Chapter 6
Alien Freshwater Fauna in South Africa

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Abstract Seventy-seven alien freshwater species are currently naturalised in South Africa. This list includes 7 protozoan, 1 cnidarian, 2 cestode, 13 monogenean,
1 nematode, 1 oligochaete, 6 crustacean, 16 insect, 7 mollusc and 21 fish species. Their origins include all continents except Antarctica and the main pathways for their introduction into the wild are intentional releases (42% of taxa), as parasitic contaminants (35%) or stowaways (14%). Escape from captivity has been relatively unimportant (one fish and one crayfish) and direct introductions for fisheries (49% of taxa), biological control (19%) and stowaways or contaminants (22%) are the most common vectors. The chapter provides an overview of the alien freshwater taxa that are naturalised in South Africa and offers insights into which areas of research are data deficient. Generally, the introduction pathways and vectors for intentionally introduced taxa, such as insects imported for biological control or fishes introduced for fisheries, are well understood and documented. Data on other taxa, and particularly on invertebrates, are scant and only certain groups, such as the parasites of fishes, and snails, for which there is directed research interest, are documented. As a result, increased survey effort is urgently required.

6.1 Introduction

6.1.1 Background

While alien species introductions are, after habitat modification and pollution, considered the third most important threat to freshwater biodiversity in southern Africa (Darwall et al. 2009), some are useful and important as biocontrol agents (Hill and Coetzee 2017) or provide nutritional, economic or recreational values to society (Ellender et al. 2014). Management through monitoring and control are therefore national priorities in South Africa. This requires knowledge on which taxa are present in the country and on their current distributions. Here we provide information on 77 freshwater alien taxa which include parasitic ciliates, mongeneans and nematodes; jellyfish, earthworms, molluscs, crustaceans and fishes (Table 6.1). Amphibians and reptiles are discussed in Chap. 5 (Measey et al. 2020).

Although there are many extralimital invasions of native species, this chapter focusses on biota introduced across the geopolitical boundary of South Africa. It is based on a comprehensive literature review of the introduction status, known distribution and impact of alien freshwater taxa that are documented to have naturalised in South Africa. We focus primarily on taxa that have naturalised, but discuss failed introductions where appropriate.

6.1.2 Pathways and Vectors

The origins of aquatic biota include all continents except Antarctica (Fig. 6.1a) and the main introduction pathways into the wild are intentional releases (42% of taxa),
Table 6.1  List of alien freshwater taxa documented to have naturalised in South African fresh waters

| Group        | Species               | Description                              | Origin  | Vector     | Pathway        | First reported | Introduction status | Impact status | Main reference         |
|--------------|-----------------------|------------------------------------------|---------|------------|----------------|-----------------|---------------------|---------------|------------------------|
| Invertebrates|                       |                                          |         |            |                |                 |                     |               |                        |
| Protozoa     | Ichthyobodo necator   | Ciliate parasite of C. carpio            | Eurasia | Fisheries  | Contaminant    | 1983            | N                   | DD            | Smit et al. (2017)     |
| Protozoa     | Trichodina acuta      | Ciliate parasite O. mykiss               | N. America | Fisheries | Contaminant    | 1993            | N                   | DD            | Smit et al. (2017)     |
| Protozoa     | Trichodina uniforma   | Ciliate parasite C. auratus              | Eurasia | Pet trade  | Contaminant    | 1989            | N                   | DD            | Smit et al. (2017)     |
| Protozoa     | Ichthyophthirius      | White Spot                               | Eurasia | Fisheries  | Contaminant    | 1978            | I                   | DD            | Smit et al. (2017)     |
| Protozoa     | Apiosoma piscicola    | Ciliate parasite C. auratus              | Eurasia | Fisheries  | Contaminant    | 1983            | I                   | DD            | Smit et al. (2017)     |
| Protozoa     | Chilodonella uniforma | Ciliate parasite S. trutta; C. auratus; P. reticulata; O. mykiss and two native fishes | Eurasia | Fisheries  | Contaminant    | 1952            | I                   | DD            | Smit et al. (2017)     |
| Protozoa     | Chilodonella piscicola| Ciliate parasite of M. dolomieu and two native fishes | Eurasia | Fisheries  | Contaminant    | 1982            | I                   | DD            | Smit et al. (2017)     |
| Cnidaria     | Craspedacusta sowerbii| Freshwater Jellyfish                      | Eurasia | Not known  | Contaminant    | 1970s           | I                   | DD            | Smit et al. (2017)     |
| Cestoda      | Schyzocotyle aechiognathi | Asian Tapeworm                           | Eurasia | Fisheries  | Contaminant    | 1980            | I                   | DD            | Smit et al. (2017)     |
| Cestoda      | Atractolytocestus huronensis | Fish Tapeworm                           | N. America | Fisheries | Contaminant    | 2015            | I                   | DD            | Smit et al. (2017)     |
| Monogenea    | Craspedella pedum     | Parasite of C. quadricarinatus           | Australia | Fisheries | Contaminant    | 2017            | I                   | DD            | Tavakol (2017)         |
| Monogenea    | Dicerotocephala boschmai | Parasite of C. quadricarinatus         | Australia | Fisheries | Contaminant    | 2013            | I                   | DD            | du Preez and Smit (2013)|
| Monogenea    | Didymorchis sp.       | Parasite of C. quadricarinatus           | Australia | Fisheries | Contaminant    | 2017            | I                   | DD            | Tavakol (2017)         |

