical origin.

The current study aimed to review the known freshwater fish introductions in south-western Australia and determine the past rate of introductions. It is hypothesised that past and future habitat and climatic change has favoured recent introductions and will increase the likelihood of future establishment of tropical and sub-tropical introduced fishes in this Mediterranean climatic region due to their physiological and ecological traits becoming increasingly matched to these altered aquatic environments.

## Material and methods

### *Current introduced freshwater fishes of Western and south-western Australia*

Information on current known introduced freshwater fishes in wild aquatic systems in Western Australia was obtained through reviews of Coy (1979), Allen (1982, 1989), Allen et al. (2002), Morgan et al. (1998, 2002, 2004, 2011a), Maddern (2008), Maddern et al. (2011), Morgan and Beatty (2007), Marr et al. (2010), records from Museum of Western Australia, and unpublished data from our past surveys of >1500 sites throughout the region (see Figure 1). Cumulative species introductions in wild aquatic systems (defined here as either naturally occurring lentic or lotic systems or artificial lentic habitats that connect to natural systems) were then plotted against time (of first known presence in the region) to examine temporal rates of introductions.



**Figure 1.** Sampling sites of the authors used in the current review of introduced freshwater fishes in south-western Australia. N.B. these include published (Morgan and Beatty 2007; Morgan et al., 2002, 2004, 2011a) and also the majority of the unpublished sampling sites of the authors in this region, but are additional to those 411 sites published in Morgan et al. (1998) for the extreme south-western corner.

## Results

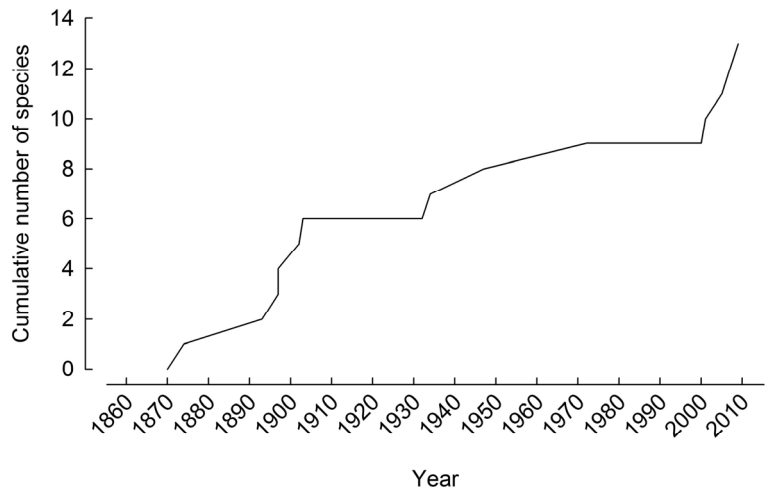
### *Introduced freshwater fishes in Western and south-western Australia*

A review of past published and unpublished information on introduced fishes in Western Australia revealed that there are currently 13 species from seven families that have been introduced into natural or artificial systems connected to natural systems in the South-west Coast Drainage Division of Australia (Table 1). These include Salmonidae (rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), brown trout *Salmo trutta* Linnaeus, 1758), Percidae (Eurasian perch *Perca fluviatilis* Linnaeus, 1758), Cyprinidae (common carp *C. carpio*, goldfish *Carassius auratus* Linnaeus, 1758, rosy barb *Puntius conchonius* (Hamilton, 1822)),

Poeciliidae (one-spot livebearer *Phalloceros caudimaculatus* (Hensel, 1868), swordtail *Xiphophorus hellerii* Heckel, 1848, eastern gambusia *G. holbrooki*), Cichlidae (*Geophagus brasiliensis* (Quoy & Gaimard, 1824), Percichthyidae (golden perch *Macquaria ambigua* (Richardson, 1845)), and Terapontidae (silver perch *Bidyanus bidyanus* (Mitchell, 1838), spangled perch *Leiopotherapon unicolor* (Günther, 1859)). Since 1970, there has been an increase of  $\approx 63\%$  (from eight to 13 species) in the number of known introduced freshwater fish species recorded in this region, with the past decade seeing an  $\approx 44\%$  increase (Table 1, Figure 2).

