

Review

A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa

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Abstract

The introduction and spread of non-native species is one of the least reversible human-induced global changes. In South Africa, non-native fish introductions have occurred over the last two and a half centuries. Resultant invasions have been cited as a primary threat to imperilled South African fishes and other aquatic fauna. Addressing a problem of this magnitude requires an organised approach. The aim of this paper is to summarise the current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. A total of 55 fishes have been introduced into novel environments in South Africa. Of these, 27 were alien and 28 were extralimital introductions. Only 11 introduced species failed to establish and of the 44 species that have established, 37% are considered fully invasive. Introductions for angling were responsible for the highest proportion (55%) of fully invasive species with the remainder linked to inter-basin water transfers (15%), bio-control (15%), ornamental fish trade (10%) and aquaculture (5%). There was a general paucity of published literature on the introduction, establishment and spread of non-native fishes, and recent research has largely focused on impacts on native biota. While documented impacts spanned multiple levels of biological organisation, most papers focused on individual and population level impacts. Large taxonomic biases were also observed, and invasive impacts were estimated for less than 50% of fully invasive fishes. There is also an extensive knowledge gap on the impacts of associated parasites and diseases introduced with non-native fishes. These knowledge gaps constrain effective management of non-native fishes in South Africa and research at all invasion stages (introduction, establishment, spread and impact) is necessary to guide conservation practitioners and managers with information to manage current invasions and curb future introductions.

Key words: alien fish, establishment, invasion, invasive impact, spread

Introduction

Globally, the introduction of non-native fishes for aquaculture, fisheries and the pet trade is increasing (Gozlan et al. 2010). Although these introductions have often achieved their desired economic objectives (Gozlan 2008), subsequent invasions and the resultant homogenization of biota (Clavero and García-Berthou 2006; Rahel 2007) are considered “one of the least reversible human-induced global changes” (Kolar and Lodge 2002). Whether the impacts of these introductions are positive or negative is context dependent (Gozlan 2008; Vitule et al. 2012; Ricciardi et al. 2013) and has been the source of much debate (e.g. Gozlan 2008; Vitule et al. 2009; Simberloff and Vitule 2013; Valéry et al.

2013). Research on the impacts of non-native fishes is therefore important for developing solutions to a difficult conservation problem (Cucherousset and Olden 2011; Richardson and Ricciardi 2013). Ecologically, impacts span multiple levels of biological organisation ranging from genes to ecosystems and although there is extensive literature on fish invasions and their impacts (Gozlan 2008; Gozlan et al. 2010; Cucherousset and Olden 2011), much still needs to be learnt, particularly in poorly studied geographical regions (Cucherousset and Olden 2011).

In South Africa, one of six global fish invasion hotspots (Leprieur et al. 2008), non-native fishes are common components of fish assemblages in all major river systems (van

Rensburg et al. 2011). Two significant publications in the mid 1980s synthesised literature on non-native aquatic species in South Africa. The first was a review on faunal invasions of aquatic ecosystems of southern Africa (Bruton and Van As 1986) and the second an ‘*Atlas of Alien and Translocated Indigenous Aquatic Animals in southern Africa*’ (de Moor and Bruton 1988). Both these publications greatly enhanced the knowledge of aquatic invasions of South Africa by summarising an extensive body of grey and peer-reviewed literature into a usable format. More recent literature has only provided an overview of fish invasions and their impacts in South Africa (Richardson et al. 2010; van Rensburg et al. 2011).

The major vectors for introductions of non-native fishes in South Africa were primarily associated with recreational angling, aquaculture, conservation translocations, ornamental fish trade, inter-basin water transfer schemes (IBTs) and bio-control (Bruton and Van As 1986). These introductions resulted in the establishment of several non-native fishes in the wild with concomitant impacts on native biota (Bruton and Van As 1986; van Rensburg et al. 2011). Early impacts were predominantly inferred from grey literature and included reports that direct predation on and competition with native fishes by non-native rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) and largemouth bass *Micropterus salmoides* (Lacepède, 1802) had resulted in the local extirpations of small native fishes including fiery redbfin *Pseudobarbus phlegethon* (Barnard, 1938), Berg River redbfin *P. burgi* (Boulenger, 1911), Maloti minnow *P. quathlambae* (Barnard, 1938), Breede River redbfin *P. burchelli* Smith, 1841, Clanwilliam redbfin *Barbus calidus* Barnard, 1938, Border barb *B. trevelyani* Günther, 1877, Treur River barb *B. treurensis* Groenewald, 1958, Cape kurper *Sandelia capensis* (Cuvier, 1829), Eastern Cape rocky *S. bairnsii* Castelnau, 1861, rock catlet *Austroglanis gilli* Barnard and Kneria *Kneria auriculata* (Pellegrin, 1905). Extralimital introductions of redbreast tilapia *Tilapia rendalli* (Boulenger, 1896) were reported to decrease aquatic macrophyte densities and the potential for hybridisation between introduced and native *Oreochromis* species was recognised (de Moor and Bruton 1988). However, a review of the literature on impacts of invasive fishes in South Africa (Bruton and Van As 1986), revealed that the examples of invasive impacts from early literature were mostly based on casual observations. For

example, statements in survey reports such as: “*What was very apparent, however, was that nowhere where there was an established population of exotics could endemic species be found*” (Gaigher 1973, p 76), when referring to an ichthyofaunal survey undertaken of the Olifants River system, Western Cape, were cited as proof of impacts.

While such observations are valuable, there is an increased need for empirical research on all facets of the invasion process in order to inform non-native species management and develop effective legislation (van Rensburg et al. 2011). It is therefore apt that more than a quarter century after the previous review (Bruton and Van As 1986), an update on the introduction, status and impacts of non-native fishes is provided. This is the purpose of the current review.

Materials and methods

An exhaustive literature search was conducted for the period 1988–2013 so as not to repeat what has already been summarised in previous invasion reviews (Bruton and Van As 1986; de Moor and Bruton 1988), and to focus instead on recent advances in the field. All publications including any aspect of the Blackburn et al. (2011) unified framework for biological invasions (transport, introduction, establishment and spread) or documenting ecological impacts were included. For the purpose of this review, alien species are defined as those that have been introduced from outside the political boundaries of South Africa. Extralimital species are species native to South Africa that have been translocated into areas where they did not naturally occur. Both alien and extralimital fishes will henceforth be referred to as non-native fishes.

The ‘*Atlas of southern African freshwater fishes*,’ was used as a baseline for presence/absences (Scott et al. 2006). Where data were considered deficient, additional updated records from the national fish collection distributions database were acquired (housed at the South African Institute for Aquatic Biodiversity). Publications with updated species lists between 2006 and 2013 were also reviewed and in some cases expert opinion from researchers whom had conducted recent surveys were consulted. The status of each non-native fish species was then evaluated using the criteria outlined in Blackburn et al. (2011) and presented in Table 1.

Table 1. A list of the non-native (alien and extralimital) species that have been introduced and translocated in South Africa between 1726 and 2013 (ANG = angling; CON = conservation; AQU = aquaculture; ORN = ornamental; IBT = Inter-basin water transfer; BCT = Bio-control) (Bruton and Merron 1985¹; de Moor and Bruton 1988²; Cambray 1997³; Impson and Tharme 1998⁴; Skelton 2001⁵; Scott et al. 2006⁶; O'Brien et al. 2012⁷; Jones et al. 2013⁸; Mäkinen et al. 2013⁹). Invasion category defined according to Blackburn et al. (2011)*.

