

REVIEW ARTICLE

A review of the biology and status of Cape Fold Ecoregion freshwater fishes

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Abstract

1. Mediterranean climate regions are globally recognized as hotspots of endemism in fishes; however, these unique assemblages are increasingly threatened by human mediated impacts including water abstraction, damming and non-native species introductions.
2. The Cape Fold aquatic ecoregion (CFR) of South Africa supports an assemblage of range-restricted endemic freshwater fishes, the majority of which are conservation priorities because they are under severe threat of extinction. Effective conservation and management are constrained by the lack of readily available information on this imperilled group of fishes because research efforts over the last century have been temporally disjointed and relatively uncoordinated.
3. This review provides an exhaustive appraisal of published literature on the taxonomy, biogeography, life history, ecology and physiology of freshwater fishes in the CFR, and the human impacts that affect them. Its aim is to direct future research needs for effective management and conservation of this imperilled group.
4. Only 103 peer-reviewed articles on CFR fishes were recorded and the majority of available research is on taxonomy and biogeography (40.8%), followed by ecological investigations (22.3%), conservation (19.4%) and human impacts (17.5%).
5. Despite a plethora of studies on taxonomy and biogeography, recent genetic evidence suggests that fish diversity in the CFR has been severely underestimated and requires urgent attention. Human impacts severely threaten the existence of many native CFR fishes and require further study. Information on the biology and ecology of CFR fishes is limited to studies on selected species; of particular note is the lack of physiological information which is particularly pertinent given projected climate change scenarios.

KEYWORDS

conservation efforts, ecology, human mediated impacts, invasive impact, taxonomy

1 | INTRODUCTION

Mediterranean climate regions (e.g. California, central Chile, south-western Australia, the Iberian peninsula and the southern fringe of Africa) are globally recognized as hotspots of endemism in fishes; however, these unique assemblages have undergone major changes owing to human impacts and are now under threat (Clavero, Blanco-Garrido, & Prenda, 2004; Gasith & Resh, 1999; Marr et al., 2010, 2013; Moyle, Kiernan, Crain, & Quinones, 2013). Traits such as high endemism, restricted geographical distribution range and isolation in headwater

refugia increase the vulnerability of fishes to human induced stressors such as temperature and flow variations associated with changing climate, non-native species introductions, pollution and habitat alteration (Collares-Pereira, Cowx, Rodrigues, Rogado, & da Costa, 1999; Meyer et al., 2007; Moyle et al., 2013). As a result, many endemic fishes in Mediterranean climate regions are red-listed as Endangered or Critically Endangered by the International Union for Conservation of Nature (IUCN). For example, 60% of native freshwater fish species in South Africa's Cape Fold Ecoregion (CFR, Abell et al., 2008; Darwall, Smith, Tweddle, & Skelton, 2009) are either Endangered (EN) or

TABLE 1 Conservation status (IUCN Redlist status), distribution and main threats (0 = no dominant threat identified; 1 = alien fish; 2 = habitat destruction; 3 = pollution; 4 = utilization; 5 = genetic integrity) to freshwater fishes native to the Cape Floristic Region, South Africa (updated from Tweddle et al. (2009) and Weyl et al. (2014). Genera for former *Barbus* species follow Yang et al. (2015). NA – not formally assessed by the IUCN. The numbers against recognized species lineages refer to the italicized numbers in Figure 1.

(Species threats status)	Threats	Status	Distribution
<i>Austroglanis barnardi</i> (Skelton, 1981)	1,2	EN	Endemic to Olifants River system, specifically three tributary streams
<i>Austroglanis gilli</i> (Barnard, 1943)	1,2	VU	Endemic to Olifants River system
<i>Enteromius anoplus</i> (Weber, 1897)	0	LC	Widely distributed throughout South Africa
<i>Enteromius</i> sp. "pallidus south" ⁵	0	LC	Widespread across the eastern CFR from the Krom River in the west to the Great Fish River system in the east
<i>Galaxias zebratus</i> Castelnau, 1861	1,2,5	DD	Type locality uncertain and requires revision
1. <i>Galaxias</i> sp. "zebratus Breede" ⁴		NA	Hex, Bothaspruit and mainstem Breede River system
2. <i>Galaxias</i> sp. "zebratus Goukou" ⁴		NA	Goukou River system
3. <i>Galaxias</i> sp. "zebratus Heuningnes" ⁴		NA	Heuningnes and Ratel River systems
4. <i>Galaxias</i> sp. "zebratus Klein" ⁴		NA	Klein, Uilkraals and Ratel River systems
5. <i>Galaxias</i> sp. "zebratus Mollis" ⁴		NA	Onrus River system and Leeu River, Berg River system
6. <i>Galaxias</i> sp. "zebratus nebula" ⁴		NA	Widespread across the CFR from the Olifants River system in the west to the Bitou River system in the east
7. <i>Galaxias</i> sp. "zebratus Rectognathus" ⁴		NA	Amandel and Du Toit Rivers, Riviersonderend sub-catchment, Breede River system
8. <i>Galaxias</i> sp. "zebratus Riviersonderend" ⁴		NA	Tributaries of the Riviersonderend River and in the Keurbooms River, Breede River system. Also occurs in the Palmiet River system
9. <i>Galaxias</i> sp. "zebratus Slender" ⁴		NA	Uilkraals River system
<i>Labeo seeberi</i> Gilchrist & Thompson, 1911	1,2	EN	Endemic to Olifants River system, specifically (currently) the Doring River main stream
<i>Labeo umbratus</i> (A. Smith, 1841)	5	LC	East coast rivers from Gouritz to Bushmans rivers and the Orange/Vaal River system
<i>Labeobarbus seeberi</i> (Gilchrist and Thompson, 1913) ⁷	1,2,4	CVU	Endemic to Olifants River system
<i>Pseudobarbus afer</i> (Peters, 1864)	1	EN	Headwater tributaries of the Baakens, Swartkops and Sundays River systems
10. <i>Pseudobarbus</i> sp. "afer Forest" ¹	0	NT	East coast from Klein Brak to Tsitsikamma rivers
11. <i>Pseudobarbus</i> sp. "afer Gamtoos" ¹	1	EN	Headwater tributaries of the Gamtoos River system,
12. <i>Pseudobarbus</i> sp. "afer Krom" ¹	1	CR	Headwater tributaries of the Krom River system
<i>Pseudobarbus asper</i> (Boulenger, 1911)	1,2	EN	Mainstream reaches of the Gamtoos and Gourits River systems
<i>Pseudobarbus burchelli</i> Smith, 1841	1,2,3	CR	Tradouw River, Breede River system
13. <i>Pseudobarbus</i> sp. "burchelli Breede" ²	1,2	NT	Headwater tributaries of the Breede, Duiwenhoks and Goukou River systems
14. <i>Pseudobarbus</i> sp. "burchelli Heuningnes" ²	1,2	CR	Heuningnes River system
<i>Pseudobarbus burgi</i> (Boulenger, 1911)	1,2,5	EN	Endemic to the Berg River system
<i>Pseudobarbus phlegethon</i> (Barnard, 1938)	1,2	EN	Occurs in the Oudste, Thee, Noordhoeks, Boskloof and Rondegat tributaries of the Olifants River system
15. <i>Pseudobarbus</i> sp. "phlegethon Doring" ⁶	1	CR	Breekrans and Drieboeks tributaries of the Doring River, Olifants River system
<i>Pseudobarbus skeltoni</i> Chakona & Swartz, 2013	1	NA	Limited to two localities within the Breede River system (upper Riviersonderend and Krom rivers)
<i>Pseudobarbus tenuis</i> (Barnard, 1938)	1,2	NT	Headwater tributaries of the Gouritz River system
16. <i>Pseudobarbus</i> sp. "tenuis Keurbooms" ²	1,2	EN	Headwater tributaries of the Keurbooms and Bitou River systems
<i>Pseudobarbus verlorenei</i> Chakona, Swartz & Skelton, 2014 ³	1,2	EN	Verlorenvlei River system
' <i>Pseudobarbus</i> ' <i>capensis</i> (Smith, 1841) ⁶	1,2,4,5	EN	Endemic to the Berg and Breede River systems
' <i>Pseudobarbus</i> ' <i>calidus</i> (Barnard, 1938)	1,2	V	Endemic to the Olifants River system
' <i>Pseudobarbus</i> ' <i>erubescens</i> (Skelton, 1974)	1,2,3	CR	Endemic to the Olifants River system, specifically the Twee River and its tributaries
' <i>Pseudobarbus</i> ' <i>serra</i> (Peters, 1864)	1,2,4	EN	Endemic to the Olifants River system
<i>Sandelia capensis</i> (Cuvier, 1831)	1,2,5	DD	Type locality uncertain and requires revision
17. <i>Sandelia</i> sp. "capensis Breede" ⁴		NA	Tributaries of the Breede, Duiwenhoks and Goukou River systems
18. <i>Sandelia</i> sp. "capensis Agulhas" ⁴		NA	Heuningnes, Haelkraal and Klein River systems

