FiSHMED
Fishes in Mediterranean Environments

sibic
Sociedad Ibérica de Ictiología
Sociedade Ibérica de Ictiologia

Review of fish community, stressors and conservation in the Rondegat River (South Africa)

Casey J. Broom*[1,2], Olaf L.F. Weyl[†1,2], Josie South[2,3]

1. Department of Ichthyology and Fisheries Science, Rhodes University, Makhanda, South Africa
2. DSI/NRF Research Chair in Inland Fisheries and Freshwater Ecology, South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa
3. School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

* correspondence to c.broom@saiab.nrf.ac.za

† deceased

SUMMARY

Anthropogenic change is a major threat to dwindling freshwater biodiversity. We present and synthesise available information regarding the fish community, ecology, threats and conservation options within The Cape Fold Ecoregion (CFE) of South Africa. The CFE is a particularly vulnerable region, with many range-restricted species and highly fragmented native fish ranges. The Rondegat River in the Olifants-Doring River System of the Western Cape province is of notable conservation value, as it hosts populations of important endemic CFE species despite being at risk from non-native invasive species, climate change, and agriculture intensification. This river is unique, being the site of the first alien fish eradication programme of its kind in South Africa. The recovering Rondegat River imperilled cyprinid assemblage is used to frame the manner in which future environmental change may continue to disturb the ecology of the system. Conservation options and priorities are discussed in the context of a southern hemisphere Mediterranean-climate freshwater system

Keywords: Cape Fold Ecoregion, cyprinids, redfin minnows, restoration, stressors, threatened species

Citation: Broom CJ, Weyl OLF, South J (2023) Fish community, stressors and conservation in the Rondegat River (Olifants-Doring system, Western Cape, South Africa). Fishes in Mediterranean Environments 2023.001: 21p. https://doi.org/10.29094/FiSHMED.2023.001

THE CAPE FOLD ECOREGION

Freshwater systems are among the most threatened globally, largely owing to their comparatively high species and habitat diversity while occupying <1% of the Earth's surface (Dudgeon *et al*., 2005; Abell, Allan & Lehner, 2007). Fish are the most imperilled of all vertebrates, yet play an important role in ecosystem functioning and food webs beyond the boundaries of the aquatic environment (Fausch *et al*., 2002; Jackson *et al*., 2016b; Jackson, Pawar & Woodward, 2021). Freshwater systems are often overlooked in the formation of protected areas and are a low priority in conservation efforts (Jordaan, Chakona & van der Colff, 2020). Additionally, conservation and restoration efforts are often inadequate or poorly implemented (Lintermans, 2013; Jordaan *et al*., 2020). Globally and within the South African context, effective conservation and restoration of highly impacted stream fish is a multi-faceted, complex, "wicked" problem (Lintermans, 2013; Ellender & Weyl, 2014; Jordaan *et al*., 2020).

South African freshwater ecosystems are no exception to the vulnerable state of systems further afield and are imperilled by a variety of threats, primarily as a result of anthropogenic interference (Darwall *et al*., 2009; Weyl *et al*., 2020). Among these threats, one of the most pressing are invasive organisms introduced to local freshwater systems, particularly predatory fish, alongside anthropogenic climate change and habitat degradation (Abell *et al*., 2007; Darwall *et al*., 2009; Tweddle *et al*., 2009; Filipe, Lawrence & Bonada, 2013; Ellender *et al*., 2017; Shelton *et al*., 2018a; Weyl *et al*., 2020). In South Africa, the Cape Fold Ecoregion (CFE) is recognised as biodiversity hotspot for freshwater fish, as despite a relative paucity of species, there is a very high degree of endemism (Tweddle *et al*., 2009; Ellender *et al*., 2017; Shelton *et al*., 2018a). Current baseline scientific knowledge on the native fishes of the CFE is fairly narrow and tends to focus on either specific inquiries or notable biological traits (Ellender *et al*., 2017). For example, a single study exists on the physiology of CFE fishes, investigating survival strategies in *Galaxias* sp. when faced with aerial exposure in response to drought conditions (Chakona, Swartz & Magellan, 2011). Reizenberg *et al*. (2019) investigated the thermal tolerances and preferences of a range of CFE fishes including *Galaxias zebratus*, *Pseudobarbus* spp., *Sedercypris calidus*, *Austroglanis gilli* and other species, with no other examples of studies on critical thermal limits available across the CFE.

In general, CFE fish literature is scarce, with 103 peer-reviewed articles focusing primarily on taxonomy and biogeography, and to a lesser degree ecology, conservation and human impacts as of 2017 (Ellender *et al*., 2017). The strong focus on taxonomy and biogeography of researchers is necessary for conservation of genetic lineages, and particularly for enabling researchers from other disciplines to appropriately define targets of research and conservation endeavours. Native fishes in the CFE are united by a series of pressures such as high levels of invasion, depleted natural range and suitable habitats through water abstraction and damming (but see Beatty *et al*. (2017) for consideration of dam removal with impacts on artificial refugia under climate change), while research and conservation efforts are usually sporadic and uncoordinated (Ellender *et al*., 2017). The majority of native small stream fishes have narrow and highly fragmented ranges. Many species have been only recently discovered, as genetically distinct and/or reclassified species (Chakona *et al*., 2020). As a result, knowledge of the exact distributions and available ecological information on these species is limited. The contemporary distributions and biogeographic history of these highly endemic lineages represent an invaluable library of material as to the natural history and freshwater biodiversity heritage of South Africa. This information is crucial for the understanding of freshwater systems both in their present state and in predicting future responses to change (Chakona *et al*., 2020).

The Olifants-Doring River System (ODRS) is characterised by a relatively high diversity of endemic and threatened fishes. In particular, the Cederberg Mountains

DOI: 10.29094/FiSHMED.2023.001

within the ODRS catchment have been identified as "vulnerability hotspots" within an already vulnerable region (Shelton *et al.*, 2018a). Ten of the 19 freshwater fish species endemic to the CFE are found the ODRS (Weyl *et al.*, 2014). The fish species that are native, non-native and extra-limital (i.e., species native to South Africa that have been moved out of their natural range) in the ODRS are summarised in Table 1. Rivers in the CFE have been devastated by invasive predatory fish, with endemic species being limited to refugia through natural barriers as the only means of survival in much of these systems (Tweddle *et al.*, 2009).

The interacting multiple anthropogenic stressors occurring in freshwater systems in the ODRS, including habitat degradation through water abstraction, alien riparian vegetation, pollution and damming activities associated with agriculture (Impson *et al.*, 2007) are common across Mediterranean freshwater ecosystems. Globally distributed Mediterranean ecosystems pose a potential learning and conservation opportunity in the future given the similarities in threats and high endemicity. Here, we synthesise the available literature on the fish of the ODRS, with a particular focus on the flagship Rondegat River restoration project with the aim of summarising the state of knowledge, threats and conservation opportunities.

THE RONDEGAT RIVER

The Rondegat River (32°24'S; 19°05'E; Figure 1) is a 25 km long, 2nd order perennial tributary of the Olifants River, opening into the Clanwilliam Dam, with a catchment area of approximately 111 km² (Lowe *et al.*, 2008; van der Walt, 2014). Rainfall falls mainly in winter, from June until August (Lowe *et al.*, 2008), and temperatures are hottest in February and coldest in June (de Moor & Day, 2013). The river originates as a pristine headwater stream in the Cederberg Mountains, progressing through fynbos and other indigenous terrestrial vegetation and passing areas of alien tree plantations, citrus fruit orchards and associated abstraction points and weirs in the lower reaches (Lowe *et al.*, 2008). The river is characteristic of a typical CFE tributary as a perennial clear, oligotrophic, acidic mountain stream (Swartz, 2000; de Moor & Day, 2013).