Species	Date	Vector	Origin	Status	Category
<i>Austroglanis sclateri</i> (Boulenger, 1901)	1975 ²	IBT	Extralimital	Uncertain	C1
<i>Barbus anoplus</i> Weber, 1897	1975 ²	IBT	Extralimital	Established, widespread	E
<i>Barbus calidus</i> Barnard, 1938	1998 ⁴	CON	Extralimital	Established, localised	C3
<i>Barbus gurneyi</i> (Günther, 1868)	1970 ²	ANG	Extralimital	Failed	F
<i>Barbus serra</i> Peters, 1864	1998 ⁴	CON	Extralimital	Established, localised	C3
<i>Barbus treurenensis</i> Groenewald, 1958	1977 ²	CON	Extralimital	Established	C3
<i>Carassius auratus</i> (Linnaeus, 1758)	1726 ²	ORN	Alien	Established	E
<i>Chetia brevis</i> Jubb, 1968	1975 ⁵	CON	Extralimital	Established, localised	C3
<i>Clarias gariepinus</i> (Burchell, 1822)	1975 ²	IBT	Extralimital	Established, widespread	E
<i>Ctenopharyngodon idella</i> (Valenciennes, 1844)	1967 ²	BCT	Alien	Established	E
<i>Cyprinus carpio</i> Linnaeus, 1758	1859 ²	ANG	Alien	Established	E
<i>Gambusia affinis</i> (Baird & Girard, 1853)	1936 ²	BCT	Alien	Established, widespread	E
<i>Gilchristella aestuaria</i> (Gilchrist, 1913)	1990 ²	ANG	Extralimital	Established, localised	E
<i>Hydrocynus vittatus</i> Castelnau, 1861	2012 ⁷	ANG	Extralimital	Established, localised	C3
<i>Hypophthalmichthys molitrix</i> (Valenciennes, 1844)	1975 ²	AQU	Alien	Established	D2
<i>Kneria auriculata</i> (Pellegrin, 1905)	1981 ²	CON	Extralimital	Established	C3
<i>Labeo capensis</i> (A. Smith, 1841)	1975 ²	IBT	Extralimital	Established	D2
<i>Labeo umbratus</i> (A. Smith, 1841)	1975 ²	IBT	Extralimital	Established	E
<i>Labeobarbus aeneus</i> (Burchell, 1822)	1953 ²	ANG	Extralimital	Established	E
<i>Labeobarbus capensis</i> (A. Smith, 1841)	1985 ²	CON	Extralimital	Established, localised	C3
<i>Labeobarbus natalensis</i> (Castelnau, 1861)	1964 ²	CON	Extralimital	Established	C3
<i>Lepomis macrochirus</i> Rafinesque, 1819	1939 ²	ANG	Alien	Established, widespread	E
<i>Micropterus dolomieu</i> (Lacepède, 1802)	1937 ²	ANG	Alien	Established, widespread	E
<i>Micropterus floridanus</i> (Lesueur, 1822)	1984 ²	ANG	Alien	Established	E
<i>Micropterus punctulatus</i> (Rafinesque, 1819)	1940 ²	ANG	Alien	Established, widespread	E
<i>Micropterus salmoides</i> (Lacepède, 1802)	1928 ²	ANG	Alien	Established, widespread	E
<i>Mugil cephalus</i> Linnaeus, 1758	1975 ²	AQU	Extralimital	Failed	C1
<i>Myxus capensis</i> (Valenciennes, 1836)	1975 ²	AQU	Extralimital	Failed	C1
<i>Notobranchius orthonatus</i> (Peters, 1844)	1975 ²	CON	Extralimital	Failed	F
<i>Notobranchius rachovii</i> Ahl, 1926	1976 ²	CON	Extralimital	Established, localised	C3
<i>Oncorhynchus mykiss</i> (Walbaum, 1792)	1897 ²	ANG	Alien	Established, widespread	E
<i>Oreochromis andersonii</i> (Castelnau, 1861)	1982 ²	AQU	Alien	Failed	F
<i>Oreochromis aureus</i> (Steindachner, 1864)	1910 ²	AQU	Alien	Failed	F
<i>Oreochromis mossambicus</i> (Peters, 1852)	1936 ²	AQU	Extralimital	Established, widespread	E
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	1955 ²	AQU	Alien	Established	D2
<i>Pangasius sanitwongsei</i> Smith, 1931	2012 ⁹	ORN	Alien	Uncertain	B3
<i>Perca fluviatilis</i> Linnaeus, 1758	1915 ²	ANG	Alien	Established, localised	C3
<i>Poecilia reticulata</i> (Peters, 1859)	1912 ²	ORN	Alien	Established, localised	E
<i>Protopterus annectens brienii</i> Poll, 1961	1987 ²	CON	Extralimital	Established, localised	F
<i>Pseudobarbus burchelli</i> (Smith, 1841)	1970 ²	CON	Extralimital	Unknown	B3
<i>Pseudocrenilabrus philander</i> (Weber, 1897)	1941 ¹	BCT	Extralimital	Established	B3
<i>Pterygoplichthys disjunctivus</i> (Weber, 1991)	2000 ⁸	ORN	Alien	Established, localised	D2
<i>Salmo salar</i> Linnaeus, 1758	1896 ²	ANG	Alien	Failed	F
<i>Salmo trutta</i> Linnaeus, 1758	1892 ²	ANG	Alien	Established, widespread	E
<i>Salvelinus fontinalis</i> (Mitchill, 1815)	1890 ²	ANG	Alien	Failed	F
<i>Sandelia bainsii</i> Castelnau, 1861	1995 ³	CON	Extralimital	Uncertain	B3
<i>Sandelia capensis</i> (Cuvier, 1831)	1982 ²	ANG	Extralimital	Established, localised	C3
<i>Sarotherodon galilaeus</i> (Linnaeus, 1758)	1959 ²	AQU	Alien	Failed	F
<i>Serranochromis robustus</i> (Günther, 1864)	1960 ²	ANG	Alien	Failed	F
<i>Tilapia rendalli</i> (Boulenger, 1896)	1952 ²	BCT	Extralimital	Established, widespread	E
<i>Tilapia sparrmanii</i> A. Smith, 1840	1941 ²	ANG	Extralimital	Established, widespread	E
<i>Tilapia zilli</i> (Gervais, 1848)	1959 ²	AQU	Alien	Failed	F
<i>Tinca tinca</i> (Linnaeus, 1758)	1896 ²	ANG	Alien	Established, localised	C3
<i>Xiphophorus hellerii</i> Heckel, 1848	1974 ²	ORN	Alien	Established, localised	D2
<i>Xiphophorus maculatus</i> (Günther, 1866)	2006 ⁶	ORN	Alien	Uncertain	B3

*B3 = Individuals transported beyond limits of native range, and directly released into novel environment; C1 = Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction; C3 = Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining; D2 = Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction; E = Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence (Blackburn et al. 2011); F = Failed introduction.

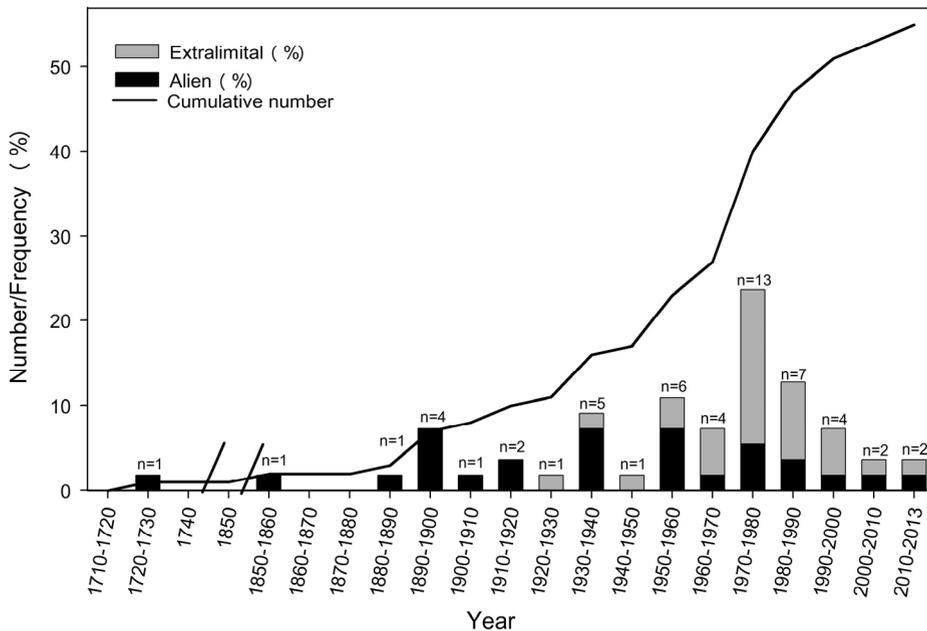


Figure 1. The number and rate of non-native and translocated fish introductions in South Africa from the early 1700's until present (only first time records of introductions into the wild were included).

Results and discussion

Literature review

During the assessment period only 38 studies have investigated invasive fishes. The majority (66%) focussed on impacts, while 34% considered the introduction, establishment or spread stages.

Introduction, establishment and spread

Introduction phase

South Africa has a long history of non-native fish introductions (Figure 1) dating back from the 2012 introduction of the giant pangasius *Pangasius sanitwongsei* Smith, 1931 (Mäkinen et al. 2013) to the first introduction of goldfish *Carassius auratus* (Linnaeus, 1758) in 1726 (de Moor and Bruton 1988). In total, 55 fishes (27 alien, 28 extralimital) have been introduced into or translocated within South African freshwater ecosystems (Table 1). This number exceeds that reported for Portugal, the Azores and Madeira Islands (Ribeiro et al. 2009), and Spain (Elvira and Almodóvar 2001) but is less than that reported for California, USA (Marchetti et al. 2004a).

Due to the lack of adequate technologies for effective fish transportation, the rate of introductions was initially low (Bruton and Van As 1986), but from 1900 onwards an average of four species

were introduced or translocated per decade (Figure 1). All early introductions were of aliens, but as a result of biodiversity concerns in the 1960s (McCafferty et al. 2012) the first native species were translocated for conservation reasons (Figure 1). This was followed by an insurgence of conservation-related introductions in the 1970s and 1980s. From the 1990s onwards, the overall introduction rate has slowed.

The leading cause of introductions in South Africa is angling (35%) followed by translocations for conservation purposes (22%) and aquaculture (17%). Escapees from the ornamental fish trade (11%), transfer via inter basin water transfer schemes (IBTs) (9%) and fish imported as bio-control agents (9%) were also contributors (Figure 2A). These vectors for introduction are not unique to South Africa since sport fishing, aquaculture and the ornamental fish trade are also major global introductory pathways (Copp et al. 2007; Gozlan 2008; Ribeiro et al. 2009).

Angling

Initially, angling-motivated introductions were a result of state-supported formal stocking programs because of a perceived lack of suitable native species (McCafferty et al. 2012). State-supported stocking, which continued until the 1980s (*sensu* de Moor and Bruton 1988), facilitated the successful

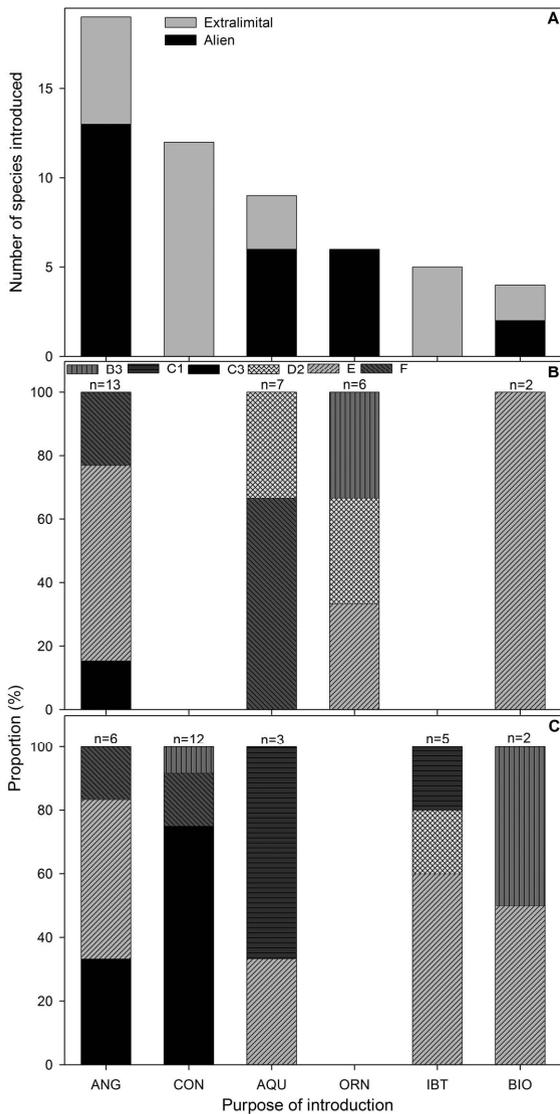


Figure 2. A) The primary purpose for the introduction or translocation of alien and extralimital fishes in South Africa (ANG = angling; CON = conservation; AQU = aquaculture; ORN = ornamental; IBT = Inter-basin water transfer; BCT = Bio-control). Categorisation of the status of fishes introduced into South Africa for each of the five vectors using the criteria from Blackburn et al. (2011)* for alien (B) and extralimital fishes (C) *(B3 = Individuals transported beyond limits of native range, and directly released into novel environment; C1 = Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction; C3 = Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining; D2 = Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction; E = Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence (Blackburn et al. 2011); F = Failed introduction.