(Continues)

TABLE 1 (Continued)

(Species threats status)	Threats	Status	Distribution
19. <i>Sandelia</i> sp. "capensis Klein" ⁴		NA	Klein River system
20. <i>Sandelia</i> sp. "capensis Koekedou" ⁴		NA	Titus and Koekedou, tributaries of the Breede River system
21. <i>Sandelia</i> sp. "capensis Riviersonderend" ⁴		NA	Tributaries of the Riviersonderend River, Breede River system

¹Swartz et al., 2007;

²Swartz et al., 2009;

³Chakona et al., 2014;

⁴Chakona, Swartz, & Gouws, 2013;

⁵Chakona, Malherbe, Gouws, & Swartz, 2015;

⁶Swartz et al. 2004;

⁷Vreven, Musschoot, Snoeks, & Schliewen, 2016.

Critically Endangered (CR) (Table 1); in the State of California USA, 80% of freshwater fish species are either extinct or threatened with extinction within 100 years (Moyle et al., 2013) and in the Iberian Peninsula in Europe, 52% of fish species are listed as CR, EN or vulnerable (VU) (Maceda-Veiga, 2013). Conservation action is therefore a high priority in these regions.

The Cape Fold aquatic ecoregion (Abell et al., 2008; Thieme et al., 2005) incorporates the drainages that flow off the Cape Fold mountains that are situated in the Mediterranean climate region along the southern fringe of the African continent (De Moor & Day, 2013). The area is best known for its exceptional diversity (9000 species) and endemism (69%) of vascular plants (Goldblatt & Manning, 2002) and aquatic biologists have often used the term Cape Floristic Region as a synonym for the Cape Fold Ecoregion (Marr, Sutcliffe, Day, Griffiths, & Skelton, 2009; Shelton, Samways, & Day, 2014; Weyl, Finlayson, Impson, Woodford, & Steinkjer, 2014). River basins in the Cape Fold Ecoregion are relatively small, and typically comprise geographically isolated, short, clear coastal rivers which descend rapidly from mountain ranges into the ocean. This historic isolation has resulted in exceptional levels of regional endemism in aquatic invertebrates, amphibians and fishes (Darwall et al., 2009). In particular, it is recognized as a hotspot of endemism for freshwater fishes, the majority of which are under severe threat of extinction (Skelton, 1990; Tweddle et al., 2009). Streams within this region are also subject to major human induced changes, including high levels of water abstraction, flow modifications (construction of weirs and impoundments) and widespread introduction of non-native invasive predatory fishes (Tweddle et al., 2009).

Based on recognized habitat discontinuities as well as the distribution of endemic freshwater fishes, Skelton (1980a) identified eight main catchments or biogeographic zones in the CFR, namely (1) Olifants, (2) Berg, (3) western Agulhas, (4) Breede and adjacent rivers, (5) Gourits, (6) south coastal rivers, (7) Gamtoos and adjacent rivers, and (8) Swartkops, Sundays and adjacent rivers. These catchments currently contain 21 formally described native freshwater fishes (Table 1). Accumulating evidence from DNA-based studies suggests that the taxonomic status of almost all CFR fishes studied thus far requires revision (Chakona, Swartz, & Gouws, 2013; Swartz, Chakona, Skelton, & Bloomer, 2014; Swartz, Flemming, & Mouton, 2004; Swartz, Skelton, & Bloomer, 2007, 2009; Waters & Cambray, 1997; Wishart, Hughes, Stewart, & Impson, 2006). Recent genetic work suggests that there are at least 42 genetically distinguishable fish lineages in the CFR

(Linder et al., 2010) with species-level divergence suggesting the existence of several species within the genera *Pseudobarbus*, *Galaxias* and *Sandelia* (Bloomer & Impson, 2000; Chakona, Swartz, & Gouws, 2013; Swartz et al., 2007, 2009; Wishart et al., 2006 Table 1). It is therefore likely that increased taxonomic survey effort in the region will result in new species descriptions as is demonstrated by the recent discovery and description of two new redfin species, *Pseudobarbus skeltoni* (Chakona & Swartz, 2013) and *Pseudobarbus verloreni* (Chakona, Swartz, & Skelton, 2014) from the CFR.

The current status of almost all endemic CFR fishes is influenced by their narrow distribution ranges. Only a few taxa have distribution ranges that span across geographically isolated river systems (Chakona, Swartz, & Chakona, 2015; Chakona, Swartz, Gouws, & Bloomer, 2013; Swartz et al., 2014; Chakona, Malherbe, Gouws, & Swartz, 2015) with most being narrow-range endemics that are either restricted to single river systems or even single tributaries within river systems (Chakona & Swartz, 2013; Chakona, Swartz, & Gouws, 2013; Chakona, Swartz, & Chakona, 2015) (Figure 1). Many of these taxa are highly fragmented, with remnant populations now confined to undisturbed and uninvaded mountain tributaries (Chakona, Swartz, & Gouws, 2013; Clark, Impson, & Rall, 2009; Ellender, Weyl, & Swartz, 2011). Survey data (Van der Walt, Weyl, Woodford, & Radloff, 2016) suggest that mainstem populations of many CFR endemics have been extirpated. The primary threats to the stream fishes of the CFR are non-native invasive fishes, while hydrological modifications and habitat degradation are also significant stressors (Ellender et al., 2011; Shelton et al., 2014; Tweddle et al., 2009; Weyl, Ellender, Woodford, & Jordaan, 2013; Weyl et al., 2014).