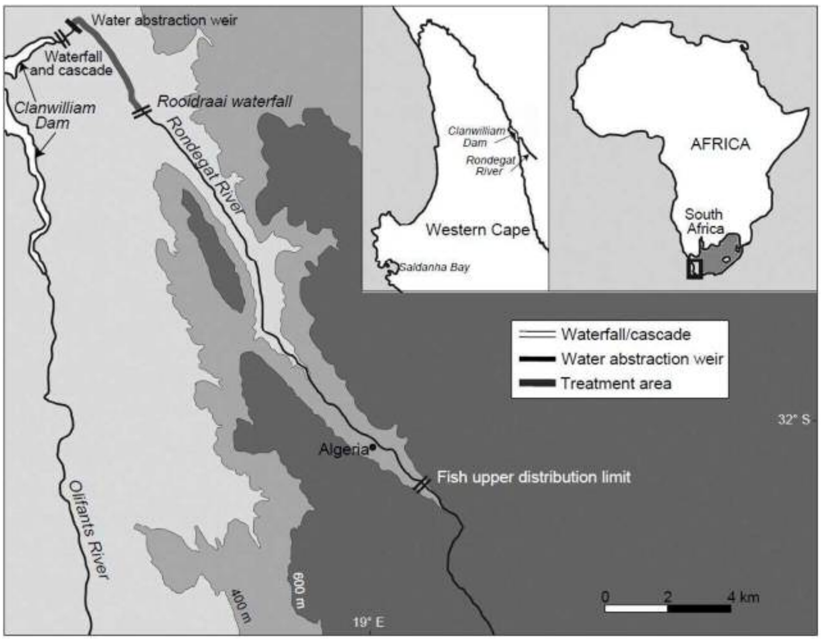

Figure 1. The location of the Rondegat River within the Olifants-Doring system, part of the Cape Fold Ecoregion of the Western Cape, South Africa. Notable features limiting fish distributions are indicated, as well as the extent of the alien fish eradication efforts utilising the piscicide Rotenone and the position of the focal river in relation to the Clanwilliam Dam and the Olifants River. Adapted from Weyl *et al.* (2013).

DOI: 10.29094/FiSHMED.2023.001

Table 1. Conservation status (IUCN Redlist; EL = extralimital, NN = non-native) and descriptive summary of native and non-native fish species found in the Olifants-Doring River System. Adapted from Ellender *et al.* (2017) and Jordaan *et al.* (2020) unless otherwise cited.

Species	Status	Notes and major threats (impact if non-native)
Austroglanis barnardi (Skelton, 1981)	EN	Endemic to ODRS. Alien fish, habitat degradation
Austroglanis gilli (Barnard, 1943)	NT	Endemic. Alien fish, habitat degradation
Cheilobarbus serra (Peters, 1864)	NT	Endemic. Alien fish, habitat degradation, utilization
Clarias gariepinus (Burchell, 1822)	EL	Widespread and resilient predator with strong dispersal ability (Skelton, 2001)
Cyprinus carpio Linnaeus, 1758	NN	Widespread in lentic water bodies, degrades habitat through feeding behaviour (Skelton, 2001)
Enteromius anoplus (Weber, 1897)	LC	Widespread, not found in mountain streams of ODRS (Skelton, 2001)
Galaxias zebratus species complex Castelnau, 1861	DD	Endemic to CFE. Ongoing taxonomic revision may classify ODRS populations as genetically distinct. Alien fish, habitat degradation, genetic integrity/population fragmentation (Chakona *et al.*, 2020)
Labeo seeberi Gilchrist & Thompson, 1911	EN	Endemic, found only in the Doring system after extirpation from the Olifants. Alien fish, habitat destruction, migratory barriers (Jordaan *et al.*, 2017)
Labeobarbus seeberi (Gilchrist and Thompson, 1913)	NT	Endemic, recognised as flagship conservation species. Alien fish, habitat degradation, utilization, physical barriers
Lepomis macrochirus Rafinesque, 1819	NN	Predatory, displaces native species through overpopulation in slow-flowing vegetated systems (Skelton, 2001)
Micropterus dolomieu (Lacepède, 1802)	NN	Predatory, adapted to flowing rocky habitats favoured by native fish (Skelton, 2001)
Micropterus punctulatus (Rafinesque, 1819)	NN	Predatory, less successful than other black bass (Skelton, 2001)
Micropterus salmoides (Lacepède, 1802)	NN	Predatory, prefers lentic systems (Skelton, 2001)
Oncorhynchus mykiss (Walbaum, 1792)	NN	Predatory, cool flowing stream specialist (Skelton, 2001)
Pseudobarbus phlegethon (Barnard, 1938)	EN	Endemic. Alien fish, habitat degradation. Five highly fragmented subpopulations remain, restricted to protected areas (van der Walt, Impson & Jordaan, 2017a)
Pseudobarbus sp. nov. "Doring"	CR	Endemic, currently undergoing taxonomic revision. Alien fish and highly limited distribution
Salmo trutta Linnaeus, 1758	NN	Predatory, cool flowing stream specialist
Sandelia capensis (Cuvier, 1829)	EL	Widespread in the CFE, translocated to the ODRS, threatens sensitive species (Skelton, 2001)
Sedercypris calidus (Barnard, 1938)	NT	Endemic. Alien fish and habitat degradation
Sedercypris erubescens (Skelton, 1974)	CR	Endemic. Alien fish (including extra-limital *S. capensis*), habitat degradation, pollution
Tilapia sparrmanii Smith, 1840	EL	Minor extralimital impact, usually introduced alongside black bass (Skelton, 2001; Ellender & Weyl, 2014)

The Rondegat River is of notable conservation concern, as it hosts populations of important endemic CFE species including *Sedercypris calidus*, *Pseudobarbus phlegethon*, *Labeobarbus seeberi*, and *Austroglanis gilli* (Woodford *et al*., 2005; Garrow & Marr, 2012; Weyl *et al*., 2013). The native fish in this system were in danger of extirpation by non-native fishes present in the system, which led to the extirpation of minnows below a natural barrier (Rooidraai waterfall, see Figure 1) and high predation pressure on Clanwilliam Yellowfish recruitment (Woodford *et al*., 2005; Marr, Impson & Tweddle, 2012). Weyl *et al*. (2013) estimated fish density in the uninvaded reaches as 97 fish per 100 m² compared to 7 per 100 m² in the invaded reaches. The Rondegat River served as the site for the first alien fish eradication project in the CFE, performed through a collaboration between the local conservation body CapeNature, the American Fisheries Society and the South African Institute for Aquatic Biodiversity (SAIAB) (Marr *et al*., 2012; Weyl *et al*., 2013, 2014, 2016). This project treated a 4 km stretch of the Rondegat River with the piscicide rotenone to remove alien smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) and thus provide additional habitat for the existing native fish populations (Marr *et al*., 2012; Weyl *et al*., 2013, 2016; Slabbert, Jordaan & Weyl, 2014).

The Rondegat River restoration project was intended to be the first of four CFE river treatments and was chosen owing to its ideal characteristics (including uninvaded headwater reaches with favourable habitat for native fishes, physical barriers to re-invasion upstream and a lack of angling importance) and invasion situation following an environmental impact assessment (Marr *et al*., 2012; Weyl *et al*., 2016). A series of studies and restoration actions were carried out concurrently with the alien fish eradication efforts, such as alien plant clearing and assessments of the effects of the rotenone application on the invertebrate communities (Woodford *et al*., 2013; Bellingan *et al.,* 2015; Weyl *et al*., 2016; Fill, Kritzinger-Klopper & van Wilgen, 2018). Alien plant clearing and fynbos restoration efforts resulted in rapid recovery of native shrubs; however, secondary invasion by alien and native grasses prevented a full recovery to a pre-invasion state (Fill *et al*., 2018). The rapid re-invasion by grasses is thought to be a result of raised nitrogen levels in the riverbank soils, and is likely to require a longer period to recover completely (Fill *et al*., 2018). The altered nutrient state may have cascading effects on river resource availability and trophic interactions that are difficult to anticipate. The application of rotenone had an immediate impact on invertebrate density, especially reducing the density of the sensitive Ephemeroptera, with a catastrophic drift event being triggered in response to the rotenone treatment (Woodford *et al*., 2013). Recolonisation and recovery of the aquatic invertebrate assemblage was anticipated through drift from unaffected upstream populations, and losses in diversity were much less marked than that recorded in comparable studies (Woodford *et al*., 2013). A rapid bioassessment of the impacts of rotenone on the invertebrate community of the river revealed these taxa were both resilient to the treatment (community returned to pre-treatment health) and resistant to lower concentrations of rotenone in the application of the second treatment, despite short term population extirpation (Bellingan *et al*., 2015).