(continued)
| Group     | Species                  | Description                 | Origin    | Vector     | Pathway          | First reported | Introduction status | Impact status | Main reference          |
|-----------|--------------------------|-----------------------------|-----------|------------|------------------|----------------|---------------------|---------------|-------------------------|
| Monogenea | *Clavunculus bursatus*    | Parasite of *M. salmoides*  | N. America| Fisheries  | Contaminant 2017 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Oncholeidus dispar*      | Parasite of *M. salmoides*  | N. America| Fisheries  | Contaminant 2017 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Oncholeidus furcatus*    | Parasite of *M. salmoides*  | N. America| Fisheries  | Contaminant 2012 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Oncholeidus principalis*| Parasite of *M. salmoides*  | N. America| Fisheries  | Contaminant 2017 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Synceleithrium fusiformis*| Parasite of *M. salmoides*  | N. America| Fisheries  | Contaminant 2012 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Acolpenteron ureteroecetes*| Parasite of *M. salmoides; M. punctulatus; M. dolomieu*| N. America| Fisheries  | Contaminant 2010 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Dactylogyrus extensus*   | Parasite of *C. carpio*     | Eurasia   | Fisheries  | Contaminant 2014 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Dactylogyrus tamellatus* | Parasite of *C. idella*     | Eurasia   | Biocontrol | Contaminant 2014 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Dactylogyrus minutus*    | Parasite of *C. carpio*     | Eurasia   | Fisheries  | Contaminant 2014 | I              | DD                  | Smit et al. (2017) |
| Monogenea | *Gyrodactylus kherulensis*| Fish Skin Fluke             | Eurasia   | Fisheries  | Contaminant 2010 | I              | DD                  | Smit et al. (2017) |
| Nematoda  | *Camallanus cotti*        | Parasite of *P. reticulata* | Eurasia   | Pet trade  | Contaminant 2017 | I              | DD                  | Smit et al. (2017) |
| Oligochaeta | *Eukerria saltensis*    | Aquatic Earthworm           | S. America| Not known  | Not known         | I              | DD                  | Smit et al. (2017) |
| Crustacea | *Argulus japonicus*       | Fish Louse                  | Eurasia   | Fisheries  | Contaminant 1982 | I              | MI                  | Smit et al. (2017) |
| Crustacea | *Artemia franciscana*     | Brine Shrimp                | N. America| Fisheries  | Release 2002    | I              | DD                  | Smit et al. (2017) |
| Crustacea | *Atyoida serrata*         | Shrimp                      | Madagascar| Not known  | Not known 1987  | N              | DD                  | Kaiser et al. (2006) |
| Kingdom  | Genus          | Species                        | Habitat          | Origin     | Release Date | Status   | Publication                                      |
|----------|----------------|--------------------------------|------------------|------------|--------------|----------|-------------------------------------------------|
| Crustacea| *Cherax*       | *quadricarinatus*              | Australia         | Fisheries  | 1988         | I        | Nunes et al. (2017)                              |
| Crustacea| *Lernaea*      | *cyprinacea*                   | Eurasia           | Fisheries  | 1982         | I        | Smit et al. (2017)                               |
| Crustacea| *Procambarus*  | *clarkii*                      | N. America        | Pet trade  | 1962         | I        | Nunes et al. (2017)                              |
| Insecta  | *Aedes*        | *albopictus*                   | Eurasia           | Trade      | 1970         | I        | Picker and Griffiths (2011)                      |
| Insecta  | *Culex*        | *pipiens*                      | Africa            | Trade      | 1962         | I        | SANBI                                           |
| Insecta  | *Trichocorixa* | *verticalis*                   | N. America        | Stowaway   | ND           | I        | SANBI                                           |
| Mollusca | *Aplexa*       | *marmorata*                    | S. America        | Pet trade  | 1986         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Gyraulus*     | *chinensis*                    | Eurasia           | Pet trade  | 2006         | N        | Appleton and Miranda (2015)                      |
| Mollusca | *Helisoma*     | *duryi*                        | N. America        | Pet trade  | 1966         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Lymnaea*      | *columella*                    | N. America        | Pet trade  | 1942         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Physa*        | *acuta*                        | S. America        | Pet trade  | 1956         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Pomacea*      | *diffusa*                      | S. America        | Pet trade  | 1981         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Radix*        | *rubiginosa*                   | Eurasia           | Pet trade  | 2004         | I        | Appleton and Miranda (2015)                      |
| Mollusca | *Tarebia*      | *granifera*                    | Eurasia           | Pet trade  | 1999         | I        | Appleton and Miranda (2015)                      |