Effective conservation of threatened species requires accurate taxonomic classification and information on their ecology, life histories, distribution, abundance and physiological tolerances (Moyle et al., 2013). While Gaigher, Hamman, and Thorne (1980), Skelton, Cambray, Lombard, and Benn (1995), Skelton (1996) and Tweddle et al. (2009) provided overviews on the taxonomy, biogeography, distribution and conservation status of native fishes in the CFR, there has never been an in-depth appraisal of available published information. The lack of such information has been identified as one of the major factors impeding the implementation of effective conservation strategies as there is no basis for assessing potential responses of threatened taxa to environmental impacts (Moyle et al., 2013).

In the CFR, conservation efforts are based on the effective transferral of knowledge from data collected through scientific surveys

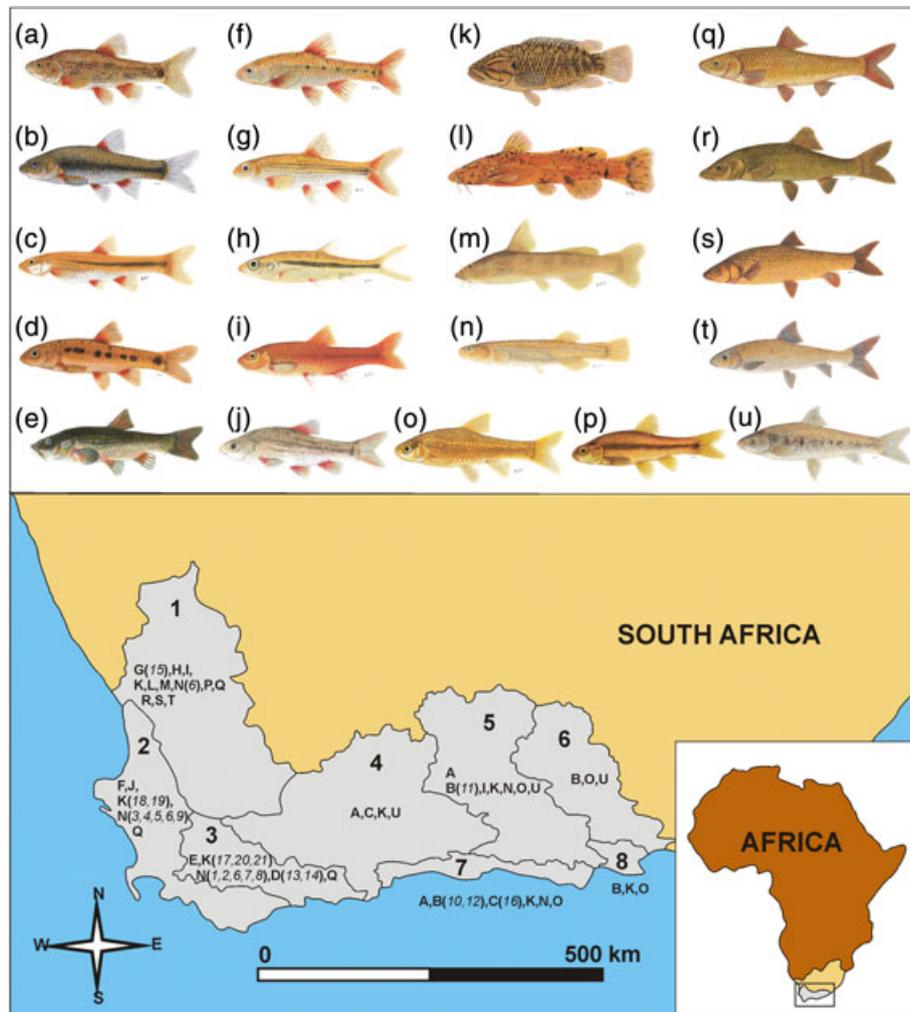


FIGURE 1 Distribution of described (letters) and undescribed (italicized numbers corresponding to Table 1) primary freshwater fishes in the eight river basins in Cape Fold Ecoregion. River basins: 1 = Olifants, 2 = Berg, 3 = Breede, 4 = Gouritz, 5 = Gamtoos, 6 = Sundays, 7 = Coastal drainages, 8 = Baakens. Fish: a = smallscale redfin (*Pseudobarbus asper*), b = Eastern Cape redfin (*P. afer*), c = slender redfin (*P. tenuis*), d = Burchell's redfin (*P. burchelli*), e = giant redfin (*P. skeltoni*), f = Berg River redfin (*P. burgii*), g = fiery redfin (*P. phlegethon*), h = Clanwilliam redfin (*'Pseudobarbus' calidus*), i = Twee River redfin (*'P. erubescens*), j = Verlorenvlei redfin (*P. verlorenei*), k = Cape kurper (*Sandelia capensis*), l = Barnard's rock catfish (*Austroglanis barnardi*), m = Clanwilliam rock catfish (*A. gilli*), n = Cape galaxias (*Galaxias zebratus*), o = goldie barb (*Enteromius pallidus*), p = chubbyhead barb (*E. anoplus*), q = whitefish (*'P. capensis*), r = sawfin (*'P. serra*), s = Clanwilliam yellowfish (*Labeobarbus seeberi*), t = Clanwilliam sandfish (*Labeo seeberi*), u = moggel (*Labeo umbratus*)

by academic institutions or national research facilities to conservation agencies. A good example of this was the collaborative effort to rehabilitate the Rondegat River whose native fishes had almost been completely extirpated from reaches invaded by smallmouth bass *Micropterus dolomieu*. Scientific institutions provided information on distribution, abundance and status of native fishes within the Rondegat River from their long-term monitoring programmes. This resulted in the proposal by Cape Nature, (the implementing agency) to eradicate *M. dolomieu* from invaded reaches of the Rondegat River using the piscicide rotenone. This was undertaken and subsequently no *M. dolomieu* have since been detected while native fishes are showing impressive recovery (Weyl et al., 2014).

For this reason, the present review is an exhaustive appraisal of published literature on the taxonomy, biogeography, life history, ecology and physiology of endemic and near endemic freshwater fishes in the CFR, and the human impacts that affect them. Its aim is to provide a benchmark of current knowledge to direct future research needs for

effective management and conservation of this imperilled group of fishes.