Only one other successful eradication of invasive fishes from a river has been achieved in South Africa, involving the mechanical removal of spotted bass (*Micropterus punctulatus* Rafinesque, 1819) from the Thee river (van der Walt et al., 2019). The Thee shares many characteristics with the Rondegat; it is a similar size, has pristine upper reaches with water abstraction and habitat alteration in the lower reaches, and has a similar fish assemblage (van der Walt, 2014; van der Walt *et al*., 2019). The specific characteristics of the Thee river and the naïve nature of the spotted bass made it a prime candidate for mechanical removal rather than piscicide application. However, this is a rare case and chemical eradication of invasive species is likely to be the preferred method for future restoration actions in the CFE (Weyl *et al*., 2016; van der Walt *et al*., 2019).

A comprehensive assessment of the composition and distribution of native fishes in the Rondegat River prior to the invasive fish removal programme in 2012 was first performed in 2005, followed by another intensive survey in 2013 (Woodford *et al*., 2005; Weyl *et al*., 2013, 2016). By that time, native fish populations were in direct danger of local extirpation by smallmouth bass. The success of the rotenone treatment has led to the river having significant value for research, representing a natural experiment in terms of an undisturbed headwater section, with the lower reaches now devoid of invasive fish (Weyl *et al*., 2014). Ongoing monitoring is anticipated to reveal further insights into the recruitment of native fishes and the expansion of natural fish assemblages in a novel environment (Weyl *et al*., 2016).

FISH SPECIES

The hydro-geological and climatic history of the CFE river systems has given rise to a hotbed of fine-scale speciation and divergence events, and is reflected in the biogeographical histories of the Rondegat River's species cohort (Swartz, Flemming & Mouton, 2004; Swartz, Skelton & Bloomer, 2007, 2009; Chakona, Swartz & Gouws, 2013). Currently, the river is host to five recognised teleost species, including three cyprinids, a galaxiid (recently re-discovered following a lengthy period of no sightings), and one austroglanid catfish species.

Sedercypris calidus (Barnard, 1938), formerly *Barbus* and *Pseudobarbus calidus* (Skelton, Swartz & Vreven, 2018), the Clanwilliam redfin minnow, is currently evaluated as near-threatened using IUCN Red List criteria (van der Walt, Jordaan & Impson, 2017c) (Figure 2). *Sedercypris calidus* is likely to have differentiated from its sister species *S. erubescens* in the Doring catchment (Swartz *et al*., 2004, 2009). Niche preferences, morphological and behavioural differences likely enabled greater dispersal ability in *S. calidus* over *Pseudobarbus phlegethon*, which itself underwent a divergence between the Olifants and Doring catchments (Swartz *et al*., 2004, 2009; Skelton *et al*., 2018).

In the Rondegat River, *S. calidus* is the more abundant of the two redfin species present and primarily feeds on suspended aquatic invertebrates and detritus through drift feeding, in addition to foraging on submerged natural structures (rock, aquatic and immersed vegetation), occasionally taking items from the surface with terminal mouths (Garrow & Marr 2012, pp. 49). *Sedercypris calidus* has notably large eyes, which are supplemented by two pairs of barbels and chemosensory cells on the head. Gut content analysis indicates baetid mayfly nymphs and chironomid larvae as the most important prey items for this species, with mayfly nymphs constituting >90% of prey items year-round (Nthimo, 1997). Terrestrial insects (Formicidae) form a riparian diet subsidy, consumed through feeding from the water surface (Nthimo, 1997). A predominantly carnivorous diet is further supported by a short gut length and smooth pharyngeal teeth (Nthimo, 1997).

Spawning and recruitment of this species occurs in the austral summer, with adults reaching sexual maturity at ~45 mm SL, reflecting that of sister species *S. erubescens* (Nthimo, 1997; Marriott, 1998). Ripe adults are found from November through to January, with gonad recrudescence initiating in August towards the end of the rainy season (Nthimo, 1997). *Sedercypris calidus* deposits eggs among rock crevices in large spawning aggregations, as opposed to the egg-scattering of *Pseudobarbus* redfin minnows (Skelton, 2001; van der Walt *et al*., 2017c). Males develop nuptial tubercles on the head and have enhanced spawning colouration, similar to other cyprinids.

Figure 2. A shoal of *Sedercypris calidus* in the Rondegat River.

Pseudobarbus phlegethon (Barnard, 1938), the fiery redfin, is endemic to the Olifants River and its tributaries (Skelton, 1996) (Figure 3). With fewer than ten populations remaining, *P. phlegethon* is listed as Endangered on the IUCN Red List (van der Walt et al., 2017a). *Pseudobarbus phlegethon* feeds on detritus attached to the rocky substrate and aquatic invertebrates (Skelton, 1996; Whitehead, Weyl & Bills, 2007; Garrow & Marr, 2012). Habitat preferences for this species tend to be slow-flowing pool environments with complex structure (Gore, King & Hamman, 1991; Broom *et al.*, 2022). A preference for substrate foraging is suggested by this species' sub-terminal mouth orientation (Whitehead *et al.*, 2007). While detritus and algae have been found in gut content analyses of limited numbers of *P. phlegethon*, the gut physiology is better suited to a carnivorous diet of aquatic invertebrate prey (Whitehead *et al.*, 2007). The primary invertebrate food items include Baetid mayflies, Chironomidae, Trichopteran pupae and Coleopteran larvae (Whitehead *et al.*, 2007). *Pseudobarbus phlegethon* tends to be smaller (up to 90 mm, with most individuals tending towards 45 – 55 mm (Whitehead *et al.*, 2007)) and less abundant than *S. calidus* (Skelton, 1996). The two redfin species tend to form transient shoals without apparent aggression behaviours despite overlap in resource and territory use (CJB unpublished data). *Pseudobarbus phlegethon* has a long summer spawning season with multiple spawning events. Sexual maturity reached is at sizes > 33 mm (Whitehead *et al.*, 2007). Males defend small territories wherein spawning takes place (Skelton, 1996) and may corral small groups of females into their territories (pers. obs.). Males have larger paired fins and develop bright red fin colouration when in breeding condition, and like *S. calidus* develop nuptial tubercles on the head (Skelton, 1996).

Figure 3. A shoal of *Pseudobarbus phlegethon* in the vegetated upper reaches of the Rondegat River

Labeobarbus seeberi (formerly *L. capensis*; Smith, 1841), the Clanwilliam yellowfish, is classified as Vulnerable by the IUCN and is the largest freshwater fish of the CFE, attaining sizes of up to 1000 mm and 11 kg (Impson, Bills & Wolhuter, 2008; Garrow & Marr, 2012) (Figure 4). In the Rondegat River, *L. seeberi* co-occurs with redfin minnows. They are generally only found abundantly in the lower reaches as older, larger individuals persist in deeper over-summering pools (Paxton, 2008; Weyl *et al.*, 2013; van der Walt *et al.*, 2016). *Labeobarbus seeberi* is likely dependent on these pools for both over-summering refugia as well as important congregation areas for drift and substrate feeding downstream of riffles (Impson *et al.*, 2008; Paxton, 2008; Broom *et al.*, 2022). *Labeobarbus seeberi* is expected to have an omnivorous diet, with a fairly even representation of plant material and invertebrate prey (Paxton, 2008). Gut content analyses by Woodford (2005) revealed high levels of ingested detritus and identified Chironomidae and Corixidae as primary invertebrate prey. *Labeobarbus seeberi* is a multiple spawning, migratory and riffle-dependent species, making it particularly sensitive to habitat alteration. In addition, it is likely that temperature is a major component of spawning cues for this species, and releases of warmer water from upstream dams may adversely affect the timing of spawning, potentially affecting survival of the offspring (King, Cambray & Impson, 1998; Dallas, 2008). Impacted migratory pathways and disrupted spawning locations owing to increased drought conditions, water abstraction and damming in crucial riffle habitats are serious conservation concerns (Impson *et al.*, 2008; Paxton, 2008).