establishment of several globally esteemed angling species such as *M. salmoides*, smallmouth bass *M. dolomieu* (Lacépède, 1802), common carp *Cyprinus carpio* (Linnaeus, 1758), brown trout *Salmo trutta* Linnaeus, 1758 and *O. mykiss*. Non-native fodder fish such as bluegill sunfish *Lepomis macrochirus* Rafinesque, 1819 and banded tilapia *Tilapia sparrmanii* A. Smith, 1840 were also introduced (de Moor and Bruton 1988). A substantial recreational fishery based largely on non-native fishes, subsequently developed (McCafferty et al. 2012). The extensive establishment of non-native sport fishes in South Africa has reduced pressures for further new introductions. The recent translocation of tigerfish *Hydrocynus vittatus* Castelnau, 1861 (O'Brien et al. 2012), however, indicates that angling is still a vector for the spread of fish.

Ornamental fish trade

Currently, South Africa permits the import and sale of ~1600 freshwater fish species (Anon. 1994) and although the ornamental trade is the second-most important vector for fish introductions into the wild, it has not resulted in the high magnitude of introductions reported from England (Copp et al. 2007), the United States or Canada (Duggan et al. 2006). The ornamental fish trade has however, facilitated the most recent reported introductions, including *P. sanitwongsei* (Mäkinen et al. 2013) and the vermiculated sailfin *Pterigoplichthys disjunctivus* (Weber, 1991) (Jones et al. 2013). These recent introductions are cause for concern and highlight the potential risks associated with the importation of new species via this vector. Due to consistent imports and the possible release of fish by aquarists, the potential for introductions via this vector is high. To compound this, globally the ornamental species trade is generally an unregulated industry (Padilla and Williams 2004). This was exemplified recently in South Africa using DNA barcoding where it was demonstrated that from a random sample of 120 aquarium trade fish species, 19 were not on the permitted species list, resulting in a misidentification rate of 15% (van der Walt 2012). Positively identifying species is also complicated by hybridisation between congeners, as demonstrated for *P. disjunctivus* (Jones et al. 2013), or confusion over common names (van der Walt 2012). Both forms of misidentification illustrate the lack of control in the ornamental fish trade and the risk of further unwanted introductions via this vector.

Aquaculture

Currently, the non-native *O. mykiss* are the mainstay of South Africa's freshwater aquaculture sector (van Rensburg et al. 2011), however, their introduction has resulted in negative impacts on native fishes in South Africa (Woodford and Impson 2004) and elsewhere (Crowl et al. 1992). In developing countries, economic pressure often dictates management decisions (Pelicice et al. 2013), therefore, the import of new popular aquaculture species or the spread of currently restricted species in South Africa is likely. Brazil, for example, has recently allowed non-native fish cage culture in any hydroelectric reservoir of the country, which will facilitate the introduction and spread of some of the world's worst invasive fish species (Pelicice et al. 2013). *Oreochromis niloticus* (Linnaeus, 1758) was introduced into South Africa for aquaculture in 1955 and is thought to be confined to the Limpopo River system and small coastal river systems in the Kwa-Zulu Natal Province, although their current status in the latter is uncertain (de Moor and Bruton 1988; van Rensburg et al. 2011). *Oreochromis niloticus* is a popular aquaculture species that is also highly invasive (Weyl 2008) and has had devastating impacts through competition or hybridisation with native congeners (Canonica et al. 2005; Firmat et al. 2013; Moralee et al. 2000). Another recently recognised issue is that of accurately identifying the species that are being cultured. This was shown in a recent study, tilapiine individuals identified taxonomically as *O. mossambicus*, when analysed genetically, turned out to carry mtDNA of several introduced *Oreochromis* species (D'Amato et al. 2007).

Introductions for conservation

In South Africa, more native species have been translocated than numbers of aliens introduced (Table 1). Ironically, the large number of translocations for conservation purposes may in many cases be attributed to counteracting their extirpation by non-native fish predation from core distributions within their native range (Kleynhans 1985; Impson and Tharme 1998; Engelbrecht et al. 2001). For example, the threat of imminent extinction of the endangered *S. bairdii* resulted in its translocation to sanctuaries within its native range (Cambray 1997) and three imperilled native fishes, *B. treurenensis* (Limpopo River system), *B. serra* Peters, 1864 and *B. calidus* (Olifants River

system) were translocated within their native river systems to above waterfalls that originally marked the upper limit of fish distributions (Engelbrecht et al. 2001). No mention is made of any risk assessments conducted to assess their impacts in fishless zones, which may be extensive (Knapp et al. 2001). Although the authors of the translocation studies had good intentions, many amphibians and invertebrates require fishless zones for their persistence (Adams et al. 2001; Knapp et al. 2001; Knapp et al. 2007). For example, after the eradication of introduced salmonids from previously fishless lakes, the mountain yellow-legged frog, *Rana muscosa* Camp, 1917, significantly increased in abundance and partly reversed formerly observed declines (Knapp et al. 2007).

Inter-basin water transfer schemes (IBTs)

South Africa is a water-scarce country and, to stabilise water supplies (Ashton 2007), 26 major IBTs have been constructed (Slabbert 2007). Literature on IBT-facilitated introductions deals almost entirely with the Orange/Fish River IBT, which resulted in the transfer of five fish species from the Orange/Vaal to the Great Fish River system (smallmouth yellowfish *Labeobarbus aeneus* (Burchell, 1822), African sharptooth catfish *Clarias gariepinus* (Burchell, 1822), Orange-River mudfish *Labeo capensis* (Smith, 1841), rock catfish *Austroglanis sclateri* (Boulenger, 1901) and moggel *Labeo umbratus* (Smith, 1841)) (Laurenson and Hocutt 1986; Laurenson et al. 1989).

Bio-control

Only three fish species have been introduced for bio-control: mosquitofish *Gambusia affinis* (Baird and Girard), grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) and *T. rendalli* (Bruton and Van As 1986; de Moor and Bruton 1988). These introductions were all prior to 1967 and because invasion risks are now better understood, the threat of new introductions via this vector is considered negligible.

Establishment

Only 21% (11) of all introductions to South Africa were reported to have failed and, although this establishment rate seems high (79%), establishment rates were similar to those in Portugal, the Azores, the Madeira Islands and Spain (Elvira and Almodóvar 2001; Ribeiro et al. 2009). Determining the establishment rates of fishes relies on accurate introduction data, which are

often unavailable and failed introductions are not often reported (Ribeiro and Leunda 2012). While recognising the limitations of inaccurate introduction data, such as inflated establishment estimates, the data presented in Table 1 are the most accurate currently available. Overall, establishment rates in South Africa were high for all vectors responsible for introductions: the highest was for IBTs (80%), followed by angling (79%), bio-control (75%), conservation (73%), ornamental purposes (67%) and lowest was for aquaculture (33%). Applying the Blackburn et al. (2011) classifications, 20 fishes (37%) are considered fully invasive (E). Introductions for angling were responsible for the highest proportion (55%) of invaders (E) with IBTs (15%), bio-control (15%), the ornamental trade (10%) and aquaculture (5%) constituting the remainder (Figure 2B). Translocation of fishes for conservation purposes has not resulted in any species fully invasive species (E) in South Africa, but populations are predominantly self-sustaining where released (C3) (Figure 2C).

The mechanisms responsible for the high establishment rates of introduced fishes in South Africa may be a reflection of high human interest in the species, which also often masks underlying biological characteristics determining establishment success (Marchetti et al. 2004b). These mechanisms include: specifically chosen species with proven establishment rates and prior invasion success elsewhere (Marchetti et al. 2004b; Ribeiro et al. 2007; Ruesink 2005); high propagule pressure (Copp et al. 2007; Leprieur et al. 2008) and physiological tolerances (Marchetti et al. 2004b).

This was also the case in South Africa, where intentional stocking programmes by government institutions and angling organisations (McCafferty et al. 2012) used species that were carefully chosen and imported to fill specific niches (van Rensburg et al. 2011). Intensive stocking regimes also resulted in high propagule pressure, further increasing chances of successful establishment (Lockwood et al. 2005; Lockwood et al. 2009). For example, after the successful establishment of salmonids (*O. mykiss* and *S. trutta*) in mountain streams, three centrarchid fishes were imported to fill specific niches not occupied by salmonids. *Micropterus salmoides* were introduced for lentic environments and the lower reaches of rivers; *M. dolomieu* for the swifter warm water lotic habitats and spotted bass *Micropterus punctulatus* (Rafinesque, 1819) for larger more turbid environments (de Moor and Bruton 1988). Considering

that these fishes were chosen according to their abilities to successfully establish elsewhere, their success in South Africa is not surprising. High rates of establishment for intentionally introduced sport fishes are consistent with Ruesink (2005) who documented that intentionally introduced fishes were more likely ($384/506 = 76\%$) to establish.