2 | LITERATURE REVIEW

An exhaustive literature review indicated that there are only 103 peer-reviewed articles on CFR fishes. Although some information is available as project reports (Paxton & King, 2009; Water Research Commission report) and research theses (Mthombeni, 2010; Paxton, 2008), these are largely outside the public domain. Before 1980 research predominantly focused on the taxonomy and biogeography of CFR fishes (Figure 2). This was most likely a consequence of the low interest in native species by anglers and the prioritization of non-native species for sport fisheries by the State (Ellender, Woodford, Weyl, & Cowx, 2014; Weyl et al., 2014). Observations that non-native sport fishes were having immense impacts on native species resulted in an increased interest in

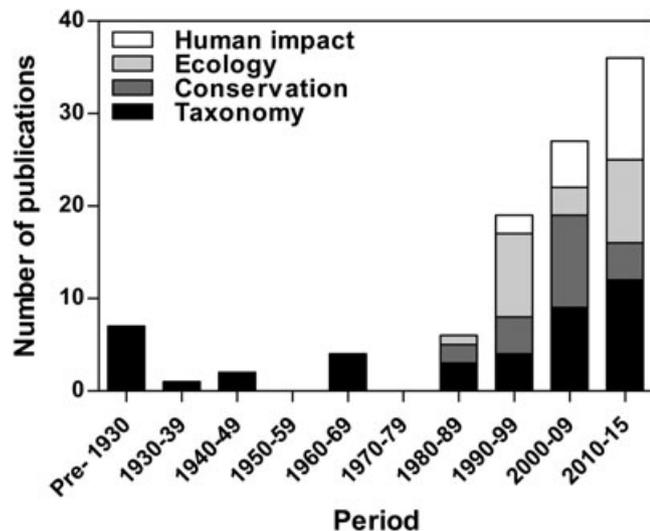


FIGURE 2 The number of peer-reviewed publications on Cape Fold Ecoregion (CFR) fishes by topic between 1822 and 2015

conservation-related research on native fishes. The need for a better understanding of the conservation status and ecology of native fishes and the impacts upon them appears to have driven an exponential increase in the publication rate observed from 1980 (Figure 2), and while most of the available research is on taxonomy and biogeography (40.8%), literature on ecological investigations (22.3%), conservation (19.4%) and human impacts (17.5%) is gaining ground. This is highlighted by the publication of the first life-history study on this group of fishes in 1985 (Cambray & Stuart, 1985), the first ecological investigation of fish ecology in 1990 (Cambray, 1990) and the presence of only two published manuscripts on the physiology of CFR fishes (Chakona, Swartz, & Magellan, 2011; Magellan, Pinchuck, & Swartz, 2014).

2.1 | Taxonomy and biogeography

The CFR has a low diversity of primary freshwater fishes, with only four families (Cyprinidae, Galaxiidae, Anabantidae and Austroglanidae) and 21 formally described species at present (Barnard, 1943; Chakona & Swartz, 2013; Chakona et al., 2014; Skelton, 1988, 2001) (Table 1). The taxonomic richness of individual river systems is low, ranging from zero to 10 species per system, with the majority of rivers that contain fish having only two to four species. Although the diversity of freshwater fishes in the CFR is much lower, this region has a distinctive fish fauna that differs from the rest of southern Africa and the continent (Skelton, 1986; Tweddle et al., 2009).

There is a long history of taxonomic research in the CFR. Written and illustrative records of the fishes of this region were reported soon after the first European settlers arrived in the 17th century (Gon & Skelton, 1997; Skelton & Skead, 1984). However, it was only in the early 19th century that the first species from the CFR was formally described (the Cape kurper *Sandelia capensis* (Cuvier, 1831) under the generic name *Spirobranchus*). This description was based on specimens in the National Museum of Natural History in Paris collected by Pierre Antoine Delalande and his nephew Jules Verreaux in the SW Cape around 1820 (Skelton & Swartz, 2011). Several CFR species were described by Sir Andrew Smith (1841) including the moggel (*Labeo*

umbratus), Clanwilliam yellowfish (*Labeobarbus seeberi*), Burchell's redbfin (*Pseudobarbus burchelli*), and the goldie barb, (*Enteromius pallidus*). Two extralimital species now invasive in the CFR were actually the first species to be described from South Africa also in the 1820s, i.e. the smallmouth yellowfish *Labeobarbus aeneus* and the sharptooth catfish *Clarias gariepinus* by Burchell (1822). To these extralimitals can be added *Tilapia sparrmanii* and *Labeo capensis*, described by Sir Andrew Smith (1841). Castelnau (1861) described *Galaxias zebratus* and the redbfin *Gnathendalia vulnerata* (now *Pseudobarbus burchelli*). Peters (1864) described *Pseudobarbus* (as *Barbus*) *afer* and '*Pseudobarbus*' (as *Barbus*) *serra*, two CFR cyprinid species from specimens collected by Ludwig Krebbs in the 1820s. An active collaboration between Dr George Boulenger at the British Museum (Natural History) and the scientists at the South African Museum, including Dr J.D.F. Gilchrist, resulted in a spike in CFR species descriptions leading to the catalogues of African freshwater fishes in both these institutions (Boulenger, 1911; Gilchrist & Thompson, 1913, 1917). The revision of the fishes of the south-western Cape (Barnard, 1938, 1943) was a thorough taxonomic revision of the fauna. Barnard (1943) described the first catfish from the CFR (*Austroglanis gilli*) and provided the first insight into the natural variation of the CFR species as well as circumscribing the geographic ranges of each species. Jubb (1965) likewise provided a focused review of Cape fishes, all of which was included in his overview of the freshwater fishes of southern Africa (Jubb, 1967).

Subsequent to these sound foundations, Skelton (1988) presented the most recent comprehensive taxonomic revision of a CFR freshwater fish lineage, focusing on the monophyletic cyprinid genus *Pseudobarbus* (commonly referred to as redbfins). In his revision, Skelton (1988) recognized six species of *Pseudobarbus* that are endemic to the CFR: *P. burchelli* Smith, 1841, *P. burgi* (Boulenger, 1911), *P. phlegethon* (Barnard, 1938), *P. tenuis* (Barnard, 1938), *P. asper* (Boulenger, 1911) and *P. afer* (Peters, 1864). Perhaps the most significant discovery regarding CFR fishes before the attention of molecular systematists was that the majority of CFR cyprinids were polyploid (Naran, Skelton, & Villet, 2006; Oellermann & Skelton, 1990; Tsigenopoulos, Rab, Naran, & Skelton, 2002).

Knowledge of the taxonomic diversity and the processes that promoted diversification and shaped distribution patterns of the CFR's freshwater fishes remains incomplete. While earlier studies assessed taxonomic diversity and the distribution of taxa based on phenotypic (morphological) characters (Barnard, 1943; Skelton, 1980a, 1980b, 1986, 1988, 1996), more recent research has relied on molecular markers to assess genetic diversity of stream fishes in the CFR (Bloomer & Impson, 2000; Chakona, Malherbe, Gouws, & Swartz, 2015; Chakona, Swartz, & Gouws, 2013; Chakona, Swartz, & Chakona, 2015; Roos, 2004; Swartz et al., 2007, 2009; Swartz et al., 2004; Waters & Cambray, 1997; Wishart et al., 2006). These studies have uncovered genetic differentiation within traditionally recognized species, indicating that earlier studies grossly underestimated biodiversity in the CFR (Linder et al., 2010). These findings have stimulated renewed interest in the taxonomy of freshwater fishes in this region.

Recently, two new species of redbfin minnows were described from the CFR, *Pseudobarbus skeltoni* (Chakona & Swartz, 2013) and *Pseudobarbus verloreini* (Chakona et al., 2014), and more species of *Pseudobarbus*, *Galaxias* and *Sandelia* await formal description (Chakona,

Malherbe, Gouws, & Swartz, 2015; Linder et al., 2010; Swartz et al., 2007, 2009). Molecular data have also suggested that generic changes may be warranted for some of the CFR fishes. For example, recent work by BurrIDGE, McDowall, Craw, Wilson, and Waters (2012) has revealed that *Galaxias zebratus*, at present the only galaxiid species recognized from South Africa, is not monophyletic with other *Galaxias* species. BurrIDGE et al. (2012) suggest that *G. zebratus* is more closely related to *Neochanna* from Australia and New Zealand. A comprehensive molecular phylogeny of the *Galaxias zebratus* group is currently being constructed to incorporate all the lineages recently identified and to determine the generic placement of the Cape *Galaxias* within a global context (Chakona pers. comm).