Figure 4. Adult *Labeobarbus seeberi* feeding in the lower reaches of the Rondegat River

Galaxias zebratus (Castelnau, 1861), the Cape galaxias, is recognised as a species complex with a highly fragmented distribution in the CFE (Wishart *et al*., 2006; Chakona *et al*., 2020). It is a small fish with a high genetic diversity due to a biogeographic history involving sea level shifts and that fragmented *Galaxias* ranges in the remaining paleo-river habitat (Wishart et al., 2006; Chakona et al., 2013). The most widespread species of the complex is the *Galaxias* 'nebula' sublineage found widely across the CFE (Chakona et al., 2011). The 'nebula' sublineage has the interesting ability to survive extended periods emersed, sharing this trait with other galaxiids across the Gondwanan continents (Chakona *et al*., 2011). In the Rondegat River, the species appears to only be found in the extreme upper reaches (< 4 km from the river source) and only in slow-moving sections of the headwater environment (Woodford, 2005; CJB pers. obs.).

Austroglanis gilli (Barnard, 1943), the Clanwilliam rock catfish, is a relatively small (<140 mm standard length) nocturnal species that occurs predominantly in headwaters with complex rocky habitats (Figure 5). It is listed as Near Threatened (van der Walt *et al*., 2017b). *Austroglanis gilli* is slow-growing, reaching sexual maturity at around three years of age and at a length of approximately 10 cm, with some individuals collected from the Rondegat River aged at over 12 years (Mthombeni, 2009). This K-selected life history makes *A. gilli* susceptible to habitat alteration, particularly sedimentation, which can result in the reduction of complex habitats that provide both protection from predators in environments where they co-occur with alien piscivores and suitable food sources (Chutter, 1969; Mthombeni, 2009; Garrow & Marr, 2012). This species is likely to spawn in November (early summer) based on otolith age analysis and gonadosomatic indices (Mthombeni, 2009), similarly to the spring-summer spawning periods of the cyprinids in this system. The diet of *A. gilli* consists primarily of Ephemeroptera (predominantly baetid mayfly larvae), Diptera (Simulidae, Chironomidae) and Trichoptera (Mthombeni, 2009).

Figure 5. *Austroglanis gilli* alongside other species collected from the Rondegat River using fyke nets.

STRESSORS AND THREATS

Stressors are defined as novel or extreme environmental changes. Climate changes, such as increased temperatures and frequency of extreme events (e.g., droughts and flooding), as well as biological invasions and habitat destruction, can act synergistically wherein their cumulative effects are non-additive, i.e., "greater than the sum of their parts" (Jackson *et al.*, 2016a, 2020). Multiple stressors have likely played a role in the majority of freshwater species declines, with approximately 81% of studies investigating impacts on freshwater species being found to have nonadditive interaction effects (Jackson *et al.*, 2016a). While management-aided removal of single stressors can result in positive results, defining and eliminating interacting stressors in tandem is likely to result in greater ecological recovery (Jackson *et al.*, 2016a).

Climate change and CFE fishes

General reductions in rainfall over the rainy season (chiefly June, August and October), alongside a shortening of the rainy season, is predicted between 2040 and 2070, tempered by increases in intense short-term rainfall events (Dallas, 2008; Lötter, 2015; du Plessis & Schloms, 2017). Climatic trends indicate that high intensity extreme rainfall events and thus flash flooding are increasing in frequency (Kruger & Nxumalo, 2017). Temperatures have been rising since the beginning of observations (1961) and the hottest 10-year period was consistently reported as the last decade (2000 – 2010) in multiple studies (Lötter, 2015). Maximum and minimum temperatures are likely to increase by up to 2.5°C between 2040 and 2070, and extreme temperature events are predicted to increase in frequency between December and March (Lötter, 2015). Comparing water temperatures of the Driehoeks River in the Doring system between 2005 and 2015 indicates a trend of increasing extreme temperature events (Reizenberg et al., 2019), suggesting the potential for similar scenarios in the Rondegat.

Fish are strongly affected by their thermal environment, temperature increases metabolism and decreases dissolved oxygen resulting in a hump-shaped relationship between feeding rate and temperature (Uiterwaal & DeLong, 2020). In rivers, the thermal regime has strong effects on growth rates and distributions of aquatic organisms (Caissie, 2006). This aspect is particularly pronounced in highly fragmented populations that are limited in dispersal and when limited thermal refugia are available. The thermal regime can be affected by natural fluctuations as well as human interference through direct thermal pollution and removal of vegetation or indirectly through anthropogenic climate change (Caissie, 2006). Mean daily temperature increases downstream and the rate of increase in temperature can be particularly significant in smaller streams, owing to their low thermal capacity. In addition to these spatial temperature gradients, headwater streams tend to have lower diel variation than larger streams (Caissie, 2006).

Temperature and other environmental variability can affect fish populations through reproductive effects, such as altered triggers for gonad development and spawning behaviours; or recruitment effects, such as decreased egg and larval growth and survival through abnormal habitat conditions (Humphries & Lake, 2000; Paxton, 2008). As fish tend to be adapted to the average long-term conditions of their historical distributions, shifts in conditions beyond the usual scope of their adaptive history may have adverse effects on their ability to time reproductive cycles with prevailing conditions most conducive to successful recruitment and other effects on reproductive cues (Humphries & Lake, 2000; Poff & Zimmerman, 2010).

Mediterranean-climate freshwater biotas are likely to be disproportionately affected by climate change with expected shifts in distribution, community composition and life-history, particularly in the seasonality of physiological processes (Filipe *et al.*, 2013). Recent work predicts that many of the CFE fishes will be put under severe strain given "business as usual" climate change scenarios, although detailed conclusions are not possible due to the lack of baseline biological data for CFE species (Dallas, 2013; Dallas & Rivers-Moore, 2014; Shelton *et al*., 2018a). In the generally species-depauperate and oligotrophic systems of the ODRS, climate-related abiotic and resultant biotic shifts may have disproportionately devastating effects as a result of relatively minor fluctuations (Shelton *et al*., 2018a; Reizenberg *et al*., 2019). *Galaxias zebratus* and *Pseudobarbus* species (including the re-classified *S. calidus*) were the most thermally sensitive (Reizenberg *et al*., 2019). These authors suggest that most CFE species are differentiated in thermal tolerance at the species level, and have not diverged in this trait across river systems (i.e., at the population level). However, the thermal physiological limits of larger cyprinids, such as *L. seeberi*, have not been examined. Climate change is predicted to increase feeding rates of *L. seeberi* and *S. calidus*, however, there was no significant change between 18°C and 25°C, suggesting community resilience (Broom *et al*., 2021).

The effects of climate change on invasive species are considerably better understood. For example, trout (*Salmo trutta* and *Oncorhynchus mykiss*), which are cool mountain stream-specialized species, are expected to decrease in abundance and viable population distribution in shrinking refugia within the CFE (Ellender *et al*. 2016; Shelton *et al*., 2018b; Dallas *et al*., 2020). Conversely, warm-adapted species, e.g., black basses (*Micropterus* spp), as well as extra-limital *Tilapia* species, may increase in abundance and invasive range (Khosa *et al*., 2019; Weyl *et al*. 2020). Black basses have a high invasion debt in South Africa as a result of rising temperatures and increased dam construction in response to drought (Khosa *et al*., 2019, 2020). Furthermore, increasing temperatures are likely to enhance invasive species ecological impact in South African freshwaters (Khosa *et al*. 2019; Mofu *et al*. 2019).

Water abstraction

Mediterranean-climate areas such as the CFE are especially vulnerable to water diversion owing to their semi-arid and strongly seasonal flow fluctuations (Gasith & Resh, 1999; Filipe *et al*., 2013; de Moor & Day, 2013). Fish assemblage responses are usually more strongly affected directly by flow variability as opposed to resource or biotic constraints (Gasith & Resh, 1999). Water abstraction and other flow-regulating anthropogenic activities are common in the lower reaches of CFE rivers, and the Rondegat River is one such example (Beatty *et al*., 2017). de Moor and Day (2013) identified the increasing demand for abstraction as the most pressing threat to aquatic biota in the CFE. The importance of this threat is expected to increase due to the predicted increase in aridity, and the extended drought conditions in recent years are a particular concern (de Moor & Day, 2013).