Seven ( $\approx 54\%$  of total species) introductions have natural distributions that include tropical (*G. brasiliensis*, *P. caudimaculatus*, *X. hellerii*) or sub-tropical (*G. holbrooki*, *C. carpio*, *C. auratus*, *P. conchonius*) climatic regions (Table 1). Moreover, 80% of introductions since

**Figure 2.** Cumulative number of introduced freshwater fishes in natural aquatic systems or artificial systems connected to natural systems in Western Australia over time. (information from Coy 1979; Allen 1982, 1989; Allen et al. 2002; Morgan and Beatty 2007; Morgan et al. 1998, 2002, 2004, 2011a; Western Australian Museum; Morgan and Beatty unpubl. data).



**Table 1.** Species name, climatic and geographical origin, year of first introduction (Intro. year), introduction vector (A = aquarium, O = ornamental, BC = biological control, SF = sport fishing), and diet (O = omnivorous, D = detritivorous, C = carnivorous) of introduced freshwater fishes in south-western Australia. N.B. limited to those currently known to be present in naturally occurring systems or artificial systems connected to natural systems (Coy 1979; Allen 1982, 1989; Allen et al. 2002; Morgan and Beatty 2007; Maddern 2008; Maddern et al. 2011; Morgan et al. 1998, 2002, 2004, 2011a; Western Australian Museum; Morgan and Beatty, unpublished data).

Species	Climatic origin	Geographical origin	Intro. year	Vector of introduction	Diet
<b>Cichlidae</b>					
<i>Geophagus brasiliensis</i>	Tropical	South America	2006	A/O	O
<b>Cyprinidae</b>					
<i>Carassius auratus</i>	Sub-tropical	Asia	1893	A/O	O/D
<i>Cyprinus carpio</i>	Sub-tropical	Europe and Asia	1947	A/O	O/D
<i>Puntius conchonius</i>	Sub-tropical	Asia	2007	A/O	O
<b>Poeciliidae</b>					
<i>Gambusia holbrooki</i>	Temperate/ Sub-tropical	North America	1934	B/C	C
<i>Phalloceros caudimaculatus</i>	Tropical	South America	1972	A/O	O
<i>Xiphophorus hellerii</i>	Tropical	North and Central America	2001	A/O	O
<b>Salmonidae</b>					
<i>Salmo trutta</i>	Temperate	Europe	1874	SF	C
<i>Oncorhynchus mykiss</i>	Cold/temperate	North America	1902	SF	C
<b>Percidae</b>					
<i>Perca fluviatilis</i>	Temperate	Europe and Asia	1903	SF	C
<b>Percichthyidae</b>					
<i>Macquaria ambigua</i>	Temperate/dry	Australia (eastern)	1897	SF	C
<b>Terapontidae</b>					
<i>Bidyanus bidyanus</i>	Temperate/dry	Australian (eastern)	1897	SF	O
<i>Leiopotherapon unicolor</i>	Temperate/tropical/dry	Australian (north-western, northern, eastern)	2009	SF	O

1970 and  $\approx 46\%$  of all introduced fishes are recognised as aquarium species, with the remainder originally being introduced for sport fishing ( $\approx 46\%$ ), or biological control ( $\approx 8\%$ ). Several temperate Australian species that do not naturally occur in this Drainage Division are

now found in this region including the eastern Australian *B. bidyanus* and *M. ambigua* and the widespread *L. unicolor* that naturally occurs throughout northern, north-western, north/central-eastern Australia (Allen et al. 2002; Morgan et al. 2004).

In terms of overall Western Australian introduced freshwater fishes, there has been an  $\approx 88\%$  increase to 15 species over the last  $\approx 40$  years, with the introduction of another cichlid (Mozambique mouthbrooder *Oreochromis mossambicus* (Peters, 1852)), into rivers of the Pilbara Drainage Division, and a poeciliid (guppy *Poecilia reticulata* Peters, 1859) into pools on the North West Cape and Christmas Island (Morgan et al. 2004). Importantly, the Kimberley Drainage Division, which houses the majority of Western Australia's freshwater fish diversity, currently remains free from introduced freshwater fishes, although *G. holbrooki* was reported from an isolated water body (Allen et al. 2002; Morgan et al. 2004; Morgan et al. 2011b).

