Fishes of Australia's Great Artesian Basin Springs – An Overview

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Abstract

Patterns of fish distribution within Great Artesian Basin springs fall into two distinct categories: the opportunistic colonisation of springs by widespread riverine species following flooding, and long-term habitation – and speciation – within isolated spring complexes by fishes endemic to certain spring complexes. The endemic fishes of Australia's Great Artesian Basin springs persist in what some would consider the most unlikely fish habitats imaginable. Within predominantly hot and dry landscapes, they inhabit the only reliable wet areas, which are frequently the same temperature as the surrounding plains and as shallow as the body depth of some of the species. There are seven narrow-range fish species endemic to Great Artesian Basin springs: the Dalhousie catfish (*Neosiluris gloveri*), Dalhousie hardyhead (*Craterocephalus dalhousiensis*), red-finned blue-eye (*Scaturiginichthys vermeilipinnis*), three localised species of gobies (*Chlamydogobius gloveri*, *C. micropterus* and *C. squamigenus*) and the Dalhousie mogurnda (*Mogurnda thermophila*). These species occur at only three locations: Dalhousie in South Australia; and the Pelican Creek and Elizabeth Springs complexes, which are both in Queensland. An eighth species, the desert goby (*Chlamydogobius eremius*) has a wider range across multiple spring complexes in South Australia. All GAB endemic spring species should be considered endangered due to their small ranges and small populations; however, their formal status varies widely between state, national and international legislation and/or lists. Additionally, all fish endemic to GAB springs are threatened by a broad suite of factors that endanger inland aquatic ecosystems, such as water extraction, pollution, and the possibility that alien or unwanted species may become established. Persisting as they do in such unique and specialised habitats, the study of these GAB fish – and all GAB springs endemics – can reveal much about evolution, speciation and resilience. Although there is a growing recognition that conservation of the fishes and their habitats is important, this is complicated by the confusing variability of their conservation status and a lack of basic knowledge regarding their ecology and precise distribution.

Keywords: endemic species, Dalhousie, Edgbaston and Elizabeth Springs, conservation status, state, national and international legislation, threatened species

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Evolution in Isolation

At three spring complexes across Australia's arid interior, locally endemic fishes are extant. Although this fact may not appear exceptional at first glance – after all, they are springs, so there's water, so why wouldn't there be fish? – the complex ecology of Great Artesian Basin (GAB) springs illustrates a fascinating story about these unique fishes.

GAB springs are the exact opposite of islands. Just as an island is an isolated piece of land surrounded by water, a spring is an isolated area of water surrounded by land. Extending the island analogy to the biota of springs, there are similar and expected patterns. As Darwin famously observed, islands offer us tangible evidence of evolution in action: if a species is confined to an island, it may – over many generations – adapt and transform to make best use of the available resources. Speciation – the formation of new and genetically distinct species – is the inevitable end-result. Biogeography is therefore littered with examples of creatures that evolved into new species in isolation on islands: Darwin's finches, the giant tortoises, Komodo dragons and the flightless dodos of Mauritius all demonstrate what happens when animals become marooned.

The rough equation – isolation plus time equals speciation – applies to springs in exactly the same way it does to islands. Isolation is relatively easy to understand: populations evolve differently in different areas. African elephants live on the savannah and have big ears and long tusks, whereas Asiatic elephants are smaller, live in the jungle and have small ears and smaller tusks. They have a common ancestor, but each went their own way.

Time is harder for us to understand, especially given our lifespans: it is difficult enough to envisage one thousand years of evolution, let alone 50,000, or 50 million. Yet in the context of GAB springs, we have to accept that: (a) the GAB springs were not *always* isolated oases surrounded by desert; and (b) the species we know now are a subset or a variation of what was there before. In other words, when diprotodons wallowed and disturbed the spring sediments as feral pigs and cattle do today, the fish fauna may have been slightly different. The entire fauna was likely very different several million years ago when crocodiles and lungfishes inhabited a permanent Lake Eyre (Byrne et al., 2008).