Invasive species

The main invasive fish threat in this system are members of the black bass genus *Micropterus* (van der Walt *et al*., 2016). In the ODRS, an estimated 81% of the natural cyprinid range has been invaded by black bass (van der Walt *et al*., 2016). The mainstem Olifants and Doring Rivers are completely invaded by black bass, and their distribution in the tributaries is primarily limited by natural barriers, which are in most cases the only factor preventing local extirpation of native fishes (van der Walt *et al*., 2016; Weyl *et al*., 2020). The bass invasions completely eradicated all small (<10 cm total length) native species and prevented recruitment of species with an adult length of >10 cm (van der Walt *et al*., 2016). Where bass and other invasive fishes co-occur, local habitat loss to native species is accelerated and multiple predator effects may act to further increase the threat of invasive fish for all local fish life (Wasserman *et al*., 2016). Currently, relationships between invasive predatory fish and the endemic fish species in this system are only partially understood (Ellender *et al*., 2017). Within the ODRS, the primary and most damaging interactions of non-native and extra-limital species interactions is direct predation, although there is evidence of some displacement of native fishes, introduction of novel parasites or diseases, and habitat degradation (Table 1) (Ellender & Weyl, 2014; Weyl *et al*., 2020).

Stream flow and drought

In the context of a drought-prone and seasonally variable river system, stream flow is of paramount importance as it regulates abiotic drivers of abundance and distribution (Bunn & Arthington, 2002; Poff & Zimmerman, 2010). Across systems, fish consistently react negatively to alterations of flow magnitude (Poff & Zimmerman, 2010), for example as a result of damming or unseasonal flooding. The life history traits of some species can affect their ability to cope with altered flow, particularly drought-like conditions as a result of human activity (Matthews & Marsh-Matthews, 2003). Damming and other human activities can have strong effects on flow as well as affecting water quality, with associated effects on fish population health, in addition to reducing connectivity of habitats for migratory fishes (Doeg & Koehn, 1994; Beatty *et al.,* 2017). Small-scale damming and the associated effects on flow downstream, as well as weir failures or removals releasing sediment downstream, are a common situation in the middle and lower reaches of the Rondegat River (Woodford, 2005). Changes to the timing and intensity of flow, as well as indirect effects on shifts in temperature, have impacts on the phenology of the system as a whole, as well as affecting the timing of triggers for breeding in species such as *L. seeberi* (Gore *et al*., 1991; Cambray, King & Bruwer, 1997; King *et al*., 1998).

Summer drought is exacerbated by strong and persistent south-easterly winds that desiccate the landscape and vegetation. Fish resilience within river reaches is likely enhanced by deep and complex habitats that can be used as refugia during times of both increased (e.g. flash floods) and decreased (e.g. drought) flow (Fausch & Bramblett, 1991). Large, deep and complex pool environments support *L. seeberi* populations during the dry season in the CFE, thus reductions in size and abundance of deep pool refugia are likely to be a major threat (Paxton, 2008; Weyl *et al*., 2013). The physicochemical stressors and reductions in viable habitat produced by drought can lead to higher incidences of competition in available refugia as fish densities increase (Magoulick & Kobza, 2003; Castañeda et al., 2020). It is during these "crunch" periods in low-flow conditions within refugia wherein the greatest competition for diminished resources should occur.

Flooding

While the Mediterranean climate of the CFE may not experience the extremes of tropical seasonal flooding events, winter rainfall spates and resultant flooding are likely to be significant drivers of resource availability within the oligotrophic Rondegat River. Jackson *et al*. (2020) suggest that the predicted decrease in rainfall and increase in frequency of extreme events in South Africa are likely to result in higher vulnerability of freshwater vertebrates to local land use patterns. Further shifts in phenology and abundance of prey items, particularly sensitive aquatic invertebrate taxa and their larvae, are likely to strongly affect nutrient flow and resource availability for freshwater fishes. In addition to temperature increase and flow regime change (Dallas & Rivers-Moore, 2014; Dallas *et al*., 2020), the predicted increase in frequency of extreme weather events such as flash flooding, may have major effects on the trajectory and intensity of invasive species through release of captive alien species into natural systems. The Rondegat river is currently recovering from a major drought, with areas below a 2m weir designed to prevent re-invasion from the Olifants River (Lowe et al., 2008; Weyl et al., 2013) consisting of isolated pools with confirmed alien fish presence, which may wash invasive *Tilapia sparmanii*, *Lepomis macrochirus* and *Clarias gariepinus* back into the system. On the other extreme, patterns of drying rivers may have either positive or negative impacts on fish species. For example, while drought may reduce available habitat for native species, it may in some cases act as a facilitator of important physical barriers protecting native species through drying of reaches required

DOI: 10.29094/FiSHMED.2023.001

for the upstream movement of bass (Ellender *et al.*, 2018).

Fire and siltation

Mediterranean climate areas tend to burn at natural frequencies to which the vegetation is adapted during hot dry summer months. The Cederberg region has a propensity to burn at intervals of less than five years under the influence of anthropogenic accidental ignitions (Southey, 2009). Natural ignition events vary from 5 to 20 years between fires (Southey, 2009), suggesting that the local vegetation and river fauna are likely adapted to relatively frequent fire events. The Rondegat has been subjected to two intense unseasonal burns in the last 20 years (Southey, 2009; Fill *et al.*, 2018; Figure 6). In both instances there was then increased rainfall over the winter months which resulted in high turbidity and altered physical characteristics through the release of a sand slug downstream of burnt areas, Sediment loads often peak in post-fire rainfall flash flooding as a result of multiple fire-related soil erosion-enhancing effects (Bozek & Young, 1994; Burton, 2005; Lyon & O'Connor, 2008; Ebner *et al.*, 2014). Sediment slugs can in many cases cause near-complete local extirpation of fish populations and loss of habitat complexity as a result of siltation (Chutter, 1969). Increased siltation and sand deposition will affect all fish species in the Rondegat assemblage; further to the removal of suitable habitat for *A. gilli*, all three cyprinid species are dependent on rocky, complex habitats (redfins) or riffles (yellowfish) for successful spawning. The *P. phlegethon* population of the nearby Noordhoeks River has been impacted by such siltation of suitable habitat brought about by anthropogenic actions (Whitehead et al., 2007).

In addition to sediment slugs, a major danger to fish from fire events is increased barriers to re-colonisation of affected areas and their subsequent re-population success during recovery. Thus, the need for barriers to prevent alien fish from extirpating native fish may inadvertently affect successful recovery after fire events (Burton, 2005). Sediment slug formation and siltation of habitats can be a delayed process (Bozek & Young, 1994; Lyon & O'Connor, 2008); which was the situation in the Rondegat in February 2019, a year after a major fire event. Delayed mortality following fire events as observed by Bozek and Young (1994) is a notable conservation concern, as direct fish kills multiple years after an initial event can be devastating and unpredictable. Populations of *G. zebratus* are very small and limited in distribution in the Rondegat River (most recently found in one near-stagnant pool <5km from the river source, with no other reported sightings in the last decade; CJB pers. obs.), and fire events in the upper reaches of the Rondegat may lead to local extirpation. Isolated populations are particularly important for conservation in *G. zebratus*, as very fine-scale differentiation and speciation is commonly observed in this putative species complex (Wishart *et al.*, 2006). The limited distribution and low number of known populations of *P. phlegethon* also warrant attention in the context of fire events affecting the Rondegat River (Broom *et al.*, 2022).

The direct effects of fire on small. Low order streams are often more pronounced than in larger rivers (Lyon & O'Connor, 2008). Fire can result in multiple concurrent stressors in river environments, such as increased temperatures from reduced riparian vegetation, siltation of pools, altered nutrient inputs from burnt material, as well as altered flow regimes as a result of shifts in vegetation water uptake demands (Bozek & Young, 1994; Burton, 2005; Lyon & O'Connor, 2008). Alongside these, physicochemical changes such as increased pH and decreased oxygen concentration have the potential for to lead to fish kills, especially in smaller streams. Less direct effects of fires may include habitat alteration through reduction of woody debris, followed by increases in woody debris and rocky environments as a result of sediment inputs in later flood events (Burton, 2005; Ebner *et al.*, 2009, 2014).