(continued)
Table 6.1 (continued)

| Group            | Species                        | Description | Origin      | Vector   | Pathway | First reported | Introduction status | Impact status | Main reference     |
|------------------|--------------------------------|-------------|-------------|----------|---------|----------------|---------------------|---------------|-------------------|
| **Fishes**       |                                |             |             |          |         |                |                     |               |                   |
| Centrarchidae    | *Lepomis macrochirus*          | Bluegill    | N. America  | Fisheries| Release | 1939           | I                   | MD            | Marr et al. (2017) |
| Centrarchidae    | *Micropterus dolomieu*         | Smallmouth Bass | N. America | Fisheries| Release | 1937           | I                   | Major         | Marr et al. (2017) |
| Centrarchidae    | *Micropterus floridanus*       | Florida Bass | N. America  | Fisheries| Release | 1980           | I                   | MD            | Weyl et al. (2017b) |
| Centrarchidae    | *Micropterus punctulatus*      | Spotted Bass | N. America  | Fisheries| Release | 1940           | I                   | MD            | Marr et al. (2017) |
| Centrarchidae    | *Micropterus salmoides*        | Largemouth Bass | N. America | Fisheries| Release | 1928           | I                   | MA            | Marr et al. (2017) |
| Cichlidae        | *Oreochromis aureus*           | Blue Tilapia | Africa      | Fisheries| Release | 1910           | N                   | DD            | Marr et al. (2018) |
| Cichlidae        | *Oreochromis niloticus*        | Nile Tilapia | Africa      | Fisheries| Release | 1955           | I                   | MA            | Marr et al. (2017) |
| Cyprinidae       | *Carassius auratus*            | Goldfish    | Asia        | Pet trade| Release | 1726           | N                   | DD            | Marr et al. (2017) |
| Cyprinidae       | *Ctenopharyngodon idella*      | GrassCarp   | Eurasia     | Biocontrol| Release | 1967           | I                   | MD            | Marr et al. (2017) |
| Cyprinidae       | *Cyprinus carpio*              | Common Carp | Eurasia     | Fisheries| Release | 1859           | I                   | DD            | Marr et al. (2017) |
| Cyprinidae       | *Hypophthalmichthys molitrix* | Silver Carp | Eurasia     | Fisheries| Escape  | 1975           | I                   | DD            | Marr et al. (2017) |
| Cyprinidae       | *Tinca tinca*                  | Tench       | Eurasia     | Fisheries| Release | 1896           | N                   | DD            | Marr et al. (2017) |
| Percidae         | *Perca fluviatilis*            | European Perch | Eurasia   | Fisheries| Release | 1915           | N                   | DD            | Marr et al. (2017) |
| Poecilidae       | *Gambusia affinis*             | Western Mosquito Fish | N. America | Biocontrol| Release | 1936           | I                   | DD            | Marr et al. (2017) |
| Poecilidae       | *Poecilia reticulata*          | Guppy       | N. America  | Fisheries| Release | 1912           | N                   | DD            | Marr et al. (2017) |
| Poecilidae       | *Xiphophorus helleri*          | Green Swordtail | N. America | Pet trade| Release | 1974           | N                   | DD            | Marr et al. (2017) |
| Poecilidae       | *Xiphophorus maculatus*        | Southern Platymish | N. America | Pet trade| Release | 2006           | N                   | DD            | Marr et al. (2017) |
| Family         | Genus        | Species          | Origin      | Introduction | Year | Impact | Status | Reference                |
|----------------|--------------|-------------------|-------------|--------------|------|--------|--------|--------------------------|
| Salmonidae     | Oncorhynchus | mykiss            | N. America  | Release      | 1897 | I      | MI     | Marr et al. (2017)       |
| Salmonidae     | Salmo        | trutta            | Eurasia     | Release      | 1890 | I      | MI     | Weyl et al. (2017a)      |
| Siluroidei     | Pterygoplichthys | disjunctivus     | S. America  | Escape       | 2000 | I      | DD     | Marr et al. (2017)       |