Freshwater fishes are most speciose in tropical areas where there are large rivers, multiple habitats and plenty of rainfall. As such, the Amazon and equatorial Africa are hotspots for diversity, and Australia is an extremely poor relation – arid Australia even more so (Kerezsy, 2017). The boom-bust cycle of Australia's inland ecosystems is driven by unpredictable flooding as opposed to a regular monsoon (Kingsford, 2017), and the paucity of freshwater fishes in the interior reflects the harshness of aquatic and surrounding terrestrial habitats: the interior is basically hard country for fish (Arthington & Balcombe, 2017).

Nevertheless, when the rains come and the rivers flow, plenty of itinerants end up making temporary homes in GAB springs. Glassfishes or perchlets (Ambassidae), colourful rainbowfishes (Melanotaeniidae) and hardyheads (Atherinidae) are all commonly encountered vagrants, as is the larger spangled perch (*Leiopotherapon unicolor*), a widespread carnivore with legendary colonisation ability and tolerances (to temperature, dissolved oxygen and other water quality parameters; Kerezsy et al., 2017). Members of these species appear to take their chances during the rare times when the desert is in flood and they can disperse widely (Kerezsy et al., 2013). If they are lucky, they may make it to a GAB spring – an area where water is likely to remain for far longer than the temporary habitat afforded by a sporadic flood. They may inhabit a spring for weeks, months or years, depending on whether enough individuals have colonised the particular spring and whether they can complete their life cycles within it. However, in most cases, opportunistic vagrants are there one year and gone the next. Returning to the island analogy, these are similar to the finches that may have visited certain islands in the Galapagos a few times, but lacked the adaptations to persist.

Endemic Fishes of GAB Springs

The narrow-range endemic fishes that today inhabit Dalhousie Springs (South Australia), the Pelican Creek Springs complex within the Barcaldine Springs supergroup, and the Elizabeth Springs complex within the Springvale supergroup (both in Queensland; Figure 1) are descended from various colonists of long ago. It's just that these species, rather than staying for months or years, survived and persisted for millennia, and became part of their localised ecosystems. Within this context, the opening sentence ("At three spring complexes across Australia's arid interior, locally endemic fish are extant") may become more intriguing, especially when it is considered that these species occur in harsh desert landscapes that could sometimes be considered the *least likely* places to offer aquatic habitats suitable to support viable fish populations.

Dalhousie Springs

At Dalhousie, in northern South Australia (Figure 1), the spring complex is surrounded by desert and gibber plain (Figure 2). Part of Witjira National Park, Dalhousie is most popular as either a starting- or end-point for tourists and adventurers to undertake four-wheel-drive crossings of the Simpson Desert. This means that in the tourist season (roughly centred on the Australian winter, so May–September), the Park is busy, and on most afternoons tourists laze in the warm waters of one of the springs, swapping stories of dune-driving and breathtaking sunsets.

One of the endemic fish species from Dalhousie – the Dalhousie hardyhead (*Craterocephalus dalhousiensis*) – schools in the open water of the bigger springs, which can be longer than 100 m and deeper than 3 m (Glover, 1989; Figure 3). A hardyhead is a small, bullet-shaped fish that rarely exceeds 5 cm. They have distant relatives throughout Australia, including *C. eyresii* and *C. centralis* from catchments in the Lake Eyre Basin in South Australia and the Northern Territory, but are most closely related to *C. lentigenosus* from north-west Australia (Unmack & Dowling, 2010). The most likely evolutionary explanation for *C. dalhousiensis* is that an ancestral *Craterocephalus* – or perhaps one of the extant species – colonised Dalhousie in a flood, and then – gradually – evolved into a separate species in the isolated warm and constant spring habitat. As the tourists float and sip their beer in the springs at Dalhousie, it is hardyheads of the same name that peck morsels of food and detritus from their skin. Until recently it was considered that there were two species of hardyhead at Dalhousie – *C. dalhousiensis* and *C. gloveri* – however, fish biologists and geneticists acquainted with the springs and hardyheads now agree that only one species appears to be present (P. Unmack, M. Hammer, pers. comm.).

Figure 1. Map of Great Artesian Basin spring supergroups (within dotted lines) where spring complexes (black circles) at Dalhousie, Barcaldine (Pelican Creek complex) and Springvale (Elizabeth Springs complex) support endemic fish species.