Figure 6. Effects of wildfires in the Rondegat River. Above, major sand deposition on the banks, following a fire event and heavy rainfall. Below, burnt and recovering vegetation on the banks of the Rondegat River, following a major fire event in February 2018.

Restoration and links to other Mediterranean-climate systems

Looking further afield to international models for contrast and lessons in restoration, Australian freshwater systems and aquatic fauna encounter similar challenges to those of South African systems, and thus are useful as a knowledge base and template for conservation and restoration actions locally (Lintermans, 2013). Australian native freshwater species are often threatened by a similar suite of threats including alien fish invasions, drought, fire and other anthropogenic impacts, and some survive in fragmented refugia (Koehn & Lintermans, 2012; Saddlier, Koehn & Hammer, 2013; Ward *et al.*, 2020), reflecting the plight of many South African species. Saddlier *et al.* (2013) provide an account of the conservation and restoration approaches towards confronting the decline of imperilled small native fishes in south-eastern Australia. Important milestones for the restoration of these highly vulnerable species are applicable to South African native species, especially in the context

DOI: 10.29094/FiSHMED.2023.001

of moving from monitoring programmes into sustainable conservation action (Lintermans, 2013). In particular, the recent Australian wildfires represent an example of highly damaging events that are likely to increase in frequency in a scenario of global change. Drought conditions and associated increases in fires and their cascading effects are paralleled between the CFE and Australian conditions; in particular, the western CFE is expected to have reduced rainfall during the historically wet season, having potential knock-on effects over an extended dry season (Dallas & Rivers-Moore, 2014). The impacts of and responses to these climate-related events in the Australian context hold much value for the prediction and mitigation of these events in the South African context, through collaborating with and studying Australian conservation and restoration efforts.

In conclusion, the CFE in general and the Rondegat River in particular provide important lessons for Mediterranean aquatic ecosystems, from their threats to their envisioned restoration. While the threat of invasive alien species is not unique to Mediterranean systems, their interactions with other stressors such as drought, fire, habitat degradation and other effects of anthropogenic global change are important aspects that can be used in case studies to improve conservation actions across systems. The imperilled freshwater fish species of the CFE share many characteristics with other Mediterranean species further afield, further enhancing the applicability of mitigation and restoration actions borne out of projects such as the Rondegat restoration project and other efforts in the CFE.

Coordinated, focused and multi-disciplinary action is required across these vital conservation regions; ideally with the collaboration of researchers from across national boundaries and applying lessons learned in their unique contexts. Only through the combined efforts of researchers and conservation practitioners from a range of backgrounds and experiences in a variety of challenges applying mitigation, conservation and restoration approaches, will a cohesive and suitably agile restorative impact be realised.

ACKNOWLEDGEMENTS

This study is dedicated to the memory of Professor Olaf Weyl, whose guidance and devotion to South African freshwater ecology made the Rondegat River restoration project and all work flowing therefrom possible.

Rika du Plessis of CapeNature facilitated research activities in the Cederberg Wilderness Area. Jannie and Cecile Nieuwoudt (of Keurbos farm), and Jannie and Katrin Nieuwoudt (Grootkloof / Jamaka farms) are thanked for land access and discussion about the history of the Rondegat River valley. Permission for land access was granted by local conservation authority CapeNature and private land owners. This study was funded by the National Research Foundation (NRF)—South African Research Chairs Initiative of the Department of Science and Innovation (DSI) (Grant No. 110507). Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF. We hereby acknowledge the use of equipment provided by the NRF-SAIAB Marine Remote Imagery Platform and the funding channelled through the NRF-SAIAB Institutional Support System. Photographs are property of the authors except where otherwise credited.

AUTHORS' CONTRIBUTIONS

CJB led the writing of the manuscript; CJB and OLFW conceptualised the study; OLFW provided primary insights and references pertaining to the Rondegat River restoration project; JS contributed significantly to editing and writing direction. All authors contributed critically to the drafts and gave final approval for publication.

CITED REFERENCES

Abell R., Allan J.D. & Lehner B. (2007). Unlocking the potential of protected areas for freshwaters. *Biological Conservation* **134**, 48–63.

Beatty S., Allen M., Lymbery A., Jordaan M.S., Morgan D., Impson D., *et al.* (2017). Rethinking refuges: Implications of climate change for dam busting. *Biological Conservation* **209**, 188–195.

Bellingan T., Woodford D., Gouws J., Villet M. & Weyl O. (2015). Rapid bioassessment of the effects of repeated rotenone treatments on invertebrate assemblages in the Rondegat River, South Africa. *African Journal of Aquatic Science* **40**, 89–94.

Bozek M.A. & Young M.K. (1994). Fish mortality resulting from delayed effects of fire in the greater Yellowstone ecosystem. *The Great Basin Naturalist* **54**, 91–95

Broom C. J., South J. & Weyl O.L.F. (2021). Prey type and temperature influence functional responses of threatened endemic Cape Floristic Ecoregion fishes. *Environmental Biology of Fishes* **104**, 797–810.

Broom, C. J., Weyl, O. L. F. & South, J. (2022). Habitat associations of imperilled fishes after conservation intervention in the Cape Fold Ecoregion, South Africa. *Journal of Fish Biology* **102**, 317-327.

Bunn S.E. & Arthington A.H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**, 492–507

Burton T.A. (2005). Fish and stream habitat risks from uncharacteristic wildfire: Observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management* **211**, 140–149.

Caissie D. (2006). The thermal regime of rivers: a review. *Freshwater Biology* **51**, 1389–1406.

Cambray J.A., King J.M. & Bruwer C. (1997). Spawning behaviour and early development of the Clanwilliam yellowfish (*Barbus capensis*; Cyprinidae), linked to experimental dam releases in the Olifants River, South Africa. *Regulated Rivers: Research & Management* **13**, 579–602.

Castañeda R.A., Mandrak N.E., Barrow S. & Weyl O.L.F. (2020). Occupancy dynamics of rare cyprinids after invasive fish eradication. *Aquatic Conservation: Marine and Freshwater Ecosystems* **30**, 1424–1436.

Chakona A., Gouws G., Kadye W.T., Jordaan M.S. & Swartz E.R. (2020). Reconstruction of the historical distribution ranges of imperilled stream fishes from a global endemic hotspot based on molecular data: Implications for conservation of threatened taxa. *Aquatic Conservation: Marine and Freshwater Ecosystems* **30**, 144–158.

Chakona A., Swartz E.R. & Gouws G. (2013). Evolutionary drivers of diversification and distribution of a southern temperate stream fish assemblage: testing the role of historical isolation and spatial range expansion. *PLoS ONE* **8**, e70953.

Chakona A., Swartz E.R. & Magellan K. (2011). Aerial exposure tolerance of a newly discovered galaxiid. *Journal of Fish Biology* **78**, 912–922.

Chutter F.M. (1969). The effects of silt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia* **34**, 57–76.

Dallas H. (2008). Water temperature and riverine ecosystems: An overview of knowledge and approaches for assessing biotic responses, with special reference to South Africa. *Water SA* **34**, 393–404

Dallas H., Shelton J., Paxton B., Weyl O., Reizenberg J.-L., Bloy L., *et al.* (2020). *Assessing the Effect of Climate Change on Native and Non-Native Freshwater Fishes of the Cape Fold Ecoregion, South Africa.*

Water Research Commission, WRC Report No. TT 801/19, Pretoria, South Africa.

Dallas H.F. (2013). Ecological status assessment in Mediterranean rivers: complexities and challenges in developing tools for assessing ecological status and defining reference conditions. *Hydrobiologia* **719**, 483–507.

Dallas H.F. & Rivers-Moore N. (2014). Ecological consequences of global climate change for freshwater ecosystems in South Africa. *South African Journal of Science* **110**.

Darwall W.R.T., Smith K.G., Tweddle D. & Skelton P. (2009). *The status and distribution of freshwater biodiversity in southern Africa.* IUCN, Gland.

Doeg T. & Koehn J. (1994). Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *Regulated Rivers: Research & Management* **9**, 263–277

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.-I., Knowler D.J., Lévêque C., *et al.* (2005). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163–182.