## Discussion

### *Introduced freshwater fishes of Western and south-western Australia*

The study has revealed a sharp increase ( $\approx 44\%$ ) in the number of introduced freshwater fish species in wild aquatic systems in the South-west Coast Drainage Division of Australia in the past decade (to 13 species) and a nearly doubling of the introduced freshwater fish species in Western Australia over that period (to 15 species). Furthermore, there have been five additional species recorded since the last comprehensive assessment by Morgan et al. (2004). The rate of increase in Western Australia therefore approximates the global increase in freshwater fish introductions that have doubled in the past  $\approx 30$  years (Gozlan 2008; Gozlan et al. 2010). South-western Australia now houses several of the most widely introduced freshwater fishes globally including *G. holbrooki*, *C. auratus*, *S. trutta*, and *O. mykiss* (Allen et al. 2002; Morgan et al. 1998, 2004, 2011a; Morgan and Beatty 2007). The fact that  $\approx 54\%$  of these species have natural distributions that include tropical or sub-tropical climatic regions and nearly half are classed as aquarium species is notable and an exception to global introductions (Gozlan et al. 2010) but consistent with a past assessment of Australian releases (Lintermans 2004). As outlined below, we propose that past and future habitat and climatic change in the Mediterranean-climatic south-west region, has and will continue to create, favourable conditions for invasive freshwater fishes to become established to the detriment of the highly

endemic native species in this global biodiversity hotspot.

The tropical *G. brasiliensis* is an example of a recently discovered established species in the region and has been shown to have a greater abundance, broader salinity tolerance, more generalist diet, longer breeding period, grow faster and to a larger maximum size than all sympatric native species and almost all south-western Australian native freshwater fishes (De Graaf and Coutes 2010; Beatty et al. in press). Relatively rapid attainment of maturity and short generation time of many introduced species in the current study such as the small-bodied poeciliids, i.e. *G. holbrooki*, *X. hellerii* and *P. caudimaculatus*, are typically characteristics of r-strategists that are often rapid colonisers of new and variable habitats (Pianka 1970). Furthermore, protracted breeding in more stable environments by r-strategists can also allow large recruitment potential (Pianka 1970).

The eastern Australian *M. ambigua* was also recently recorded in lakes connected to the Swan River (Beatty et al. in press). The simultaneous discovery of *B. bidyanus* in the latter study was also of note, although the species had previously been reported from the Swan River and the Harvey Dam and was counted as one of the eight introduced fishes in the region by Morgan et al. (2004). *Bidyanus bidyanus* is a common inland aquaculture species and Morgan et al. (2004) predicted expansion of the aquaculture industry in Western Australia may lead to further introductions of this and potentially other aquaculture species into wild systems. Both species grow much larger than all native freshwater fish species of this region, with the diet of *B. bidyanus* being omnivorous (Rowland and Barlow 1991) and *M. ambigua* feeding as a generalist carnivore (Baumgartner 2007; Sternberg et al. 2008). Both these species would undoubtedly predate on the relatively small native fishes and also crayfishes of the region, as do the existing top order introduced teleosts *P. fluviatilis* (Morgan et al. 2002), *O. mykiss* (Tay et al. 2007) and *Salmo trutta* (Morgan et al. 2004). In their native range, spawning in both species generally occurs during spring and summer with *M. ambigua* generally thought to move upstream to spawn during flood events when temperature exceeds  $20^{\circ}\text{C}$  (Reynolds 1983; Lintermans 2009). Although summer flood events are less common in south-western Australia, they do nonetheless occur. Furthermore, Ebner et al. (2009) found that *M. ambigua*

in lake systems in the Darling River could breed in all seasons, at lower temperatures than previously believed (18.8°C), and did not require floods. Whilst the viability of current populations of these two species remains to be determined, such reproductive flexibility increases the chances of populations becoming self-maintaining in south-western Australia.