High propagule pressure is most likely the mechanism responsible for high establishment rates from IBT-linked introductions. Regular water releases from IBTs create a corridor for fish translocation (Snaddon et al. 1998) which ensures a fairly regular propagule supply from donor to recipient systems. This is evident when examining establishment of fishes translocated from the Orange River system to the Great Fish River system by IBT. Those fish species abundant in Lake Gariep in the vicinity of the IBT tunnel intake (e.g. *C. gariepinus*, *L. aeneus*, *L. capensis*; (Ellender et al. 2012)) have also established in the Great Fish River, while those that were rare in the lake (e.g. *A. sclateri*, largemouth yellowfish *Labeobarbus kimberleyensis* (Gilchrist and Thompson, 1913)) have not (Laurenson et al. 1989; Weyl et al. 2009). A study on the drivers of establishment for fishes introduced into the irrigation dams in South Africa indicated that propagule pressure was a significant determinant of establishment success (Woodford et al. 2013).

There is an increasing threat of introduction, establishment and consequent threats to biodiversity via the ornamental fish trade (Padilla and Williams 2004; Magalhães and Vitule 2013). Ornamental fishes that have established in South Africa (*P. disjunctivus*, *C. auratus*, the guppy *Poecilia reticulata* Peters, 1859, swordtails *Xiphophorus hellerii* Heckel, 1848 and platy *X. maculatus* Günther, 1866) are all common and popular aquarium species, a significant determinant of establishment success in Canada and the USA (Duggan et al. 2006). Although hundreds of ornamental fish species are currently being imported into South Africa, introductions into the wild are mainly facilitated by aquarists releasing unwanted pets. It is therefore impossible to quantify the number of fish species that have been released.

Fish introduced for conservation purposes were predominantly translocated within the same river system but into areas where they did not previously occur, such as above waterfalls that would have originally limited their natural distribution. Fishes were also often stocked in previously fishless reaches of the river systems

without other fish competitors or predators. Despite both low propagule size and number (Simberloff 2009) (often only a single introduction event), establishment rates were high (73%). As these areas were often geographically close and had conditions similar to their native range, this may explain the high establishment rates.

Determining establishment success on a country-wide scale may be misleading as finer-scale studies investigating system and stream-scale establishment rates are rare. Records of failed introductions are also scarce, which hampers accurately determining establishment rates (Ribeiro and Leunda 2012). This indicates that at drainage basin scale, establishment rates are most likely lower. For example, Woodford et al. (2013) demonstrated that, while an irrigation network resulted in the transport of nine fish species from donor to recipient environments, only five species successfully established. This establishment was a result of high propagule pressure and reproductive guild: benthic spawners (*C. carpio* and *C. gariepinus*) were less successful than live bearers (*G. affinis*), pelagic spawners (estuarine roundherring *Gilchristella aestuaria* (Gilchrist, 1913) and river goby *Glossogobius callidus* (Smith, 1937)) and mouth brooders (*O. mossambicus*) in irrigation ponds where water levels fluctuated daily (Woodford et al. 2013).

Due to the variable rates of spread, introduced species may take decades to fulfil their invasive potential (Strayer 2010). An example is the establishment of *L. aeneus* in the Great Fish River after their introduction via an IBT (Laurenson et al. 1989). Assessments eight years after the completion of the IBT found no evidence of establishment (Laurenson et al. 1989) but follow-up study 30 years later confirmed that *L. aeneus* had subsequently established, and indicated that there was an extensive 'lag' phase between their initial introduction and establishment (Weyl et al. 2009). Even if a non-native fish species becomes established, this does not necessarily mean that it is able to establish in all parts of the river system. Establishment comparisons between populations in the mainstream Great Fish River and the Glen Melville reservoir, an off-stream impoundment, indicated that *L. aeneus* was only established in the Great Fish River and that persistence in the impoundment was due to continued recruitment from the Great Fish River (Weyl et al. 2009). Similarly, the *O. niloticus* introduction into the Limpopo River system has yet to fulfil its potential for establishment and spread in South Africa (Zengeya et al. 2013a; b). In the

Blindekloof stream, a headwater tributary of the Swartkops River system, Eastern Cape, South Africa, four (*M. salmoides*, *M. dolomieu*, *C. gariepinus* and *T. sparrmanii*) out of six non-native species recorded from the river system had managed to invade the stream, and only one of these (*T. sparrmanii*) had successfully established (Ellender et al. 2011).

While many freshwater fishes are stenohaline and unable to invade estuaries, some non-native freshwater fishes have managed to establish in estuarine or brackish water environments. In the Wilderness Lakes system, a series of interconnected estuarine lakes, two euryhaline non-natives (*O. mossambicus* and *G. affinis*) were established and the less salinity tolerant *C. carpio* were in the early stages of invasion and *M. salmoides* (recorded 15 years previously) were absent (Olds et al. 2011). There may therefore be a threat of freshwater species introduced into estuaries dispersing via the marine environment and invading other coastal river systems. For example, Gutierre et al. (2013) demonstrated that introduced non-native freshwater fish species display greater physiological plasticity when exposed to high salinities than do the native freshwater fishes.

Spread

There is a paucity of drainage-specific distributions data for South Africa and, for those that do exist there is a lack of spatial resolution for system wide assessments (de Moor 1996). The most current distributions data are available in the '*Atlas of southern African freshwater fishes*' (Scott et al. 2006). However, inconsistencies, and the lack of accurate data for the various drainages of South Africa hampers analyses. An example of this is that in many instances only native fishes were collected and their specimens added to fish collections during past ichthyological surveys, while non-native species were ignored or discarded (E.R Swartz pers. comm.). This severely constrains documenting the spread of introduced fishes in South Africa. Data on the spread of non-native fishes from their initial introduction sites are scarce. However, using two common angling species *C. carpio* and *M. salmoides* as an indication of the potential to spread, following their introductions in 1859 and 1928 respectively, they now inhabit every major river system in South Africa (van Rensburg et al. 2011). The invasive potential of *C. carpio* was illustrated in a study on their life history and population dynamics in Lake Gariep, South Africa's largest

impoundment (Winker et al. 2011). Compared to populations in their native range, introduced *C. carpio* matured earlier and grew faster but had high mortality rates, traits indicative of rapid population growth potential (Winker et al. 2011). In the case of *M. salmoides*, in the 10 years following their introduction, they were spread into five major catchments on the east coast of South Africa from the Clanwilliam/Olifants drainage on the west coast to the upper Incomati system on the east coast, a distance of >1500 km (de Moor 1996). This further illustrates the fervour with which people moved fish between drainages during early introduction phases. The extent non-native fishes are spread between drainages is also a function of time (Copp et al. 2007), and all currently widespread fishes (van Rensburg et al. 2011) have been established in South Africa for longer than 35 years.

Invasive impact studies in South Africa

Research on the invasive impact of fishes in South Africa is in its infancy. In the period since the previous invasions review (Bruton and Van As 1986), only 25 studies demonstrating the impact of non-native fish species on recipient ecosystems have been published. Included in this list are two perspective papers that document observational evidence on the impact of salmonids (*S. trutta* and *O. mykiss*) and *C. gariepinus* on native fishes in South Africa (Cambrey 2003a; b). Research has predominantly focussed on competitive or predatory impacts at individual and population levels, with some research on genetic impacts.

Genetic impacts, hybridisation and introgression

Human-mediated hybridisation is the leading cause of global biodiversity loss (Muhlfeld et al. 2009). Hybridisation is defined as the mating between individuals from two genetically distinct populations and introgression results when the offspring are fertile and backcross to parental populations (Allendorf et al. 2013). The level and type of impact therefore depends on the viability of offspring. Viable offspring may result in a hybrid swarm and eventual genomic extinction (Muhlfeld et al. 2009). In South Africa, studies on the impact of *O. niloticus* introductions into the Limpopo River system indicate extensive hybridisation and introgression with native *O. mossambicus* (D'Amato et al. 2007; Moralee et al. 2000). Further complicating the matter,

specimens also contained mtDNA from non-native Kariba tilapia *Oreochromis mortimeri* (Trewavas, 1966) and three-spot tilapia *Oreochromis andersonii* (Castelnau, 1861), indicating the presence of a hybrid swarm (Firmat et al. 2013). In addition, phylogeographic analysis of native *O. mossambicus* within their native range recognised three lineages: a Zambezi basin lineage; a Malawian lineage and a southern lineage (including South African coastal estuarine populations) (D'Amato et al. 2007). These historically isolated lineages may be under threat as individuals sequenced from aquaculture facilities in the Limpopo basin grouped with the Zambezi and Malawian lineages, indicating extensive translocations and a threat of hybridisation with native lineages (D'Amato et al. 2007). D'Amato et al. (2007) recommended that efforts should be made to preserve these unique lineages and that the introduction of any *O. mossambicus* into these regions should be prevented. Hybridisation is recognised as a primary threat to *O. mossambicus* and they are consequently IUCN redlisted as 'Near Threatened' (Cambrey and Swartz 2007).

Threats to the genetic integrity of a species may also result from a breakdown of biogeographical barriers resulting in mixing of previously isolated populations of the same species or between congeners. For example, the genetic integrity of *L. umbratus* is being threatened in numerous southern coastal river populations by introductions of congeners via IBTs (Rameojane 2011). The natural distribution of *L. umbratus* encompasses the Vaal and upper Orange River systems and the Gouritz, Gamtoos, Sundays, Great Fish, Buffalo and Nahoon River systems on the east coast (Skelton 2001). Genetic analyses have indicated that each of these river systems harbours unique genetic diversity (Rameojane 2011). Via the Orange Fish tunnel IBT, which also links the Great Fish and Sundays River systems, Orange River *L. umbratus* and its congener *L. capensis* were translocated from the Orange River system into the Fish River. There is therefore the threat of mixing within *L. umbratus* and additionally *L. umbratus* x *L. capensis* hybrids have been documented (Rameojane 2011). The 25 other IBTs in South Africa also provide vectors for mixing previously isolated populations or species.