Ebner B.C., Clear R., Godschalx S. & Beitzel M. (2009). In-stream behaviour of threatened fishes and their food organisms based on remote video monitoring. *Aquatic Ecology* **43**, 569–576.

Ebner B.C., Starrs D., Morgan D.L., Fulton C., , *et al.* (2014). Emergence of field-based underwater video for understanding the ecology of freshwater fishes and crustaceans in Australia. *Journal of the Royal Society of Western Australia* **97**, 287–296

Ellender B.R., Rivers-Moore N.A., Coppinger C.R., Bellingan T.A. & Weyl O.L.F. (2016). Towards using thermal stress thresholds to predict salmonid invasion potential. *Biological Invasions* **18**, 3513–3525.

Ellender B.R., Wasserman R.J., Chakona A., Skelton P.H. & Weyl O.L.F. (2017). A review of the biology and status of Cape Fold Ecoregion freshwater fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* **27**, 867–879.

Ellender B.R. & Weyl O.L.F. (2014). A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. *Aquatic Invasions* **9**, 117–132.

Ellender B.R., Weyl O.L.F., Alexander M.E., Luger A.M., Nagelkerke L.A.J. & Woodford D.J. (2018). Out of the pot and into the fire: Explaining the vulnerability of an endangered small headwater stream fish to black-bass *Micropterus* spp. invasion. *Journal of Fish Biology* **92**, 1035–1050.

Fausch K.D. & Bramblett R.G. (1991). Disturbance and fish communities in intermittent tributaries of a Western Great Plains river. *Copeia* **1991**, 659-674.

Fausch K.D., Torgersen C.E., Baxter C.V. & Li H.W. (2002). Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. *BioScience* **52**, 483-498.

Filipe A.F., Lawrence J.E. & Bonada N. (2013). Vulnerability of stream biota to climate change in Mediterranean climate regions: a synthesis of ecological responses and conservation challenges. *Hydrobiologia* **719**, 331–351.

Fill J.M., Kritzinger-Klopper S. & van Wilgen B.W. (2018). Short-term vegetation recovery after alien plant clearing along the Rondegat River, South Africa. *Restoration Ecology* **26**, 434–438.

Garrow C. & Marr S. (2012). *Swimming on the Edge of Extinction: The Perilous State of the Indigenous Freshwater Fishes of the Western Cape*. NISC.

Gasith A. & Resh V.H. (1999). Streams in Mediterranean Climate Regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events. *Annual Review of Ecology and Systematics* **30**, 51–81.

Gore J., King J. & Hamman K. (1991). Application of the instream flow incremental methodology to Southern African rivers: Protecting endemic fish of the Olifants River. *Water SA* **17**, 225–236

Humphries P. & Lake P.S. (2000). Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management* **16**, 421–432.

Impson N.D., Bills I.R. & Wolhuter L.E. (2008). *Technical report on the state of yellowfishes in South Africa 2007*. Water Research Commission, Pretoria, South Africa.

Impson N.D., Marriott M., Bills I.R. & Skelton P.H. (2007). Conservation biology and management of a critically endangered cyprinid, the Twee River redfin, *Barbus erubescens* (Teleostei: Cyprinidae), of the Cape Floristic Region, South Africa. *African Journal of Aquatic Science* **32**, 27–33.

Jackson M.C., Fourie H.E., Dalu T., Woodford D.J., Wasserman R.J., Zengeya T.A., *et al.* (2020). Food web properties vary with climate and land use in South African streams. *Functional Ecology* **34**, 1653–1665.

Jackson M.C., Loewen C.J.G., Vinebrooke R.D. & Chimimba C.T. (2016a). Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology* **22**, 180–189.

Jackson M.C., Pawar S. & Woodward G. (2021). The temporal dynamics of multiple stressor effects: from individuals to ecosystems. *Trends in Ecology & Evolution* **36**, 402–410.

Jackson M.C., Woodford D.J., Bellingan T.A., Weyl O.L.F., Potgieter M.J., Rivers-Moore N.A., *et al.* (2016b). Trophic overlap between fish and riparian spiders: potential impacts of an invasive fish on terrestrial consumers. *Ecology and Evolution* **6**, 1745–1752.

Jordaan M.S., Chakona A. & van der Colff D. (2020). protected areas and endemic freshwater fishes of the Cape Fold Ecoregion: missing the boat for fish conservation? *Frontiers in Environmental Science* **8**, 502042.

Jordaan M.S., Lubbe A., Bragg C., Paxton B.R., Schumann M., Van Der Walt R., *et al.* (2017). *Labeo seeberi* (errata version published in 2020). *The IUCN Red List of Threatened Species 2017: e.T11071A174778890*.

Khosa D., Marr S.M., Wasserman R.J., Zengeya T.A. & Weyl O.L.F. (2019). An evaluation of the current extent and potential spread of Black Bass invasions in South Africa. *Biological Invasions* **21**, 1721–1736.

Khosa D., South J., Cuthbert R.N., Wasserman R.J. & Weyl O.L. (2020). Temperature regime drives differential predatory performance in Largemouth Bass and Florida Bass. *Environmental Biology of Fishes* **103**, 67–76

King J., Cambray J.A. & Impson N.D. (1998). Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologica* **384**, 245–265

Koehn J.D. & Lintermans M. (2012). A strategy to rehabilitate fishes of the Murray-Darling Basin, south-eastern Australia. *Endangered Species Research* **16**, 165–181

Kruger A.C. & Nxumalo M.P. (2017). Historical rainfall trends in South Africa: 1921–2015. *Water SA* **43**, 285.

Lintermans M. (2013). A review of on-ground recovery actions for threatened freshwater fish in Australia. *Marine and Freshwater Research* **64**, 775–791.

Lötter D. (2015). *Potential implications of climate change for Rooibos (A.Linearis) production and distribution in the greater Cederberg Region, South Africa*. University of Cape Town, Cape Town.

Lowe S.R., Woodford D.J., Impson D.N. & Day J.A. (2008). The impact of invasive fish and invasive riparian plants on the invertebrate fauna of the Rondegat River, Cape Floristic Region, South Africa. *African Journal of Aquatic Science* **33**, 51–62.

Lyon J.P. & O'Connor J.P. (2008). Smoke on the water: Can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology* **33**, 794–806.

Magoulick D.D. & Kobza R.M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* **48**, 1186–1198.

Marr S.M., Impson N.D. & Tweddle D. (2012). An assessment of a proposal to eradicate non-native fish from priority rivers in the Cape Floristic Region, South Africa. *African Journal of Aquatic Science* **37**, 131–142.

Marriott M.S. (1998). *Conservation biology and management of the Twee River redfin,* Barbus erubescens *(Pisces: Cyprinidae)*. Rhodes University, Grahamstown.

Matthews W.J. (2012). *Patterns in freshwater fish ecology*. Springer Science & Business Media.

Matthews W.J. & Marsh-Matthews E. (2003). Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* **48**, 1232–1253.

Mofu L., South J., Wasserman R.J., Dalu T., Woodford D.J., Dick J.T.A., *et al.* (2019). Inter-specific differences in invader and native fish functional responses illustrate neutral effects on prey but superior invader competitive ability. *Freshwater Biology* **64**, 1655–1663.

de Moor F.C. & Day J.A. (2013). Aquatic biodiversity in the Mediterranean region of South Africa. *Hydrobiologia* **719**, 237–268.

Mthombeni V.G. (2009). *The biology* of Austroglanis gilli *and* Austroglanis barnardi *(Siluriformes: Austroglanididae) in the Olifants River system, South Africa*. Rhodes University, Grahamstown.

Nthimo M. (1997). *The reproductive and feeding biology of Clanwilliam redfin minnow,* Barbus calidus *(Pisces: Cyprinidae)*. Rhodes University, Grahamstown.

Paxton B.R. (2008). *The influence of hydraulics, hydrology and temperature on the distribution, habitat use and recruitment of threatened cyprinids in a Western Cape river, South Africa*. University of Cape Town.

du Plessis J.A. & Schloms B. (2017). An investigation into the evidence of seasonal rainfall pattern shifts in the Western Cape, South Africa. *Journal of the South African Institution of Civil Engineering* **59**, 47–55.