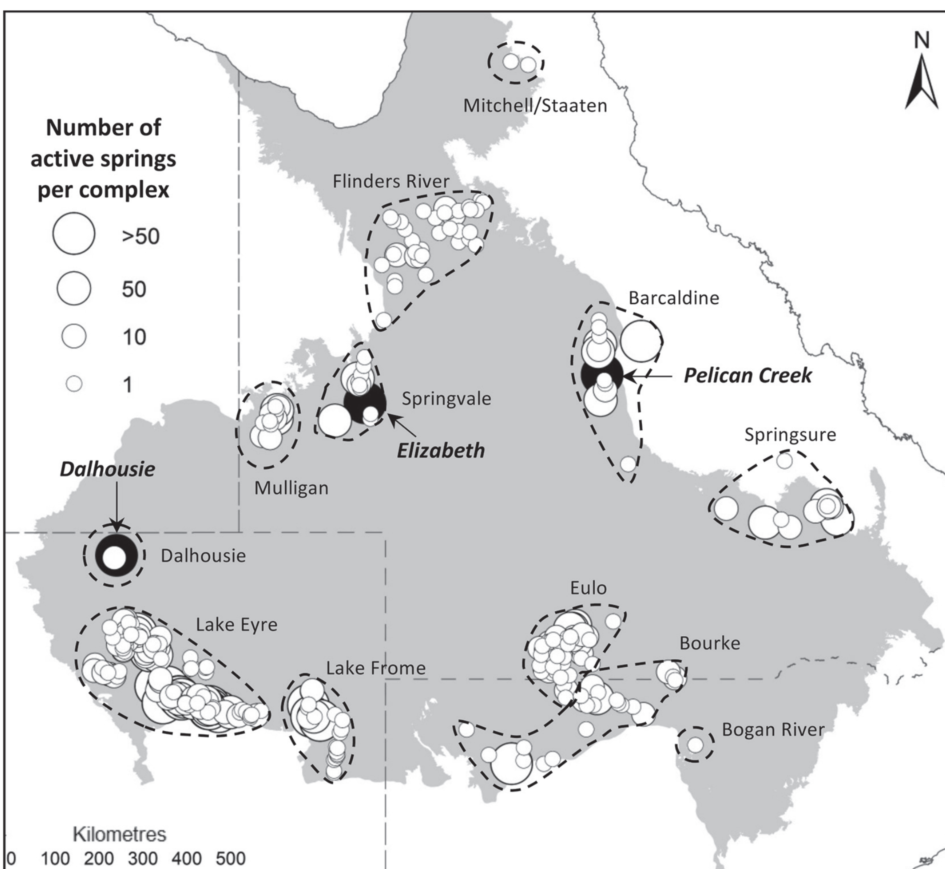
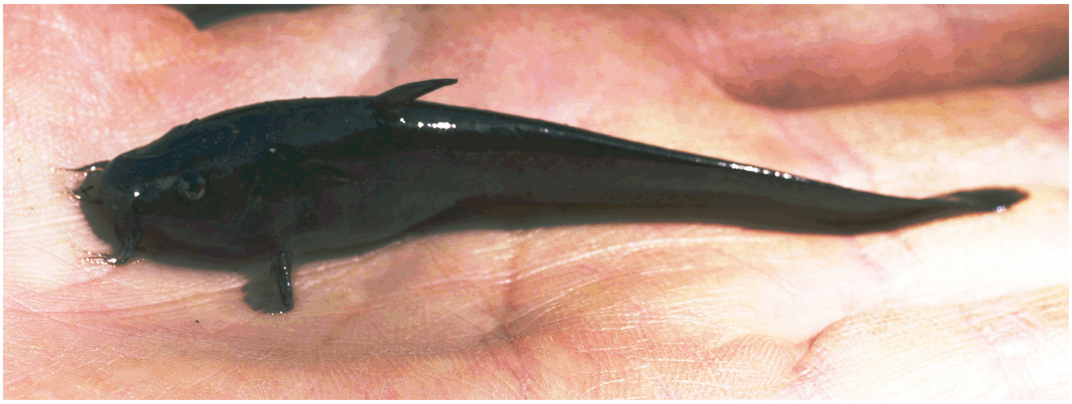


Figure 2. The desert landscape around Dalhousie (above) is in stark contrast to the springs (below). All photographs in this paper by the author.