Competition and predation

Impacts of non-natives on native fishes at the individual level include: alterations in behaviour;

suppression of vital rates such as growth and reproduction (Fraser and Gilliam 1992); and morphological changes in response to invader presence/absence (Latta et al. 2007). Few studies have addressed impacts at the individual level in South Africa. However, in the upper Berg River where *P. burgi* co-occur with non-native *O. mykiss*, *P. burgi* juveniles exhibited predator avoidance along a depth gradient, only occupying shallow littoral habitats (Woodford and Impson 2004). In the Driehoeks River (Olifants River system) another small endemic, the Cape galaxias *Galaxias zebratus* (Castelnau, 1861) occupied deeper more complex habitats in the presence of *M. salmoides*, than in non-invaded sites (Shelton et al. 2008). These studies were primarily descriptive, however, the mechanisms responsible for the observed patterns are most likely related to the threat of predation by introduced fishes. A major bottleneck in quantifying behavioural impacts is that, in most cases native and non-native fish species do not co-occur (Woodford et al. 2005; Ellender et al. 2011; Weyl et al. 2013). Predation generally results in local extirpation of native fishes and therefore individual level sub-lethal impacts are difficult to document due to lack of co-occurrence between native and non-natives.

At small spatial scales in the Blindekloof stream (Swartkops River system), Skelton (1993) and Ellender et al. (2011) recorded the complete absence of native fishes from stream reaches invaded by *M. salmoides*, and similar trends were observed from the nearby Wit River (Sundays River system) (Traas 2009). Similar within stream patterns have been observed in invaded rivers throughout the Cape Floristic Region (Woodford et al. 2005; Lowe et al. 2008; Weyl et al. 2013). There is evidence that vulnerability to invasion is also size- and species-specific. In the Rondegat River, a headwater tributary of the Olifants River system, three studies consistently recorded the same patterns where four out of five native species were absent at sites invaded by *M. dolomieu*, and the fifth, Clanwilliam yellowfish *Labeobarbus capensis* (Smith, 1841), was only present as large adults (Woodford et al. 2005; Lowe et al. 2008; Weyl et al. 2013). In the upper Berg River, predation and spatial interactions between *O. mykiss* and three native species (*G. zebratus*, *P. burgi* and *S. capensis*) were investigated (Woodford and Impson 2004). The study documented low levels of native fish predation by *O. mykiss* (only *G. zebratus* were recorded from *O. mykiss* stomachs) and possible predator avoidance behaviour by *G. zebratus*

(Woodford and Impson 2004). Non-native fishes have also been documented to prey on estuarine fishes, and in the Kowie River system, *M. salmoides* preyed on three native estuarine species: oval moony *Monodactylus falciformis* Lacepède, 1801; flathead mullet *Mugil cephalus* Linnaeus, 1758; and freshwater mullet *Myxus capensis* (Valenciennes, 1836) (Weyl and Lewis 2006).

At system scale, a study on the Berg River noted range contractions from historical distribution data for three endemic native fishes (*P. burgi*, *G. zebratus* and *S. capensis*) which were now limited to non-invaded stream reaches often above natural barriers such as waterfalls which inhibit non-native fish dispersal (Clark et al. 2009). While a suite of non-native fishes have been introduced into the Berg River system (*O. mykiss*, *M. dolomieu*, *M. punctulatus*, *M. salmoides*, *O. mossambicus*, *T. sparrmanii*, *C. gariepinus*, *L. macrochirus*, *C. carpio* and *G. affinis*), disentangling impacts of non-native species from other anthropogenic stressors such as pollution and water abstraction was considered unrealistic (Clark et al. 2009). However, given the invasive nature of the non-native fishes present in the Berg River system, and the limitation of native fish distributions to non-invaded stream reaches, impacts on native fishes are inferred. Such findings highlight the low degree of biotic resistance of native stream fishes to invasion. This vulnerability to invasion displayed by native fishes is also reflected by other biota.

In two salmonid (*O. mykiss* and *S. trutta*) invaded streams (Mobovaneni and Sterkspruit streams) of the uKhahlamba Drakensberg Park World Heritage site, there were major differences in the abundance of tadpoles of the Natal cascade frog *Hadromophryne natalensis* Hewitt, 1913 above and below *O. mykiss* and *S. trutta* invasion barriers (Karssing et al. 2012). In both cases, tadpole abundances were greatly reduced (4.7 and 15.7 times lower) in salmonid invaded zones of the Mobovaneni and Sterkspruit Rivers respectively (Karssing et al. 2012).

Some studies have investigated possible mechanisms of community-level competition between native and non-native species. In the Tyume River, a Keiskamma River system headwater tributary, the endangered *S. bainsii* occurred sympatrically with *O. mykiss* in the upper reaches and with *M. salmoides* in the lower reaches (Mayekiso and Hecht 1988). High degrees of dietary overlap were observed between *S. bainsii* and both *O. mykiss* and *M. salmoides* (Mayekiso and Hecht 1988). Low abundances in the lower

reaches were ascribed to competition with *M. salmoides*, however, predation was more likely the cause, but overall population level impacts were not detectable (Mayekiso and Hecht 1988).

In the Limpopo River system, stomach content analysis revealed high levels of dietary overlap between invasive *O. niloticus* and native *O. mossambicus*, however, stable isotope analyses, which provides increased accuracy on long-term dietary carbon and nitrogen assimilation, indicated strong selective resource partitioning (Zengeya et al. 2011). It was therefore unclear whether *O. niloticus* would be a strong competitor in the Limpopo River system (Zengeya et al. 2011). A broader-scale study on the Sundays and Great Fish River systems indicated that *C. gariepinus* exhibited trophic diversity and plasticity (Kadye and Booth 2012a). *Clarias gariepinus* also exhibited ontogenetic dietary shifts, from feeding predominantly on aquatic invertebrates at smaller sizes to an increased proclivity for piscivory at larger sizes (Kadye and Booth 2012b). Three native species formed part of its diet: *O. mossambicus* in the lower Great Fish River system; *L. umbratus* from Glen Melville reservoir; and *Barbus pallidus* Smith, 1841 in the Sundays River (Kadye and Booth 2012b). The authors predicted that *C. gariepinus* may impact on invaded communities due to predation and interference in habitats where they co-occur with native fishes (Kadye and Booth 2012a; b).

Four studies have attempted to document the impact of non-native fishes on invertebrate communities. The first was conducted on the Rondegat River in the Western Cape, where Lowe et al. (2008) described the impact of *M. dolomieu* invasion on the invertebrate community. Shifts in invertebrate assemblage were noted and certain grazing taxa showed reduced abundances whereas all other taxa exhibited abundance increases in areas invaded by *M. dolomieu* (Lowe et al. 2008). Similar community-level effects were observed in *M. salmoides* invaded zones from the Wit River in the Eastern Cape (Weyl et al. 2010). Both studies postulated that top down control on invertebrates was decreased as native invertebrate fish predators had been extirpated by centrarchids and therefore overall invertebrate predator biomass was reduced in invaded stream reaches. The impact of salmonids (*O. mykiss* and *S. trutta*) on invertebrate communities were investigated by comparing paired sites separated by waterfalls, with invaded sites below, and non-invaded sites above waterfalls (Rivers-Moore et al. 2013). Shifts in community structure were

noted between invaded and non-invaded sites, but confounding factors such as waterfalls acting as ecotones and sampling during high flows resulting in high levels of suspended sediments, rendered inconclusive results (Rivers-Moore et al. 2013). In an attempt to understand the relationship between invasive *C. gariepinus* and aquatic invertebrates, Multiple Before-After Control-Impact (MBACI) design experiments were conducted with and without *C. gariepinus* in invaded and non-invaded tributaries of the Great Fish River system (Kadye and Booth 2012c). Macro invertebrates showed little response to predators in the invaded Koonap River communities, while in *C. gariepinus*-naïve communities in the non-invaded Brak River, there was decreased species richness, diversity and biomass (Kadye and Booth 2012c).

Introductions of associated parasites and diseases

The introduction of novel parasites and diseases into environments can be particularly severe, as fish and novel parasite communities have not co-evolved, and consequently, hosts do not possess immune responses to infection (Gozlan 2008). Numerous non-native fish parasites have been introduced into South Africa (Bruton and Van As 1986; de Moor and Bruton 1988; Picker and Griffiths 2011). The primary vector fish species for parasite/disease introductions has been *C. carpio*, which are suspected to have introduced seven species (*Ichthyobodo necator* Henneguy 1883, *Chilodonella cyprini* (Moroff, 1902), *C. hexasticha* (Kiernik, 1909), *Apiosoma piscicola* (Blanchard 1885), *Trichodina acuta* Lom, 1961, *T. nigra* Lom, 1960 and *Trichodinella epizootica* (Raabe, 1950)). *Ctenopharyngodon idella* were also implicated in the introduction of *Bothriocephalus acheilognathi* Yamaguti, 1934 (Bruton and Van As 1986). Currently a major threat for new introductions into South Africa is via species imported for the ornamental fish trade as eight million fishes are imported annually, and the industry is largely unregulated (Mouton et al. 2001). Results from a pilot study on the health of fish imported for the ornamental fish trade documented that, of the four species tested (*C. auratus*, *C. carpio*, *P. reticulata* and cardinal tetras *Paracheirodon axelrodi* (Schultz, 1956)), one harmful bacterium (*Mycobacterium fortuitum* Da Costa Cruz 1938) and numerous external parasites (*Trichodina mutabilis* Kazubski and Migala, 1968 *Ichthyophthirius multifiliis* Fouquet, 1876 ciliophorans of the genus *Tetrahymena*, and

monogeneans of the genera *Dactylogyrus* and *Gyrodactylus*) were recorded (Mouton et al. 2001). *Trichodina mutabilis* had also not previously been recorded in South Africa (Mouton et al. 2001).