While the use of molecular approaches has enabled the discovery of hidden diversity, many of the newly identified lineages remain in taxonomic crypsis owing to the lack of taxonomic and systematic capacity to describe new species, not only in the CFR but in southern Africa as a whole (Skelton & Swartz, 2011). This 'taxonomic impediment' has ramifications for biodiversity conservation, ecology and biogeographic studies, because the species remains the basic unit and focal means of communication for these various fields of biological research that require accurate delimitation of species (Collares-Pereira, Skelton, & Cowx, 2016).

In addition to facilitating more accurate documentation of biological diversity, DNA-based studies are also providing valuable information about the processes that promoted diversification and shaped the distribution patterns of freshwater fishes in the CFR (Chakona, Malherbe, Gouws, & Swartz, 2015; Chakona, Swartz, & Gouws, 2013; Chakona, Swartz, Gouws, & Bloomer, 2013; Chakona, Swartz, & Chakona, 2015; Swartz et al., 2014, 2007, 2009). Drainage rearrangements and isolation by mountain ranges have largely been invoked as the predominant mechanisms that had a major impact on the diversity and distribution of freshwater fishes in multiple isolated river systems in the CFR (Barnard, 1943; Skelton, 1986). Although studies have found patterns consistent with expectations of river captures (Swartz et al., 2007), emerging patterns indicate that the evolutionary histories of CFR fishes have been more complex (Chakona, Malherbe, Gouws, & Swartz, 2015; Chakona, Swartz, & Gouws, 2013; Chakona, Swartz, Gouws, & Bloomer, 2013; Chakona, Swartz, & Chakona, 2015; Swartz et al., 2014, 2009). Findings from these studies suggest the role of alternative mechanisms, including inter-drainage dispersal through intermittent freshwater connections (Chakona, Swartz, Gouws, & Bloomer, 2013) and connectivity associated with sea-level changes (Swartz et al., 2014, 2007; Chakona, Swartz, Gouws, & Bloomer, 2013). In addition, some taxa (e.g. *S. capensis*) reflect a pattern consistent with human-assisted translocation (Chakona, Malherbe, Gouws, & Swartz, 2015; Chakona, Swartz, & Chakona, 2015). Such work indicates that the biogeographic patterns of the fish fauna of the CFR and biogeographic zones of Skelton (1980a) need to be re-evaluated incorporating new information from recent studies (Chakona, Malherbe, Gouws, & Swartz, 2015; Chakona, Swartz, & Gouws, 2013; Chakona, Swartz, Gouws, & Bloomer, 2013; Chakona, Swartz, & Chakona, 2015; Swartz et al., 2014, 2009).

Studies of the higher level lineages with representatives in the CFR, notably to date the cypriniform lineages (Yang et al., 2015) including *Labeobarbus* (Tsigonopoulos, Kasapidis, & Berrebi, 2010) and *Labeo* (Yang & Mayden, 2010), add to the growing body of

information about timing and diversification of the species and lineages and will inform the re-evaluation. The realization that there are no barbine elements in the Afrotropical realm is a particularly significant move forward (Yang et al., 2015) with considerable taxonomic implications. The finding by Yang et al. (2015) that most of the CFR cyprinids are members of a distinct polyploid (tetraploid) smiliogastrine lineage necessitates both new generic determination and biogeographic and evolutionary explanation. More clarification about the higher relationships of the galaxiid, siluriform and anabantid lineages is needed to complete this understanding.

2.2 | Life history

Autecological and ecological work on the CFR fishes is relatively scant. Most life-history related research on CFR fishes has been done on cyprinids. For the purposes of this review these are discussed in two groups: small-bodied minnows and large cyprinids.

2.2.1 | Small-bodied minnows

Life-history data are available for five minnow species: '*Pseudobarbus erubescens*, *P. afer*, *P. asper*, *P. phlegethon* and *P. burchelli*, but available data differ between species. *Pseudobarbus asper* inhabits turbid main-stream sections of the Gamtoos River system located in the arid Karoo region where flows and environmental conditions are highly variable (Cambray, 1990, 1991). The other four species inhabit headwater to lower foothill reaches of clear fold-mountain streams. All spawn in spring to early summer (Cambray & Stuart, 1985; Cambray, 1994b; Impson, Marriott, Bills, & Skelton, 2007; Whitehead, Weyl, & Bills, 2007) and histological data suggest that at least '*P. erubescens* and *P. phlegethon* are serial spawners (Impson et al., 2007; Whitehead et al., 2007) and maturity is attained early in life (ages 1–2 years) at 35–50% of maximum length. Fecundity varies between species and absolute fecundity has been estimated as 3922 ova per fish for *P. afer* (73 mm SL), 4771 ova per fish for *P. afer* (64 mm SL) and 10678 ova per fish for *P. burchelli* (123 mm SL) (Cambray & Stuart, 1985; Cambray, 1994b). Longevity has been estimated at between 3 years (*P. asper*) and 6 years (*P. erubescens*, *P. afer* and *P. burchelli*) using scales (Cambray & Stuart, 1985; Cambray & Hecht, 1995; Impson et al., 2007). For *P. burchelli* and *P. afer*, females have been shown to grow faster and live longer than the males (Cambray & Stuart, 1985; Cambray & Hecht, 1995).

Comparative research on the sympatrically occurring *P. afer* and *P. asper* highlights some of the life-history adaptations to different environmental conditions (Cambray, 1991; Cambray, 1994a, b; Cambray & Bruton, 1994; Cambray & Hecht, 1995). In the Gamtoos River system, *P. afer* inhabits clear mountain streams while *P. asper* inhabits more turbid low-gradient streams (Cambray, 1994a, b, 1994c). These habitat preferences are reflected in the morphology of the two species whereby *P. afer* has larger neural structures related to vision than *P. asper* (Cambray, 1994d). *Pseudobarbus afer* are also slower growing, live longer and mature later than *P. asper* (Cambray & Hecht, 1995). Cambray (1994a) also demonstrated that the two *Pseudobarbus* species have contrasting sex ratios, with *P. afer* demonstrating female-biased and *P. asper* male-biased sex ratios. The adaptive significance of these differences in life-history traits are thought to be related to environmental stability, with *P. afer* inhabiting

more stable perennial streams, while *P. asper* occupies episodic environments (Cambray, 1994a, b).