Though not standard equipment on desert crossings, a mask and a snorkel are handy travel accessories at Dalhousie, for unlike the majority of waterways in central Australia, the GAB water in the springs is perfectly clear. When snorkelling, the first thing the swimmer will notice is just how common the hardyheads are; they're obviously perfectly adapted to their environment, where they feed on algae, micro-organisms and – opportunistically – on the detritus attached to visiting humans. Beneath the hardyhead, and busily shuffling across the substrate, is the second of the four fish species that occur only at Dalhousie Springs.

Dalhousie catfish (*Neosiluris gloveri*; Figure 3) belong to the catfish family Plotosidae, which are all eel-tailed (as opposed to fork-tailed). Their primary means of propulsion is the long fin/tail which extends beneath their body. Eel-tailed catfish of various species occur in most Australian catchments, and in the case of *Tandanus tandanus* from the Murray-Darling Basin, can grow to almost one metre long (Lintermans, 2007). The Dalhousie species, named after John Glover, a pioneering fish biologist from South Australia, is the smallest at less than 10 cm long, and also one of the few Australian fish species adapted to living in 40°C water (Glover, 1982). Again, other catfishes are known from catchments of the Lake Eyre Basin in central Australia, such as *Neosiluris hyrtlii* and *Porochilus argenteus* (Wager & Unmack, 2000), so the evolution of *N. gloveri* is likely due to an ancestral form becoming marooned in the hospitable habitat of these desert springs.

Figure 3. Dalhousie mogurnda (above) and Dalhousie catfish (below) are two of the four endemic fishes from the Dalhousie spring complex.



There are two main types of habitat at Dalhousie – the wide, deep, open pools, and the long, winding and often vegetation-congested 'tails'. Spring tails at Dalhousie can be several kilometres long, and are often overgrown with *Phragmites* and *Typha* that can grow to several metres tall. The tails drain the water away from the pools where the main spring vents are situated, so they are far shallower (usually less than 50 cm deep).

The spring tails are the favoured habitat of *Mogurnda thermophila*, or the Dalhousie mogurnda (Figure 3). Mogurndas are commonly known as purple-spotted gudgeons and are attractive, bottom-dwelling species that have a comparatively wide range across Australia (Allen et al., 2002). The Dalhousie mogurnda, like the hardyhead and the catfish, has evolved to tolerate water up to and occasionally over 40°C. An ambush predator, they grow up to about 15 cm so are by far the largest endemic species occurring within the spring complex. A territorial species, it appears mogurndas wait in their own 'space' within the spring tails for food – such as shrimp, yabbies or other fish – to drift within striking range (pers. ob.).

Chlamydogobius gloveri – the Dalhousie goby – is the last of the Dalhousie endemics. Like its more widespread relation *C. eremius* (the desert goby; Rossini et al., 2018), this species is tolerant of extreme temperatures and salinity, and can even extract oxygen from the atmosphere using a pharyngeal organ (Thompson & Withers, 2002). Dalhousie gobies are poor swimmers and rarely grow larger than 5 cm. They are found throughout the Dalhousie Springs complex, including small springs and soaks where the other species do not occur.

Elizabeth Springs

North-east of South Australia and into the GAB springs of Queensland, the only fish species present at the Elizabeth Springs complex in the Springvale supergroup south-east of Boulia (Figure 1) is the Elizabeth Springs goby (*C. micropterus*; Larson 1995). In stark contrast to the extensive springs and tails of Dalhousie (that occur within approximately 70 km^2), all of the extant spring vents at Elizabeth Springs are situated within an area less than 500 × 500 metres (pers. ob.). Like its relatives in Dalhousie and throughout Central Australia, the Elizabeth Springs goby is benthic, tolerant and opportunistic. However, given that the Elizabeth Springs are shallow (mostly less than 5 cm deep) and small, Elizabeth Springs gobies persist within a far more restricted range than fishes in other spring complexes such as Dalhousie and the Pelican Creek complex at Edgbaston.