The impacts of introduced parasites/diseases in South Africa may be serious and mass mortalities of native and non-native fishes have also been recorded and attributed to five introduced parasite species (*C. hexasticha*, *I. multifiliis*, *Argulus japonicus* Thiele, 1900, *B. acheilognathi*, *T. acuta*) (Bruton and Van As 1986). A few contemporary studies have documented individual and population-level prevalence, abundance and mean intensity. For example, high prevalence and abundance of *B. acheilognathi* was recorded from two native species *L. aeneus* and *L. kimberleyensis* in the Vaal Dam (Bertasso and Avenant-Oldewage 2005) and a translocated *L. aeneus* population in Glen Melville Dam on the Great Fish River system (Stadtlander et al. 2011). The native eel *Anguilla mossambica* (Peters, 1852) has also been infected by the non-native parasitic gill monogenean *Pseudodactylogyrus anguillae* (Yin and Sproston, 1948) (Christison and Baker 2011; Parker et al. 2011). High prevalence and intensity of *P. anguillae* on *A. mossambica* were recorded from the Great Fish River system (Parker et al. 2011). Another non-specific non-native fish louse *A. japonicus* infested all collected fishes from the Witbank Dam on the Olifants River system, with a maximum of 87 individual lice per fish (Avenant-Oldewage 2001). Despite the recognition that high prevalence and abundance of introduced parasites and diseases pose significant threats to native fish communities in South Africa, studies have thus far failed to highlight population-level impacts.

The way forward

Invasive Alien Species (IAS) are a recognised threat to South Africa's biodiversity and their management is a high priority in national legislation [National Environmental Management: Biodiversity Act (Act 10 of 2004) and the National Environmental Management: Protected Areas Act (Act 57 of 2003)]. Draft Alien and Invasive Species Regulations published for public comment in July 2013 (and amended in early 2014), for example, require all Government Departments and Management Authorities of protected areas to develop monitoring, control, and eradication plans for listed IAS. The legislative framework also recognises that many alien fishes are

conflict species, which have both negative environmental impact but also contribute to food security and economic development (e.g. through fisheries and aquaculture) and management measures include import controls of high risk species and the control of the movement of established IAS within South Africa. The effective implementation of IAS legislation will require a strong information base to allow for proactive decision making and allow for comprehensive risk assessments based on regional experience. The current literature review indicates that South Africa is data-poor with regard to understanding non-native fish invasions.

Recent literature has predominantly focused on the impacts of some non-native fishes (Woodford et al. 2005; Lowe et al. 2008; Weyl et al. 2013), while relatively little research has been done on their introduction, establishment and spread. This focus on impacts may result in inadequate information on the transport and introduction phases of non-native fishes. Such knowledge is essential for preventing new introductions and curbing the further spread of established non-native fishes (Copp et al. 2005; Clavero and García-Berthou 2006; Duggan et al. 2006; Gozlan et al. 2010). For example, in the UK a precautionary approach to importation of fishes is applied under the Import of Live Fish (England and Wales) Act 1980 (ILFA) and the Import of Live Fish (Scotland) Act 1978, both of which prohibit import of fish species assessed as capable of forming self-sustaining populations in British waters.

In South Africa, research on non-native fishes has tended to focus on describing individual and population level impacts (Weyl et al. 2010; Karssing et al. 2012), while some address mechanisms by which introduced non-native fishes may impact upon native biota (e.g. Woodford and Impson 2004; D'Amato et al. 2007). However, very few studies attempt to quantify these impacts at the system scale. As for other parts of the world, there are also three major issues concerning quantifying impacts: firstly, a major stumbling block for researchers is the lack of accurate baseline pre-invasion data with which to compare current status (Ribeiro and Leunda 2012); secondly, disentangling the impacts of other confounding factors such as river regulation, pollution and siltation is difficult and sometimes impossible (Didham et al. 2007); and lastly defining exactly what constitutes impacts and how these are measured (Ricciardi et al. 2013).

Analogous to international invasive fish literature (Cucherousset and Olden 2011), taxonomic biases were observed for South African impact studies. Less than 50% of fully invasive fish species had been the subject of an impact study. Most studies focussed on impacts of the centrarchids *M. salmoides* and *M. dolomieu* on native biota (Woodford et al. 2005; Weyl et al. 2010; Ellender et al. 2011; Weyl et al. 2013). The remainder of the studies were also focussed on other global pests, *O. mykiss* and *C. gariepinus*, *O. niloticus* and *G. affinis* (Woodford et al. 2004; Kadye and Booth 2012a; b; c; Howell et al. 2013; Zengeya et al. 2011; 2013a; b). This is not surprising as these are among the most widespread invaders in South Africa with the largest perceived impacts. Two highly invasive species, *C. carpio* and *L. macrochirus*, are widespread in South Africa, but little to no information exists on their impacts on invaded ecosystems. It is therefore evident that information is still required on all aspects of the invasion process, from introduction, to establishment, spread and impacts. Continued emphasis should be placed not only on describing invasion states but also on understanding the mechanisms responsible for the observed patterns of impact.

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References

- Adams SB, Frissell CA, Rieman BE (2001) Geography of invasion in mountain streams: Consequences of headwater lake fish introductions. *Ecosystems* 4: 296–307, <http://dx.doi.org/10.1007/s10021-001-0012-5>
- Allendorf FW, Luikart GH, Aitken SN (2013) Conservation and the genetics of populations 2nd edn. Wiley-Blackwell, Oxford, UK, 624 pp
- Anon. (1994) Fresh water fish species for aquarium purpose only: species allowed for importation into RSA. Directorate of Plant Production, Health and Quality, National Department of Agriculture, Pretoria, South Africa
- Ashton PJ (2007) Riverine biodiversity conservation in South Africa: current situation and future prospects. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17: 441–445, <http://dx.doi.org/10.1002/aqc.886>
- Avenant-Oldewage A (2001) *Argulus japonicus* in the Olifants River system – possible conservation threat? *South African Journal of Wildlife Research* 31: 59–63
- Bertasso A, Avenant-Oldewage A (2005) Aspects of the ecology of the Asian tapeworm, *Bothriocephalus acheilognathi* Yamaguti, 1934 in yellowfish in the Vaal Dam, South Africa. *Onderstepoort Journal of Veterinary Research* 72: 207–217, <http://dx.doi.org/10.4102/ojvr.v72i3.198>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339, <http://dx.doi.org/10.1016/j.tree.2011.03.023>
- Bruton MN, Merron SV (1985) Alien and translocated aquatic animals in southern Africa: a general introduction, checklist and bibliography. *South African National Scientific Programmes Report* 13: 1–71
- Bruton MN, Van As JG (1986) Faunal invasions of aquatic ecosystems in southern Africa, with suggestions for their management. In: MacDonald IAW, Kruger FJ, Ferrar AA, (eds), *The Ecology and Management of Biological Invasions in Southern Africa*. Oxford University Press, Cape Town, South Africa, pp 47–61
- Cambray J, Swartz E (2007) *Oreochromis mossambicus*. In: IUCN 2012 IUCN Red List of Threatened Species Version 2012.2. <http://www.iucnredlist.org> (Accessed 17 April 2013)
- Cambray JA (1997) Captive breeding and sanctuaries for the endangered African anabantid *Sandelia bainesii*, the Eastern Cape rocky. *Aquarium Sciences and Conservation* 168: 159–168, <http://dx.doi.org/10.1023/A:1018300104631>
- Cambray JA (2003a) The need for research and monitoring on the impacts of translocated sharp-tooth catfish, *Clarias gariepinus*, in South Africa. *African Journal of Aquatic Science* 28: 191–195, <http://dx.doi.org/10.2989/16085910309503786>
- Cambray JA (2003b) The global impact of alien trout species - a review; with reference to their impact in South Africa. *African Journal of Aquatic Science* 28: 61–67, <http://dx.doi.org/10.2989/16085914.2003.9626601>
- Canonica GC, Arthington A, Mccrary JK, Thieme ML (2005) The effects of introduced tilapias on native biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* 483: 463–483, <http://dx.doi.org/10.1002/aqc.699>
- Christison KW, Baker GC (2011) First record of *Pseudodactylogyrus anguillae* (Yin & Sproston, 1948) (Monogenea) from South Africa. *African Zoology* 42: 279–285, [http://dx.doi.org/10.3377/1562-7020\(2007\)42\[279:FROPAY\]2.0.CO;2](http://dx.doi.org/10.3377/1562-7020(2007)42[279:FROPAY]2.0.CO;2)
- Clark BM, Impson D, Rall J (2009) Present status and historical changes in the fish fauna of the Berg River, South Africa. *Transactions Of The Royal Society Of South Africa* 64: 142–163, <http://dx.doi.org/10.1080/00359190909519249>
- Clavero M, Garcia-Berthou E (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications* 16: 2313–2324, [http://dx.doi.org/10.1890/1051-0761\(2006\)016\[2313:HDAIRO\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2006)016[2313:HDAIRO]2.0.CO;2)
- Copp GH, Bianco PG, Bogutskaya NG, Eros T, Falka I, Ferreira MT, Fox MG, Freyhof J, Gozlan RE, Grabowska J, Kovac V, Moreno-Amich R, Naseka AM, Penaz M, Povz M, Przybylski M, Robillard M, Russell IC, Stakenas S, Sumer S, Vila-Gispert A, Wiesner C (2005) To be, or not to be, a non-native freshwater fish? *Journal of Applied Ichthyology* 21: 242–262, <http://dx.doi.org/10.1111/j.1439-0426.2005.00690.x>
- Copp GH, Templeton M, Gozlan RE (2007) Propagule pressure and the invasion risks of non-native freshwater fishes: a case study in England. *Journal of Fish Biology* 71: 148–159, <http://dx.doi.org/10.1111/j.1095-8649.2007.01680.x>
- Crowl TA, Townsend CR, McIntosh AR (1992) The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Reviews in Fish Biology and Fisheries* 2: 217–241, <http://dx.doi.org/10.1007/BF00045038>
- Cucherousset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. *Fisheries* 36: 215–230, <http://dx.doi.org/10.1080/03632415.2011.574578>