Similarly, the reproductive strategies of *P. afer* and *P. asper* reflect the stability in their respective habitat preferences. Nuptial tubercles are present in both species during the reproductive season (Cambray, 1994c). *Pseudobarbus afer* males, however, have larger and more numerous tubercles than *P. asper* males, and since the former species is more closely associated with clear-water environments, this suggests that visual stimuli are more important for *P. afer* than *P. asper* (Cambray, 1994c). *Pseudobarbus afer* and *P. asper* were found to be multiple spawners with the former spawning over a 4–5 month and the latter a 6–7 month period, both peaking in October–November (Cambray, 1994b). *Pseudobarbus afer* has larger ova than *P. asper* with the eggs of *P. asper* hatching faster than those of *P. afer* (Cambray & Bruton, 1994; Cambray & Hecht, 1995). Both species, however, have been identified as open substrate benthic spawners that lay their eggs in rocky bottom habitats and practise no guarding of their non-adhesive eggs (Cambray, 1994b). The young of both *P. afer* and *P. asper* were found to be photophobic during the first few days of the free embryo stage of their life histories, becoming photophilic by days five and four respectively (Cambray, 1994b). Days to first feeding also differed between the two species, with *P. asper* feeding after only 7 days and *P. afer* after 10 days. The survival of *P. afer* larvae was also shown to be linked to the size at first feeding, with larger individuals more successful than smaller fish (Cambray & Bruton, 1994; Cambray & Hecht, 1995). Diet has been studied in detail in three species (*P. erubescens*, *P. phlegethon* and *P. burchelli*) all of which are benthic insectivores (Cambray & Stuart, 1985; Impson et al., 2007; Whitehead et al., 2007). In addition, *P. phlegethon* were found to feed predominantly on chironomids (Whitehead et al., 2007).

2.2.2 | Large cyprinids

There are few peer reviewed publications on the life history of the larger cyprinids '*Pseudobarbus capensis*', *Labeo seeberi*, *Labeobarbus seeberi* and '*Pseudobarbus serra*'. However, research published in technical reports (Paxton & King, 2009; van Rensburg, 1966) is worth including here. *Labeobarbus seeberi*, '*Pseudobarbus capensis*' and '*P. serra*' are omnivorous, feeding primarily on aquatic macro-invertebrates and algae, while *Labeo seeberi* feeds on algae, diatoms and microscopic crustacea (van Rensburg, 1966). All large cyprinids appear to undertake spawning migrations in spring and early summer. While these spawning behaviours have not been assessed for '*P. capensis*' and *Labeo seeberi*, good descriptions are available for *L. seeberi* and '*P. serra*' (Gore, King, & Hamman, 1991; Paxton & King, 2009) which undertake upstream spawning migrations from deep, more structurally complex, habitats occupied in late summer–winter to shallow, temporally variable feeding and spawning habitats in spring and summer. Length at maturity has not been formally assessed for any of the large cyprinids but observations of spawning runs suggest that maturity occurs at between 20 and 30 cm FL (Cambray, 1999; Paxton & King, 2009).

Paxton and King (2009) demonstrated that, like *L. seeberi* (Cambray, King, & Bruwer, 1997; Cambray, 1999), '*P. serra*' are non-guarding, open substratum spawners, selecting riffles and runs with loosely embedded gravel, cobble and boulder substrata,

significantly shallower water and faster current speeds than non-spawning adults. Both species are repeat spawners that spawn over several days during each spawning bout, as well as multiple spawners throughout the 4-month reproductive season (Cambray et al., 1997; Paxton & King, 2009; van Rensburg, 1966).

There appear to be differences in spawning strategy, however, because although the eggs of both *L. seeberi* and '*P. serra*' are negatively buoyant, those of *L. seeberi* are non-adhesive (Cambray, 1999) while those of '*P. serra*' are adhesive (Paxton & King, 2009). The eggs of both species hatch out within 2–3 days and larvae remain in the river bed for 10–12 days (Cambray et al., 1997; Paxton & King, 2009). In the Doring River tributary of the Olifants River, Paxton and King (2009) observed that '*P. serra*' larvae and early juveniles occupied shallow slow-flowing marginal slack-waters as nursery areas, but at an age of about 30 days juveniles began exhibiting schooling behaviour and migrated several kilometres downstream. Paxton and King (2009) also reported on differences between species, whereby young-of-year (YOY) '*P. serra*' selected bedrock-dominated reaches, and juvenile *L. seeberi* selected riffles with higher current speeds over gravel and cobble.

Juvenile growth for '*P. serra*' was assessed based on validated daily growth zone deposition on otoliths by Paxton and King (2009). The relationship between age and length for YOY fish in the Doring River differed between 2004/2005 (TL mm = 0.3651 [age] + 7.0) and 2005/2006 (TL = 0.4413 [age] + 5.1055). Van Rensburg (1966) used scales to estimate age of *L. seeberi* and '*P. serra*' and based on the assumption of the deposition of annuli demonstrated that the two species were slow growing (*Labeobarbus seeberi* length at age 1 = 9 cm; 5 = 34 cm; 10 = 49 cm; '*P. serra*' age 1 = 9 cm, 2 = 25 cm; 10 = 39 cm).

2.3 | Ecology and behaviour

The ecological investigations on fish in the CFR are more representative than the life-history assessments (Cambray, 1990; Cambray, 1994c, 1994d; Cambray, Bok, & Smith, 1995; Chakona & Swartz, 2012; Clark et al., 2009; Ellender & Weyl, 2015; Kadye & Booth, 2012, 2014; Lowe & Skelton, 2008; Magellan, 2015; Magellan & Swartz, 2013). Work conducted on *Galaxias 'nebula'*, a recently identified lineage of the *Galaxias zebratus* complex, showed that this lineage has adaptations that may be used for respiration outside of water (Chakona et al., 2011; Magellan, 2015; Magellan et al., 2014). Its ability to withstand short- and long-term aerial exposure is thought to have implications for its distribution (Chakona et al., 2011; Chakona et al., 2013; Magellan et al., 2014) and these fish have now been observed voluntarily moving from water in unfamiliar environments in the direction of alternative water bodies (Magellan, 2015, 2016). In addition, Magellan and Swartz (2013) showed that *Galaxias 'nebula'* exhibit polymorphic colour patterns that are non-interchangeable but with elements of disruptive colouration and background pattern matching. These findings were all related to predation threat and the persistence of the species in small streams (Chakona et al., 2011; Magellan, 2015; Magellan & Swartz, 2013; Magellan et al., 2014).

A few studies have investigated behavioural and activity patterns in the *Pseudobarbus* group. Two studies have investigated their movements in relation to flooding events, with Cambray (1991) showing that *P. asper* used a flood as an opportunity to migrate upstream in

the Gamtoos River system. More recently, Ellender and Weyl (2015) found that an unpredictable high magnitude flood did not result in downstream displacement of *P. afer* in the Swartkops River system. Kadye and Booth (2012) investigated seasonal population dynamics and habitat preferences of *P. afer* and reported that the species displayed an affinity for large boulders in stream environments. Diel activity patterns of *P. afer* were investigated by Kadye and Booth (2014), who suggested that this minnow was mostly diurnal in activity and postulated that this behaviour was a result of predator avoidance as the only indigenous fish predator in the headwaters of their study area was nocturnal. The only other behavioural work conducted on the genus was by Lowe and Skelton (2008), who showed that *P. burchelli* is capable of sound production. These authors suggested that auditory communication is an aspect of the ecology of this group that should be considered further and may have implications for territoriality and reproductive success within the genus (Lowe & Skelton, 2008). There are few broader-scale studies on factors influencing distribution at a landscape level.