Pelican Creek Springs

On the eastern edge of the GAB, within the Barcaldine Springs supergroup, lies the Pelican Creek Springs complex. This complex is often referred to as 'Edgbaston Springs' because the vast majority of research to date has focused on the springs within Edgbaston Conservation Reserve. The springs at Edgbaston occur near the base of an escarpment, and contain the most diverse assemblages of invertebrates and plants (Figure 4; Fensham et al., 2011). There are up to 100 individual springs, but many are nothing more than damp areas.

In about 30 springs there are fish (Fairfax et al., 2007). Like Dalhousie and Elizabeth Springs, there is a resident goby – the Edgbaston goby, *C. squamigenus* (Figure 5) – and it is reasonable to assume, again, that speciation has been a direct consequence of isolation. Indeed, it seems likely that gobies are the most widespread endemic spring genus due to their ability to live in extremely shallow water: at Edgbaston, they frequently occur in water that is equivalent to (or less than) their body depth (of up to 1 cm; pers. ob.). Nevertheless, despite the apparent fortitude of the various gobies, the most curious inhabitant at Edgbaston – and possibly the most fascinating fish endemic in GAB springs – is the red-finned blue-eye (*Scaturiginichthys vermeilipinnis*; Figure 5).

Discovered by chance in 1990 by fish biologist Peter Unmack (Wager & Unmack, 2000), the red-finned blue-eye is the only representative of the Pseudomugilidae fish family in Central Australia, and its closest relative – *Pseudomugil tenellus*, the delicate blue-eye – is mostly associated with swamps in northern Australia and Papua New Guinea. The mysterious story of how red-finned blue-eye managed to colonise, evolve and persist in water that is frequently less than 3 cm deep and hotter than 40°C may never be known, but shortly after its discovery a far more pressing need was recognised, for it transpired that the fish was rapidly disappearing due to invasion of its unusual habitat by the alien live-bearer eastern gambusia (*Gambusia holbrooki*; Fairfax et al., 2007; Kerezsy, 2009).

In 2008, Edgbaston Station, the *only* habitat for *S. vermeilipinnis*, was purchased by the not-for-profit conservation organisation Bush Heritage Australia, and a recovery program began to take shape. Trials of the piscicide Rotenone were undertaken in order to assess its usefulness as a tool for controlling eastern gambusia, and populations of red-finned blue-eye were relocated to safer areas (Kerezsy & Fensham, 2013). Luckily, by the time the naturally occurring populations had dwindled (there is only one population left today), several 'new' populations had been established (Radford et al., 2018). Although the future of this species remains precarious, with ongoing management hopefully it can persist.

Figure 4. The landscape around Edgbaston (above) and one of the larger springs (below).