- D'Amato ME, Esterhuysen MM, van Der Waal BCW, Brink D, Volckaert FAM (2007) Hybridization and phylogeography of the Mozambique tilapia *Oreochromis mossambicus* in southern Africa evidenced by mitochondrial and microsatellite DNA genotyping. *Conservation Genetics* 8: 475–488, <http://dx.doi.org/10.1007/s10592-006-9186-x>
- De Moor IJ (1996) Case studies of the invasion by four alien fish species (*Cyprinus carpio*, *Micropterus salmoides*, *Oreochromis macrochir* and *O. mossambicus*) of freshwater ecosystems of southern Africa. *Transactions of the Royal Society of South Africa* 51: 233–255, <http://dx.doi.org/10.1080/00359199609520609>
- De Moor IJ, Bruton MN (1988) Atlas of alien and translocated indigenous aquatic animals of southern Africa. *South African National Scientific Programmes Report* 144: 78–133
- Didham RK, Tylianakis JM, Gemmill NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* 22: 489–496, <http://dx.doi.org/10.1016/j.tree.2007.07.001>
- Duggan IC, Rixon CAM, MacIsaac HJ (2006) Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biological Invasions* 8: 377–382, <http://dx.doi.org/10.1007/s10530-004-2310-2>
- Ellender BR, Weyl OLF, Swartz ER (2011) Invasion of a headwater stream by non-native fishes in the Swartkops River system, South Africa. *African Zoology* 46: 39–46, <http://dx.doi.org/10.3377/004.046.0116>
- Ellender BR, Weyl OLF, Winker H (2012) Age and growth and maturity of southern Africa's largest cyprinid fish, the largemouth yellowfish *Labeobarbus kimberleyensis*. *Journal of Fish Biology* 81: 1271–1284, <http://dx.doi.org/10.1111/j.1095-8649.2012.03395.x>
- Elvira B, Almodóvar A (2001) Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology* 59: 323–331, <http://dx.doi.org/10.1111/j.1095-8649.2001.tb01393.x>
- Engelbrecht GD, Mulder PFS, Mpherwane SK (2001) Conservation genetics of the vulnerable Treur River barb, *Barbus treurenensis*. *African Journal of Aquatic Science* 26: 39–44, <http://dx.doi.org/10.2989/16085910109503722>
- Firmat C, Alibert P, Losseau M, Baroiller J-F, Schliwien UK (2013) Successive invasion-mediated interspecific hybridizations and population structure in the endangered cichlid *Oreochromis mossambicus*. *Plos One* 8: 1–12, <http://dx.doi.org/10.1371/journal.pone.0063880>
- Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73: 959–970, <http://dx.doi.org/10.2307/1940172>
- Gaigher CM (1973) The Clanwilliam River: it is not yet too late. *Piscator* 88: 75–78
- Gozlan RE (2008) Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* 9: 106–115, <http://dx.doi.org/10.1111/j.1467-2979.2007.00267.x>
- Gozlan RE, Britton JR, Cowx IG, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 44: 751–786, <http://dx.doi.org/10.1111/j.1095-8649.2010.02566.x>
- Gutierrez SMM, Vitule JRS, Freire CA, Prodócimo V (2013) Physiological tools to predict invasiveness and spread via estuarine bridges: tolerance of Brazilian native and worldwide introduced freshwater fishes to increased salinity. *Marine and Freshwater Research* 65(5): 425–436, <http://dx.doi.org/10.1071/MF13161>
- Howell DH, Woodford DJ, Weyl OLF, Froneman W (2013) Population dynamics of the invasive fish, *Gambusia affinis*, in irrigation impoundments in the Sundays River Valley, Eastern Cape, South Africa. *Water SA* 39: 485–490, <http://dx.doi.org/10.4314/wsa.v39i4.6>
- Impson ND, Tharme R (1998) Translocation of indigenous freshwater fishes for conservation and flyfishing: the Boontjies River, Western Cape as a case study. *Piscator* 130: 87–92
- Jones RW, Weyl OLF, Swartz ER, Hill MP (2013) Using a unified invasion framework to characterize Africa's first Loricariid catfish invasion. *Biological Invasions* 15: 2139–2145, <http://dx.doi.org/10.1007/s10530-013-0438-7>
- Kadye WT, Booth AJ (2012a) An invader within an altered landscape: One catfish, two rivers and an inter-basin water transfer scheme. *River Research and Applications* 29: 1131–1146, <http://dx.doi.org/10.1002/rra.2599>
- Kadye WT, Booth AJ (2012b) Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharp-toothed catfish *Clarias gariepinus*. *Biological Invasions* 14: 779–795, <http://dx.doi.org/10.1007/s10530-011-0116-6>
- Kadye WT, Booth AJ (2012c) Detecting impacts of invasive non-native sharp-toothed catfish, *Clarias gariepinus*, within invaded and non-invaded rivers. *Biodiversity and Conservation* 21: 1997–2015, <http://dx.doi.org/10.1007/s10531-012-0291-5>
- Karssing RJ, Rivers-Moore NA, Slater K (2012) Influence of waterfalls on patterns of association between trout and Natal cascade frog *Hadromophryne natalensis* tadpoles in two headwater streams in the uKahlamba Drakensberg Park World Heritage Site, South Africa. *African Journal of Aquatic Science* 37: 102–112, <http://dx.doi.org/10.2989/16085914.2012.666381>
- Kleynhans CJ (1985) The future of rare fish species in the Transvaal. *Fauna & Flora* 42: 30–32
- Knapp RA, Boiano DM, Vredenburg VT (2007) Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). *Biological Conservation* 135: 11–20, <http://dx.doi.org/10.1016/j.biocon.2006.09.013>
- Knapp RA, Corn PS, Schindler DE (2001) The Introduction of non-native fish into wilderness lakes: good intentions, conflicting mandates and unintended consequences. *Ecosystems* 4: 275–278, <http://dx.doi.org/10.1007/s10021-001-0009-0>
- Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science* 298: 1233–1236, <http://dx.doi.org/10.1126/science.1075753>
- Latta LC, Bakelar JW, Knapp RA, Pfrender ME (2007) Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity. *BMC Evolutionary Biology* 7: 21, <http://dx.doi.org/10.1186/1471-2148-7-21>
- Laurenson LJB, Hocutt CH (1986) Colonisation theory and invasive biota: the Great Fish River, a case history. *Environmental Monitoring and Assessment* 6: 71–90, <http://dx.doi.org/10.1007/BF00394289>
- Laurenson LJB, Hocutt CH, Hecht T (1989) An evaluation of the success of invasive fish species of the Great Fish River. *Journal of Applied Ichthyology* 1: 28–34, <http://dx.doi.org/10.1111/j.1439-0426.1989.tb00566.x>
- Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology* 6(2): e28, <http://dx.doi.org/10.1371/journal.pbio.0060028>
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20: 223–228, <http://dx.doi.org/10.1016/j.tree.2005.02.004>
- Lockwood JL, Cassey P, Blackburn T (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15: 904–910, <http://dx.doi.org/10.1111/j.1472-4642.2009.00594.x>