Chakona and Swartz (2012) found that there were significant differences in environmental drivers for three genetic lineages of CFR fishes, *Sandelia* spp., *Pseudobarbus* 'Breede' and *Galaxias* 'nebula'. *Pseudobarbus* 'Breede' distributions were influenced by stream width and temperature, *Sandelia* spp. was limited by elevation, while occurrence of *Galaxias* 'nebula' was mainly influenced by stream size and depth (Chakona & Swartz, 2012).

2.4 | Physiology

Only one study has investigated physiology of CFR fishes, with Magellan et al. (2014) assessing strategies that facilitate aerial exposure in *Galaxias* 'nebula'. In this study the authors suggest that *Galaxias* 'nebula' uses contraction of abdominal cutaneous pores to cope with short-term aerial exposure, while thickening of epithelial layers of the secondary gill lamellae is a strategy that facilitates longer-term exposure (Magellan et al., 2014). The only other study that is relevant in this regard, albeit not fundamentally physiological in nature, was the work by Chakona et al. (2011) who assessed *Galaxias* 'nebula' opercular movement (as a proxy for gill ventilation rates) in relation to aerial exposure. The lack of physiological information on CFR fishes is a major gap inhibiting assessment of the potential impacts of projected climate change on the distributions of CFR fishes.

2.5 | Human impacts

A study by Clark et al. (2009) that investigated landscape level changes in assemblage structure and distributions of fishes in the Berg river system exemplifies the multitude of stressors in CFR rivers and their impacts on native fishes. Human impacts are widespread in the Berg River system and include large-scale land transformation, invasion by non-native plant species, modification of the natural flow regime of the river, changes to water chemistry, siltation, and introduction of non-native fish species (Clark et al., 2009). The large cyprinid '*P. capensis*' that was historically common in the Berg River system is now thought to have been extirpated (Clark et al., 2009). The distribution ranges of the Berg River redbfin *Pseudobarbus burgi*, Cape kurper

Sandelia capensis and Cape galaxias *G. zebratus* which were historically widespread and common throughout the river system have severely contracted. Remnant populations are now confined to relatively unaffected upper reaches of tributaries, usually above barriers that prevent invasion by non-native fishes (Clark et al., 2009). Accumulating evidence from continuing studies shows a similar pattern for many river systems across the CFR (Ellender et al., 2011; Weyl et al., 2013, 2014) and South Africa (Ellender & Weyl, 2014). Often these impacts occur simultaneously and it is therefore very difficult to tease apart causal factors of native fish declines.

South Africa is a water scarce country and as a result flow modifications such as impoundments, weirs or agricultural offtakes are common components of most river systems (Ashton, 2007). Little research has been undertaken, however, on the impacts of hydrological modifications on native fish communities in the CFR. Cambray (1990) documented that at a single small agricultural water offtake from Beervlei Dam on the Groot River, Gamtoos River system, up to 131 smallscale redbfin minnows *Pseudobarbus asper* were removed from the system by the water off-take every 5 minutes and therefore unable to survive. Instream barriers were also found to be an effective obstacle to upstream migrations of *P. asper* in the Groot River, Gamtoos River system (Cambray, 1990). The Groot River is ephemeral in nature and periodically dries up making *P. asper* reliant on refuge pools during dry periods (Cambray, 1990). There may be important adaptive significance, therefore, to these migrations as access to refuge pools during dry periods is vital for the long-term persistence of this species.

Evidence of flow release impacts on native fish spawning has been documented for *P. asper* from the Gamtoos River system and *Labeobarbus seeberi* from the Olifants River system. *Labeobarbus seeberi*, similar to other riverine cyprinids globally, is reliant on high flows for successful spawning. However, unlike other regions that receive summer rainfall, the CFR receives its rainfall in winter but the winter photoperiod and low temperatures inhibit spawning of *L. seeberi* (Cambray et al., 1997). This species therefore spawns during the dry season (summer) and relies on sporadic rainfall that results in flow pulses which trigger spawning (Cambray et al., 1997; King, Cambray, & Impson, 1998). Such reliance on summer flow pulses may be heavily influenced by instream barriers or dams that may alter the magnitude and frequency of these pulses. Cambray et al. (1997) conducted an experimental study on the impact of impoundments on *L. seeberi* spawning in the Olifants River in the CFR. Experimental pulses released from Clanwilliam Dam resulted in heightened spawning activity and good survival of larvae and juveniles (Cambray et al., 1997). During the same study period, hypolimnetic cold water pulses (16–18°C) did not result in an initiation of spawning activity, while during epilimnetic warmer water pulses (19–21°C) fish aggregated on the spawning beds and thereafter free embryos and larvae were recorded (King et al., 1998). Similarly, controlled releases from the Beervlei Dam on the Gamtoos River system induced spawning of *P. asper*, but there is no information on subsequent recruitment success (Cambray, 1991).

While flow modifications and instream artificial barriers have implications for reproduction and migration of native fishes, recent research by Van der Walt et al. (2016) has shown the role of these barriers in limiting upstream invasion by predatory non-native

centrarchid fishes in the Olifants River system, and ultimately protecting many native fish populations that are isolated by these barriers in headwater refugia from extinction. Impacts by predatory non-native fishes are considered the primary threat to all but one of the endemic and near endemic CFR species (Skelton, 1987; Tweddle et al., 2009; Weyl et al., 2014). Despite this threat fewer than 10 studies have investigated impacts empirically. This mirrors the general lack of studies on impacts by non-native fishes on native fauna in South Africa (Ellender & Weyl, 2014). The evidence that does exist, however, suggests that these impacts may be considerable.

Most studies document the complete absence or reduced abundance of native fishes in reaches invaded by predatory non-native fishes. In the Blindekloof stream where non-native centrarchid fishes (largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*) occur, small-bodied native fishes (Cape kurper *S. capensis*, Eastern Cape redfin *P. afer*, river goby *Glossogobius calidus*) were absent (Ellender et al., 2011). In the Witte River, Shelton et al. (2014) documented absence or greatly reduced abundances of Breede River redfin *P. burchelli*, and *S. capensis* in stream reaches invaded by *M. dolomieu*. A longer-term dataset from the Rondegat River had similar findings where Clanwilliam redfin '*Pseudobarbus*' *calidus*, fiery redfin *P. phlegethon* and Clanwilliam rock catlets *A. gilli* were absent from reaches invaded by *M. dolomieu*; however, the large Clanwilliam yellowfish *L. seeberi* co-exists with *M. dolomieu* as adults but no juveniles were recorded in invaded reaches (Weyl et al., 2013, 2014; Woodford, Impson, Day, & Bills, 2005). The mechanism for the decreased abundance or absence at invaded sites is most likely predation, and results from a study by Shelton et al. (2014) on the impacts of rainbow trout *Onchorynchus mykiss* on native fishes from field and experimental data demonstrate this. Native fish (*P. burchelli*, *S. capensis*, and *G. zebratus*) were absent or their abundances were 89–97% reduced in invaded streams compared with non-invaded replicates, and the field experiment showed that *O. mykiss* selectively consume small *P. burchelli*.