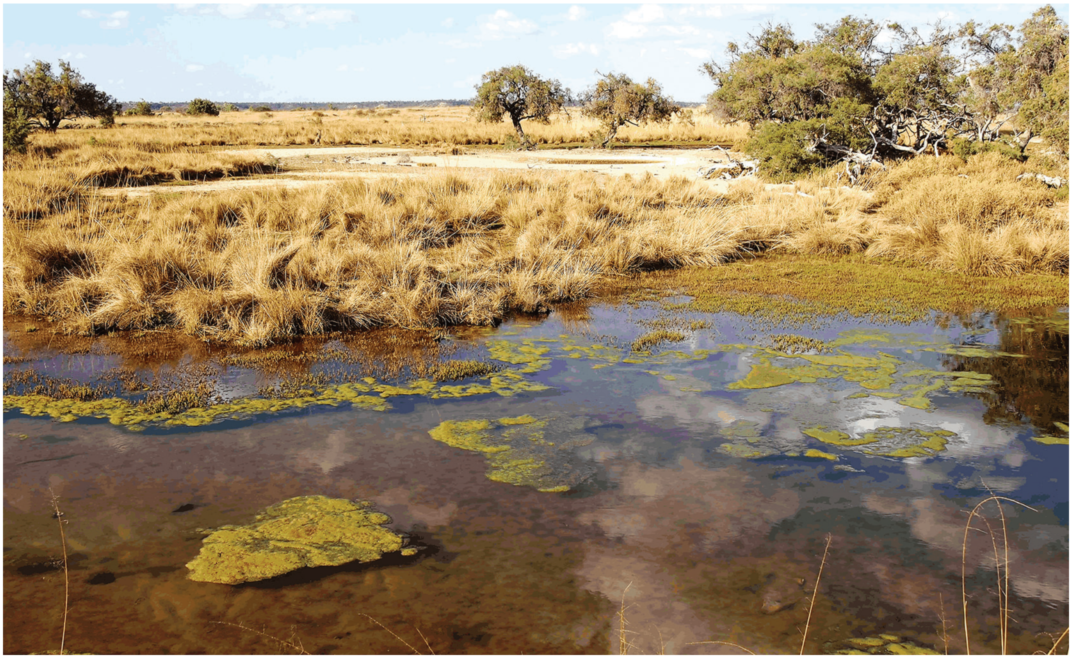


Figure 5. Edgbaston goby (above) and male red-finned blue-eye (below).

Summary

There are narrow-range endemic fish species at three spring complexes in three supergroups across Australia's Great Artesian Basin. In the past there may have been many more, but currently there are seven endemic species: four at Dalhousie, two at Edgbaston, and one at Elizabeth Springs. It is important to note that at many spring complexes, there are simply no fish; this is possibly due to prehistoric extinctions, but in many cases the evidence of spring destruction by cattle, pigs and camels points to more recent extirpations. In other words, it's possible that there were more spring endemic fish species in comparatively recent history, but they disappeared before we knew they were there.

All fishes endemic to GAB springs are threatened by a broad suite of factors that endanger inland aquatic systems (Kingsford, 2017). However, these threats are neither limited to fishes of GAB springs nor to Australia's inland ecosystems. Worldwide, fishes from marginal habitats – especially in arid

areas – face similar threats from fragmentation of habitat, the imposition of alien or translocated species, extraction of ground and surface water, and climate change (Fagan et al., 2002; Unmack & Minckley, 2008; Kerezsy et al., 2017). The seriousness of such threats is amplified in Australia's GAB springs due to two main factors: the isolated and already-fragmented nature of the springs, and the comparatively large numbers of endemic species – of all groups – that live nowhere else. In other words, there are few buffers for spring endemics. If their habitat is destroyed, species extinction is the most likely outcome.

The endemic fishes of Australia's GAB springs are all functionally endangered due to their small ranges and small populations; however, their formal conservation status varies widely between state, national and international legislation and/or lists (Table 1). Persisting as they do in such unique and specialised habitats, the study of these GAB fish species – and all GAB springs endemics – can reveal much about evolution, speciation and resilience. It is therefore imperative that we respect and conserve them and their unusual habitats.

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Table 1. The status of narrow-range endemic fishes from Australia's Great Artesian Basin springs under state and Commonwealth legislation, and their international status on the IUCN Red List of Threatened Species.

Species	Common name	State legislation	Commonwealth legislation	IUCN Red List
South Australian species				
Craterocephalus dalhousiensis	Dalhousie hardyhead	All four Dalhousie species are considered protected in South Australia as they occur within a national park; however, they are not listed under South Australian legislation (M. Hammer, pers. comm.).	All four Dalhousie species are not individually listed.*	Critically endangered (Whiterod et al., 2019a)
Neosiluris gloveri	Dalhousie catfish			Critically endangered (Whiterod et al., 2019b)
Chlamydogobius gloveri	Dalhousie goby			Critically endangered (Hammer et al., 2019)
Mogurnda thermophila	Dalhousie mogurnda			Critically endangered (Unmack et al., 2019)
Queensland species				
Chlamydogobius micropterus	Elizabeth Springs goby	Endangered (NCA, 1992)	Endangered (EPBC Act, 1999a)*	Vulnerable (Kerezsy et al., 2019)
Chlamydogobius squamigenus	Edgbaston goby	Endangered (NCA, 1992)	Vulnerable (EPBC Act, 1999b)*	Critically endangered (Kerezsy et al., 2019a)
Scaturiginichthys vermeilipinnis	Red-finned blue-eye	Endangered (NCA, 1992)	Endangered (EPBC Act, 1999a)*	Critically endangered (Kerezsy et al., 2019b)

*The community of native species dependent upon natural discharge of groundwater from the Great Artesian Basin is listed as an endangered ecological community (EPBC Act, 1999c) in addition to individually listed species.

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