Poff N.L. & Zimmerman J.K.H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows: Review of altered flow regimes. *Freshwater Biology* **55**, 194–205.

Reizenberg J.-L., Bloy L.E., Weyl O.L.F., Shelton J.M. & Dallas H.F. (2019). Variation in thermal tolerances of native freshwater fishes in South Africa's Cape Fold Ecoregion: examining the east-west gradient in species' sensitivity to climate warming. *Journal of Fish Biology* **94**, 103-112

Saddlier S., Koehn J.D. & Hammer M.P. (2013). Let's not forget the small fishes – conservation of two threatened species of pygmy perch in south-eastern Australia. *Marine and Freshwater Research* **64**, 874.

Shelton J.M., Weyl O.L.F., *et al.* (2018a). Vulnerability of Cape Fold Ecoregion freshwater fishes to climate change and other human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* **28**, 68–77.

Shelton J.M., Weyl O.L.F., Esler K.J., Paxton B.R., Impson N.D. & Dallas H.F. (2018b). Temperature mediates the impact of non-native rainbow trout on native freshwater fishes in South Africa's Cape Fold Ecoregion. *Biological Invasions* **20**, 2927–2944.

Skelton P.H. (2001). *A complete guide to the freshwater fishes of southern Africa.*, 2nd edn. Struik, Cape Town, South Africa.

Skelton P.H. (1996). Threatened fishes of the world: *Pseudobarbus phlegethon* (Barnard, 1938) (Cyprinidae). *Environmental Biology of Fishes* **45**, 214

Skelton P.H., Swartz E.R. & Vreven E.J. (2018). The identity of *Barbus capensis* Smith, 1841 and the generic status of southern African tetraploid cyprinids (Teleostei, Cyprinidae). *European Journal of Taxonomy* **410**, 1–29.

Slabbert E., Jordaan M. & Weyl O. (2014). Analysis of active rotenone concentration during treatment of the Rondegat River, Cape Floristic Region, South Africa. *African Journal of Aquatic Science* **39**, 467–472.

Southey D. (2009). *Wildfires in the Cape Floristic Region: Exploring vegetation and weather as drivers of fire frequency*. University of Cape Town, Cape Town.

Swartz E.R. (2000). *Population genetics of* Pseudobarbus phlegethon*,* Barbus calidus *and* Barbus erubescens *(Teleostei: Cyprinidae) of the Olifants River System, Western Cape Province*. University of Stellenbosch, Stellenbosch.

Swartz E.R., Flemming A.F. & Mouton P. le F.N. (2004). Contrasting genetic patterns and population histories in three threatened redfin species (Cyprinidae) from the Olifants River system, western South Africa. *Journal of Fish Biology* **64**, 1153–1167.

Swartz E.R., Skelton P.H. & Bloomer P. (2009). Phylogeny and biogeography of the genus *Pseudobarbus* (Cyprinidae): Shedding light on the drainage history of rivers associated with the Cape Floristic Region. *Molecular Phylogenetics and Evolution* **51**, 75–84.

Swartz E.R., Skelton P.H. & Bloomer P. (2007). Sea-level changes, river capture and the evolution of populations of the Eastern Cape and fiery redfins (*Pseudobarbus afer* and *Pseudobarbus phlegethon*, Cyprinidae) across multiple river systems in South Africa. *Journal of Biogeography* **34**, 2086–2099.

Tweddle D., Bills R., Swartz E., Coetzer W., da Costa L., Engelbrecht J., *et al.* (2009). The status and distribution of freshwater fishes. In: *The status and distribution of freshwater biodiversity in southern Africa*. p. 37.

Uiterwaal S.F. & DeLong J.P. (2020). Functional responses are maximized at intermediate temperatures. *Ecology* **101**, e02975.

van der Walt J.A. (2014). *Black bass (*Micropterus *spp.) in the Olifants-Doorn river system: distribution, distribution barriers, predatory impact and management*. Cape Peninsula University of Technology, Cape Town, South Africa. https://core.ac.uk/download/pdf/148364784.pdf.

van der Walt J.A., Impson D.N. & Jordaan M.S. (2017a). *Pseudobarbus phlegethon*. *The IUCN Red List of Threatened Species* e.T107649522A107654419.

van der Walt J.A., Jordaan M.S., Bills R. & Impson D.N. (2017b). *Austroglanis gilli*. *The IUCN Red List of Threatened Species* e.T2427A99448983.

van der Walt J.A., Jordaan M.S. & Impson D.N. (2017c). *Pseudobarbus calidus*. *The IUCN Red List of Threatened Species* e.T2562A100139530.

van der Walt J.A., Marr S.M., Wheeler M.J., Impson N.D., Garrow C. & Weyl O.L.F. (2019). Successful mechanical eradication of spotted bass (*Micropterus punctulatus* (Rafinesque, 1819)) from a South African river. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 303–311.

van der Walt J.A., Weyl O.L.F., Woodford D.J. & Radloff F.G.T. (2016). Spatial extent and consequences of black bass (*Micropterus* spp.) invasion in a Cape Floristic Region river basin. *Aquatic Conservation: Marine and Freshwater Ecosystems* **26**, 736–748.

Ward M., Tulloch A.I., Radford J.Q., Williams B.A., Reside A.E., Macdonald S.L., *et al.* (2020). Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nature Ecology & Evolution* **4**, 1321–1326.

Wasserman R.J., Alexander M.E., Dalu T., Ellender B.R., Kaiser H. & Weyl O.L.F. (2016). Using functional responses to quantify interaction effects among predators. *Functional Ecology* **30**, 1988–1998.

Weyl O.L.F., Barrow S., Bellingan T.A., Dalu T., Ellender B.R., Esler K., *et al.* (2016). *Monitoring of invertebrate and fish recovery following river rehabilitation using rotenone in the Rondegat River: report to the Water Research Commission*. Pretoria, South Africa.

Weyl O.L.F., Ellender B.R., Wassermann R.J., Truter M., *et al.* (2020). Alien Freshwater Fauna in South Africa. In: *Biological Invasions in South Africa.* (Eds B.W. van Wilgen, J. Measey, D.M. Richardson, J.R. Wilson & T.A. Zengeya), pp. 153–183. Springer International Publishing, Cham.

Weyl O.L.F., Ellender B.R., Woodford D.J. & Jordaan M.S. (2013). Fish distributions in the Rondegat River, Cape Floristic Region, South Africa, and the immediate impact of rotenone treatment in an invaded reach. *African Journal of Aquatic Science* **38**, 201–209.

Weyl O.L.F., Finlayson B., Impson N.D., Woodford D.J. & Steinkjer J. (2014). Threatened endemic fishes in South Africa's Cape Floristic Region: a new beginning for the Rondegat River. *Fisheries* **39**, 270–279.

Whitehead A., Weyl O. & Bills I. (2007). Reproductive and feeding biology of the endangered fiery redfin, *Pseudobarbus phlegethon* (Barnard 1938) (Teleostei: Cyprinidae), in the Noordhoeks River, South Africa. *African Journal of Aquatic Science* **32**, 281–290.

Wishart M., Hughes J., Stewart B. & Impson D. (2006). Extreme levels of intra-specific divergence among Cape Peninsula populations of the Cape galaxias, *Galaxias zebratus* Castelnau 1861, reveals a possible species complex. *African Journal of Aquatic Science* **31**, 99–106.

Woodford D.J. (2005). *The impact of alien invasive smallmouth bass (*Micropterus dolomieu*) on the indigenous fish of the Rondegat River: A quantitative assessment with implications for rehabilitation*. University of Cape Town, Cape Town, South Africa. http://hdl.handle.net/11427/6739.

Woodford D.J., Barber-James H.M., Bellingan T.A., Day J.A., de Moor F.C., Gouws J., *et al.* (2013). Immediate impact of piscicide operations on a Cape Floristic Region aquatic insect assemblage: a lesser of two evils? *Journal of Insect Conservation* **17**, 959–973.

Woodford D.J., Impson N.D., Day J.A. & Bills I.R. (2005). The predatory impact of invasive alien smallmouth bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African Journal of Aquatic Science* **30**, 167–173.