#### *Ecological impact of introduced fishes in Western Australia*

Differentiating between demonstrated and assumed impacts of introduced freshwater fishes on ecological response indicator groups such as native freshwater fishes can be very difficult due to the complexity of and interactions between other stressors (i.e. anthropogenic driven habitat and water quality changes). Nonetheless, assumed and demonstrated impacts of the alien freshwater fish species in south-western Australia include predation, competition for food and habitat and agonistic behaviour on native fishes and are likely to have resulted in major changes to the structure and function of many aquatic ecosystems (e.g. Morgan et al. 2002, 2004; Morgan and Beatty 2007; Tay et al. 2007). Moreover, these species would have undoubtedly exacerbated the impacts caused by major habitat and water quality decline such as secondary salinisation (Halse et al. 2003; Morgan et al. 2003; Beatty et al. 2011), and construction of instream barriers (e.g. Morgan and Beatty 2006).

Although studies have been conducted on the biology and agonistic behaviour of *G. holbrooki* (Pen and Potter 1991; Gill et al. 1999), the biology and diet of *C. auratus* (Morgan and Beatty 2007), *X. hellerii* (Maddern et al. 2011), and *P. fluviatilis* (Morgan et al. 2002), and the diet of *O. mykiss* (e.g. Tay et al. 2007), as with global aquatic introductions (Strayer 2010), much more research is required to quantify the direct and indirect impacts of the 13 species of introduced fishes in south-western Australia. The broad omnivorous diets of several introduced species in the region including *G. brasiliensis*, *C. auratus*, *C. carpio*, *P. caudimaculatus*, *X. hellerii*, and *P. conchonius* would help facilitate their viability in a wide range of aquatic ecosystems due to the lack of specific dietary requirements. Such omnivory contrasts with the entirely carnivorous diets of native freshwater fishes of the region (Morgan et al. 1998). Omnivorous diets would also result in those species potentially having a considerable

impact on the structure and function of the aquatic ecosystems; however, this may be difficult to predict due to the potential decoupling of trophic cascades.

The relative roles of habitat alteration versus impacts of introduced fishes in driving population declines has not yet been investigated in this region and indeed very limited research has been conducted elsewhere in Australia. It is known that introduced fishes are both a symptom and a driver of general river health decline (Kennard et al. 2005). Indices of alien fishes in south-east Queensland were related to disturbance intensity indices and not native fish diversity or abundance (Kennard et al. 2005). Although limitations existed, that study suggested that this was due to alien fishes being more likely to be introduced into urban areas, more tolerant of degraded habitats, and possessing advantageous life-history traits to exist at those degraded habitats. Therefore, factors relating to stream habitat characteristics may confound the use of introduced species as indicators of river health *per se*; although the poeciliids were identified as having potential to be used as initial indicators to help diagnose or explore other impacts (Kennard et al. 2005).

As introduced freshwater fishes often favour altered habitats (e.g. Lapointe et al. 2012) maintaining undisturbed habitats and preventing habitat fragmentation is a cost-effective way of reducing risks of establishment and impacts of invasive species in general (Marvier et al. 2004). For Californian freshwater fishes, Light and Marchetti (2007) found that invasions drove native fish declines, with habitat alteration having an indirect positive impact on introduced fishes. *Gambusia holbrooki* has been shown to be a key driver of native fish community structure in Australia with related environmental variables playing a more minor role (MacDonald et al. 2012). Quantifying the relative contributions to native freshwater fish population declines of introduced fishes, habitat alteration, and water quality decline is required in Western Australia.

#### *The future of freshwater fish introductions in Western Australia*

Due to altered thermal and flow regimes, salinisation and increased water resource developments, climate change has been predicted globally to increase the likelihood of establishment of invasive freshwater species and also

influence their ecological impact (Rahel and Olden 2009). South-western Australia has undergone severe surface flow and groundwater reductions since the mid 1970's (CSIRO 2009a, b). Rainfall reduction has caused a 2–3 fold (relative to rainfall reduction) decline in streamflow in this region (CSIRO 2009a; Department of Water Government of Western Australia 2010; Silberstein et al. 2012) and is predicted to continue to reduce aquatic habitat availability, exacerbate water quality decline, and favour introduced species with broad environmental tolerances and invasive life-history traits, such as *G. holbrooki* (Horwitz et al. 2008; Morrongiello et al. 2011).