Only two studies have recorded the competitive non-lethal impacts of non-native fishes. In the Berg River, *G. zebratus* were absent from pools invaded by *O. mykiss* but inhabited nearby backwaters, while *P. burgi* juveniles were separated from *O. mykiss* on a depth gradient (Woodford & Impson, 2004). In the Driehoeks River, a headwater tributary of the Olifants River system, *G. zebratus* selected deeper, faster-flowing microhabitats where *M. salmoides* was present and shallower slower-flowing habitats where absent (Shelton, Day, & Griffiths, 2008). Avoidance behaviour is more common in perennial streams of the CFR, such as the Berg and Driehoeks rivers. In the more episodic systems such as the Blindekloof stream, a headwater tributary of the Swartkops River system, during prolonged dry periods native fishes are isolated in small refuge pools with non-native predators, resulting in local extirpation (Ellender et al., 2011).

A major threat to CFR fishes is invasion of headwater refugia. In many cases centrarchids invade upstream until their progress is limited by instream barriers (Van der Walt et al., 2016). Other species are either introduced into the headwaters (trout) or display higher capabilities to penetrate native fish refugia. A study by Kadye and Booth (2012) predicted that the probability of invasion

by non-native African sharp-tooth catfish *Clarias gariepinus* decreased from the mainstem Great Fish River to the headwater tributaries. This is in agreement with findings from Ellender, Woodford, and Weyl (2015) who showed that although *C. gariepinus* did invade headwater tributaries, it was unlikely to become established and invasions were casual and originated from mainstem source populations.

3 | INTERVENTIONS, MANAGEMENT AND CONSERVATION IMPLICATIONS

In response to the imperilment of CFR fishes, plans for remediation have either been proposed or undertaken. Owing to the paucity of knowledge on the impacts of other stressors such as pollution, water abstraction or habitat degradation on CFR fishes, the only remedial conservation actions so far in the region have been eradication of non-native fishes to increase native fish range or provide sanctuaries for imperilled fishes (Weyl et al., 2014). As non-native fishes are considered the primary threat to the survival of native fishes in the CFR, a pilot project has begun that proposed the removal of non-native fishes using the piscicide rotenone (Marr, Impson, & Tweddle, 2012) in selected reaches of four CFR rivers: Olifants River system, Western Cape - Rondegat River - eradicate *M. dolomieu* to facilitate the recovery of '*P. calidus*, *P. phlegethon*, *L. seeberi* and *A. gilli*; Krom River - eradicate *O. mykiss* to facilitate the recovery of *Pseudobarbus* sp. ('*phlegethon* Doring'), '*P. calidus* and *A. gilli*; Suurvlei River - eradicate translocated non-native *S. capensis* to facilitate the recovery of Twee River redfin '*Pseudobarbus*' *erubescens* and an undescribed taxon of *Galaxias*; Krom River system, Eastern Cape - eradicate largemouth bass to facilitate the recovery of two undescribed taxa, Krom River redfin *Pseudobarbus* sp. ('*afer* Krom') and a *Galaxias* lineage.

In the Rondegat River two successive treatments were undertaken 1 year apart (2012, 2013) and a 2.5 km section of the river was treated with rotenone. *Micropterus dolomieu* had previously extirpated three native species ('*P. calidus*, *P. phlegethon* and *A. gilli*) and the fourth *L. seeberi* were only present as adults below a waterfall barrier that inhibited upstream dispersal of *M. dolomieu* (Woodford et al., 2005; Weyl et al., 2013, 2014). This application was successful as after the second treatment no *M. dolomieu* were detected. While CFR fishes do not display high resistance to non-native fish invasions, the natural recovery (from non-invaded upstream sources) of native fishes following the removal of *M. dolomieu* from the Rondegat River indicate that resilience may be high. In the two successive years following the removal of *M. dolomieu*, the recruitment of juvenile and sub-adult '*P. calidus*, *P. phlegethon* and *L. seeberi* has been high and native fish densities have increased from 0.68 ± 0.33 fish per 100 m^2 before treatment in 2012 to 9.6 ± 7.0 fish per 100 m^2 after the first treatment (Weyl et al., 2013) and 38.7 ± 7.0 fish per 100 m^2 after the 2013 treatment (Weyl et al., 2014). This is now considered a flagship restoration project in South Africa and a prime example of the positive impacts of remediation projects executed in areas where eradication is logistically feasible, re-invasion is unlikely and the recolonization of native fishes can occur naturally from non-invaded stream reaches upstream (Weyl et al., 2014).

4 | CONCLUSIONS AND FUTURE RESEARCH NEEDS

It is evident from this assessment of the available literature that the increase in molecular studies during the last two decades has changed the way the CFR is viewed. The fish fauna of this region was previously thought to be rather depauperate, but recent evidence shows severe underestimation of the taxonomic diversity of endemic stream fishes and a number of previously recognized species that were thought to have wide ranges are now known to occur only in single river systems or short reaches within many systems. This has a major impact on conservation status assessments as many of these fishes are under greater threat than previously thought.

There is renewed interest in reviewing the taxonomy of stream fishes of this region, although limited taxonomic capacity and expertise remains a major impediment. The use of molecular techniques has also improved an understanding of the factors that promoted diversification and shaped contemporary distributions of stream fishes of the CFR. There is a need for more comparative studies incorporating other co-distributed taxa such as invertebrates to test biogeographic and phylogeographic hypotheses proposed by Swartz et al. (2007, 2009, 2014), Chakona, Swartz, and Gouws (2013) and Chakona, Swartz, Gouws, and Bloomer (2013).

Information on the biology, ecology and physiology of CFR fishes is limited to studies on selected species. Life-history assessments are only available for a few species and most of these studies have investigated only one or two aspects of their life history, such as reproduction or diet, and do not include a comprehensive assessment. Information on aspects of the ecology of CFR fishes is also sparse with much scope for future work. Some of the more obvious ecological investigations lacking are those assessing fish movements or migrations, interactions among CFR fishes and behavioural studies, but of particular note is the lack of physiological information. Physiological and eco-physiological studies may provide insight into CFR fish response to environmental perturbations and threats such as changing climates and pollution.

Human impacts severely threaten the existence of many native CFR fishes. In particular, the impacts of invasive non-native fishes on native fishes has been relatively well documented and these can cause considerable changes to assemblage composition, abundance, behaviour and distribution of native fishes. Most of these assessments are limited to assessments at river-reach scale; therefore, quantifying impacts at landscape level should be a future research priority. Little research has also been undertaken on impacts of impounding rivers and altering flow regimes. Studies on two fishes, *L. seeberi* and *P. asper*, suggest that altered flow regimes and damming may have impacts on spawning, recruitment success and migrations of these species; however, further work on a more comprehensive suite of CFR fishes is necessary. Other human impacts such as pollution, habitat degradation through abstraction or bad land-use practices have not been assessed and require urgent attention.

Aquatic faunas in Mediterranean climates around the world are under threat (Moyle & Leidy, 1992). Given that the fish assemblages in these regions are often highly endemic, these ecoregions have been

flagged as conservation priorities (Moyle et al., 2013), but limited information often impedes conservation action (Clavero et al., 2004; Moyle et al., 2013). The CFR ecoregion is no exception, and this review has highlighted the paucity of information and the major gaps in knowledge with the aim of directing focus on future research needs.

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