- Lowe S, Woodford D, Impson D, Day J (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, <http://dx.doi.org/10.2989/AJAS.2007.33.1.6.390>
- Magalhães, AL, Vitule JR (2013) Aquarium industry threatens biodiversity. *Science (New York, NY)*, 341(6145), 457–457, <http://dx.doi.org/10.1126/science.341.6145.457-a>
- Mäkinen T, Weyl OLF, van der Walt K-A, Swartz ER (2013) First record of an introduction of the giant pangasius, *Pangasius sanitwongsei* Smith 1931, into an African river. *African Zoology* 48: 388–391, <http://dx.doi.org/10.3377/004.048.0209>
- Marchetti MP, Moyle PB, Levine R (2004a) Alien fishes in California watersheds: Characteristics of successful and failed invaders. *Ecological Applications* 14: 587–596, <http://dx.doi.org/10.1890/02-5301>
- Marchetti MP, Moyle PB, Levine R (2004b) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*: 646–661, <http://dx.doi.org/10.1111/j.1365-2427.2004.01202.x>
- Mayekiso M, Hecht T (1988) Conservation status of the anabantid fish *Sandelia bainsii* in the Tyume River, South Africa. *South African Journal of Wildlife Research* 18: 101–108
- McCafferty JR, Ellender BR, Weyl OLF, Britz P (2012) The use of water resources for inland fisheries in South Africa. *Water SA* 38: 327–344, <http://dx.doi.org/10.4314/wsa.v38i2.18>
- Moralee RD, van der Bank FH, van der Waal BCW (2000) Biochemical genetic markers to identify hybrids between the endemic *Oreochromis mossambicus* and the alien species, *O. niloticus* (Pisces: Cichlidae). *Water SA* 26: 263–268
- Mouton A, Basson L, Impson D (2001) Health status of ornamental freshwater fishes imported into South Africa: a pilot study. *Aquarium Sciences and Conservation* 3: 313–319, <http://dx.doi.org/10.1023/A:1013197928590>
- Muhlfeld CC, Kalinowski ST, McMahon TE, Taper MA, Painter S, Leary RF, Allendorf FW (2009) Hybridization rapidly reduces fitness of a native trout in the wild. *Biology Letters* 5: 328–331, <http://dx.doi.org/10.1098/rsbl.2009.0033>
- O'Brien GC, Bulfin JB, Husted A, Smit NJ (2012) Comparative behavioural assessment of an established and a new tigerfish *Hydrocynus vittatus* population in two man-made lakes in the Limpopo River catchment, southern Africa. *African Journal of Aquatic Science* 37: 253–263, <http://dx.doi.org/10.2989/16085914.2012.723196>
- Olds AA, Smith MKS, Weyl OLF, Russell IA (2011) Invasive alien freshwater fishes in the Wilderness Lake System, a wetland of international importance in the Western Cape Province, South Africa. *African Zoology* 46: 179–184, <http://dx.doi.org/10.3377/004.046.0109>
- Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2: 131–138, [http://dx.doi.org/10.1890/1540-9295\(2004\)002\[0131:BBWAAO\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2)
- Parker D, Weyl OLF, Taraschewski H (2011) Invasion of a South African *Anguilla mossambica* (Anguillidae) population by the alien gill worm *Pseudodactylogyrus anguillae* (Monogenea). *African Zoology* 46: 371–377, <http://dx.doi.org/10.3377/004.046.0216>
- Pellicice FM, Vitule JRS, Junior DPL, Orsi ML, Agostinho AA (2013) A serious new threat to Brazilian freshwater ecosystems: the naturalisation of nonnative fish by decree. *Conservation Letters* 7: 55–60, <http://dx.doi.org/10.1111/cons.12029>
- Picker M, Griffiths CL (2011) Alien & invasive animals: A South African perspective. Struik Nature, Cape Town, South Africa, 240 pp
- Rahel FJ (2007) Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology* 52: 696–710, <http://dx.doi.org/10.1111/j.1365-2427.2006.01708.x>
- Ramoejane M (2011) The genetic integrity of *Labeo capensis* and *L. umbratus* (Cyprinidae) in South Africa in relation to inter-basin water transfer schemes. MSc Thesis, Rhodes University, Grahamstown, South Africa, 125 pp
- Ribeiro F, Collares-Pereira MJ, Moyle PB (2009) Non-native fish in the fresh waters of Portugal, Azores and Madeira Islands: a growing threat to aquatic biodiversity. *Fisheries Management and Ecology* 16: 255–264, <http://dx.doi.org/10.1111/j.1365-2400.2009.00659.x>
- Ribeiro F, Elvira B, Collares-Pereira MJ, Moyle PB (2007) Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions* 10: 89–102, <http://dx.doi.org/10.1007/s10530-007-9112-2>
- Ribeiro F, Leunda PM (2012) Non-native fish impacts on Mediterranean freshwater ecosystems: current knowledge and research needs. *Fisheries Management and Ecology* 19: 142–156, <http://dx.doi.org/10.1111/j.1365-2400.2011.00842.x>
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282, <http://dx.doi.org/10.1890/13-0183.1>
- Richardson DM, Wilson JRU, Weyl O, Griffiths CL (2010) South Africa: Invasions. In: Simberloff D, Rejmánek M (eds), *Encyclopedia of Biological Invasions*. University of California Press, pp 643–651
- Richardson DM, Ricciardi A (2013) Misleading criticisms of invasion science: a field guide. *Diversity and Distributions* 19: 1461–1467, <http://dx.doi.org/10.1111/ddi.12150>
- Rivers-Moore NA, Fowles B, Karssing RJ (2013) Impacts of trout on aquatic macroinvertebrates in three Drakensberg rivers in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 38: 93–99, <http://dx.doi.org/10.2989/16085914.2012.750592>
- Ruesink JL (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology* 19: 1883–1893, <http://dx.doi.org/10.1111/j.1523-1739.2005.00267.x-i1>
- Scott LEP, Skelton PH, Booth AJ, Verheust L, Harris R, Dooley J (2006) Atlas of southern African freshwater fishes. *Smithiana Monograph* 2: 1–303
- Shelton JM, Day JA, Griffiths CL (2008) Influence of largemouth bass, *Micropterus salmoides*, on abundance and habitat selection of Cape galaxias, *Galaxias zebratus*, in a mountain stream in the Cape Floristic Region, South Africa. *African Journal of Aquatic Science* 33: 201–210, <http://dx.doi.org/10.2989/AJAS.2008.33.3.2.614>
- Simberloff D (2009) The role of propagule pressure in biological invasions. *Annual Reviews of Ecology, Evolution and Systematics* 40: 81–102, <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120304>
- Simberloff D, Vitule JRS (2013) A call for an end to calls for the end of invasion biology. *Oikos* 123: 408–413, <http://dx.doi.org/10.1111/j.1600-0706.2013.01228.x>
- Skelton PH (1993) On bass in the Blindekloof - the impact of an alien predator on a wilderness stream. *The Naturalist* 37: 27–27
- Skelton PH (2001) A Complete Guide to the Freshwater Fishes of Southern Africa. Southern Book Publishers, Cape Town, South Africa, 395 pp
- Slabbert N (2007) The potential impact of an inter-basin water transfer on the Modder and Caledon River systems. MSc Thesis, University of the Free State, Bloemfontein, South Africa, 215 pp
- Snaddon CD, Wishart MJ, Davies BR (1998) Some implications of inter-basin water transfers for river ecosystem functioning and water resources management in southern Africa. *Aquatic Ecosystem Health and Management* 1: 159–182, [http://dx.doi.org/10.1016/S1463-4988\(98\)00021-9](http://dx.doi.org/10.1016/S1463-4988(98)00021-9)

- Stadtlander T, Weyl OLF, Booth AJ (2011) New distribution record for the Asian tapeworm *Bothriocephalus acheilognathi* Yamaguti, 1934 in the Eastern Cape province, South Africa. *African Journal of Aquatic Science* 36: 339–343, <http://dx.doi.org/10.2989/16085914.2011.636914>
- Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174, <http://dx.doi.org/10.1111/j.1365-2427.2009.02380.x>
- Traas GRL (2009) The conservation and management of freshwater fishes in the Greater Addo Elephant National Park. MSc Thesis, Rhodes University, Grahamstown, South Africa, 157 pp
- Valéry L, Fritz H, Lefevre J-C (2013) Another call for the end of invasion biology. *Oikos* 122: 1143–1146, <http://dx.doi.org/10.1111/j.1600-0706.2013.00445.x>
- Van der Walt K-A (2012) Species identification in South Africa's ornamental trade – how accurate are the names? Honours Thesis, Rhodes University, Grahamstown, South Africa, 46 pp
- Van Rensburg BJ, Weyl OLF, Davies SJ, van Wilgen NJ, Spear D, Chimimba CT, Peacock F (2011) Invasive vertebrates of South Africa. In: Pimentel D (ed), *Biological invasions: Economic and environmental costs of alien plant, animal, and microbe species*. CRC Press, Boca Raton, Florida, pp 326–378
- Vitule JRS, Freire CA, Simberloff D (2009) Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10: 98–108, <http://dx.doi.org/10.1111/j.1467-2979.2008.00312.x>
- Vitule JRS, Freire CA, Vazquez DP, Nunez MA, Simberloff D (2012) Revisiting the potential conservation value of non-native species. *Conservation Biology* 26: 1153–1155, <http://dx.doi.org/10.1111/j.1523-1739.2012.01950.x>
- Weyl OLF (2008) Rapid invasion of a subtropical lake fishery in central Mozambique by Nile tilapia, *Oreochromis niloticus* (Pisces: Cichlidae). *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 839–851, <http://dx.doi.org/10.1002/aqc.897>
- Weyl OLF, Ellender BR, Woodford DJ, Jordaan MS (2013) Native fish distributions and immediate impact of rotenone treatment on alien fish abundance in the Rondegat River, Cape Floristic Region, South Africa. *African Journal of Aquatic Science* 38: 201–209, <http://dx.doi.org/10.2989/16085914.2012.753401>
- Weyl OLF, Lewis H (2006) First record of predation by the alien invasive freshwater fish *Micropterus salmoides* L. (Centrarchidae) on migrating estuarine fishes in South Africa. *African Zoology* 41: 294–296, [http://dx.doi.org/10.3377/1562-7020\(2006\)41\[294:FROPBT\]2.0.CO;2](http://dx.doi.org/10.3377/1562-7020(2006)41[294:FROPBT]2.0.CO;2)
- Weyl OLF, Stadtlander T, Booth AJ (2009) Establishment of translocated populations of smallmouth yellowfish, *Labeobarbus aeneus* (Pisces: Cyprinidae), in lentic and lotic habitats in the Great Fish River system, South Africa. *African Zoology* 44: 93–105, <http://dx.doi.org/10.3377/004.044.0109>
- Weyl PS, de Moor FC, Hill MP, Weyl OLF (2010) The effect of largemouth bass *Micropterus salmoides* on aquatic macro-invertebrate communities in the Wit River, Eastern Cape, South Africa. *African Journal of Aquatic Science* 35: 273–281, <http://dx.doi.org/10.2989/16085914.2010.540776>
- Winker H, Weyl OLF, Booth AJ, Ellender BR (2011) Life history and population dynamics of invasive common carp, *Cyprinus carpio*, within a large turbid African impoundment. *Marine and Freshwater Research* 62: 1270–1280, <http://dx.doi.org/10.1071/MF11054>
- Woodford DJ, Hui C, Richardson DM, Weyl OLF (2013) Propagule pressure drives establishment of introduced freshwater fish: quantitative evidence from an irrigation network. *Ecological Applications* 23: 1926–1937, <http://dx.doi.org/10.1890/12-1262.1>
- Woodford DJ, Impson ND (2004) A preliminary assessment of the impact of alien rainbow trout (*Oncorhynchus mykiss*) on indigenous fishes of the upper Berg River, Western Cape Province, South Africa. *African Journal of Aquatic Science* 29: 107–111, <http://dx.doi.org/10.2989/16085910409503799>
- Woodford DJ, Impson ND, Day JA, Bills IR (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, <http://dx.doi.org/10.2989/16085910509503852>
- Zengeya TA, Booth AJ, Bastos ADS, Chimimba CT (2011) Trophic interrelationships between the exotic Nile tilapia, *Oreochromis niloticus* and indigenous tilapiine cichlids in a subtropical African river system (Limpopo River, South Africa). *Environmental Biology of Fishes* 92: 479–489, <http://dx.doi.org/10.1007/s10641-011-9865-4>
- Zengeya TA, Robertson MP, Booth AJ, Chimimba CT (2013a) Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congeners. *Biological Invasions* 15: 1507–1521, <http://dx.doi.org/10.1007/s10530-012-0386-7>
- Zengeya TA, Robertson MP, Booth AJ, Chimimba CT (2013b) A qualitative ecological risk assessment of the invasive Nile tilapia, *Oreochromis niloticus* in a sub-tropical African river system (Limpopo River, South Africa). *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 51–64, <http://dx.doi.org/10.1002/aqc.2258>