The successful establishment of introduced freshwater fishes has been shown to be related to whether the new country into which they become established climatically matched their existing geographical ranges (Bomford et al. 2010). Furthermore, Marr et al. (2010) found that large numbers of tropical species, such as Characiformes, were under-represented in Mediterranean-climatic regions presumably due to temperature tolerances and other unsuitable abiotic conditions. Therefore, the results of the current study, which has revealed that  $\approx 54\%$  of introduced species in south-western Australia are tropical or sub-tropical species, represent an exception to that trend. Given the considerable increases in temperatures projected for this region (Suppiah et al. 2007; Department of Water Government of Western Australia 2010), particularly during winter when the greatest proportional increase is forecasted (i.e. 8.8–16.0% by 2050), we propose that such climatic change, coupled with an increased rate of aquarium species introductions (that are dominated by tropical species), will continue to facilitate the establishment of tropical species such as *G. brasiliensis*. The projected increase in temperature is also predicted to have a negative impact on the typically stenotherm Gondwanic aquatic fauna of south-western Australia as southward geographical distributional shifts are not possible due to the proximity to the Southern Ocean (Davies 2010).

Secondary salinisation has drastically altered the inland aquatic ecosystems of many major rivers of the region by causing stenohaline native freshwater fishes distributions to contract west and south (Morgan et al. 1998, 2003; Beatty et al. 2011). Indeed, many of the region's secondary salinised rivers have recently been colonised by typically estuarine species (Morgan

et al. 2003; Beatty et al. 2011). A relatively high tolerance of salinity by current introduced species in south-western Australia (such as *G. brasiliensis*, *G. holbrooki*, *O. mykiss*, and *C. auratus*) and in future new species introductions would convey an advantage over most native species.

Ongoing research is needed to quantify the ecological impacts of the current introduced species in this region and indeed globally (Strayer 2010). Moreover, there is an urgent need to determine the physiological thresholds (particularly salinity, temperature, and aerobic scope) and habitat requirements of the established alien fishes in order to predict future alien species distributions under habitat change scenarios and better inform monitoring and control efforts. The over representation of aquarium species in south-western Australia is also consistent with a previous review of Australian introduced fishes that found 22 of the 34 known species to be aquarium or ornamental releases (Lintermans 2004). The latter study also highlighted that, at that time, there was a general lack of a coordination to prevent new introductions and highlighted that better education and a more strategic approach to the issue was required. Copp et al. (2010) demonstrated that propagule pressure from aquarium releases in England was best predicted by human population density and numbers of fish imports. Similar research is required for this region and throughout Australia to enable targeted monitoring for detecting future introductions and to implement strategic education campaigns. Eradication of self-maintaining populations of introduced fishes is notoriously difficult; strategic control and containment can be an effective alternative to mitigate their impacts (Britton et al. 2011). A long-term control for *C. auratus* has been undertaken by the authors (Morgan and Beatty 2007) and similar programs are required for other species.

Ongoing hydrological change (driven by both rainfall reductions over-extraction of water resources) in south-western Australia will have a broad range of negative impacts on prevailing ecosystems; particular those dependant on groundwater (Horwitz et al. 2008; Barron et al. 2012). Horwitz et al. (2008) proposed that an overall attitudinal shift in how the broader communities relate to water (i.e. by becoming more 'water literate' through education) and biodiversity within this global hotspot was required if sustainable population growth could

be achieved. We propose that introduced fishes should be regarded as an additional biophysical stressor that also urgently needs to be addressed, and requires a similar attitudinal shift. As recommended globally (Strayer 2010; Britton et al. 2011), sustained increased public education on the problems of aquatic alien species and risk-based management of alien freshwater fishes is required in Western Australia to halt the alarming increase in species introductions and resultant taxonomic homogenization.

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