Entries in the column on **introduction status** are either (N) naturalised but not invasive or (I) invasive. The column on impact status is based on the EICAT scheme as Major (MA)—the species causes the local or population extinction of at least one native species, and leads to reversible changes in the structure of communities and the abiotic or biotic composition of ecosystems; Moderate (MD)—the species causes declines in the population densities of native species, but no changes to the structure of communities or to the abiotic or biotic composition of ecosystems; Minor (MI)—the species causes reductions in the fitness of individuals in the native biota, but no declines in native population densities, and has no impacts that would cause it to be classified in a higher impact category; Minimal Concern—the species is unlikely to have caused deleterious impacts on the native biota or abiotic environment. Data Deficient (DD)—species where there is either inadequate information to classify the species with respect to its impact, or insufficient time has elapsed since introduction for impacts to have become apparent; Not Evaluated (NE)—a species is Not Evaluated when it has not yet been evaluated against the criteria.
as parasitic contaminants (35%) or stowaways (14%) (Fig. 6.1b). There are regional differences in the alien taxa linked to the history and purpose of introductions. Introductions from other African countries, for example, are mostly fishes introduced to enhance fisheries and for aquaculture, while those introduced from South

Fig. 6.1 (a) Region of origin, (b) pathways and (c) vectors of alien aquatic biota present in South Africa
America are mostly insects that were intentionally introduced and released for the biological control of alien aquatic plants or molluscan stowaways on imports of aquarium plants (Picker and Griffiths 2011). Escape from captivity has been rare (one fish and one crayfish) and direct introductions for fisheries and aquaculture (49% of taxa), biological control (19%), and stowaways or contaminants of international trade (22%) are the most common vectors for introduction into the wild (Fig. 6.1c).

Although the pet trade has been a pathway for the direct introduction of hundreds of alien freshwater fishes (Box 12.1 in Faulkner et al. 2020, Chap. 12; van der Walt et al. 2017), only four have naturalised, mostly in close association with humans (Ellender and Weyl 2014). Examples include populations of Guppy Poecilia reticulata in urban streams and the occasional presence of naturalised Goldfish Carassius auratus populations in urban ponds and impoundments (Ellender and Weyl 2014). There are, however, exceptions. Vermiculated Sailfin Catfish Pterygoplichthys disjunctivus escaped from captivity in the upper Mthlatuze catchment and then invaded the Nseleni River via an artificial connection between the two rivers (Jones et al. 2013). Even more widespread is the Quilted Melania Terebia granifera, a snail that was most likely introduced into the country as a stowaway with aquatic aquarium plants and now occurs widely in subtropical rivers and estuaries (Picker and Griffiths 2011).

Fisheries and aquaculture were the motivation for the importation of at least 12 of the naturalised alien fishes (Ellender and Weyl 2014) and 1 crayfish (Nunes et al. 2017). Most naturalised populations of alien fishes in South Africa are the result of direct introductions into the wild (Ellender and Weyl 2014). The desire to develop opportunities for recreational angling was the main driver for the construction of fish hatcheries in the early to mid-twentieth century. Once constructed, imported fish were bred and their offspring released directly into suitable environments by government agencies, acclimatisation societies and angling organisations (Ellender et al. 2014). Fishes introduced for this purpose include Common Carp Cyprinus carpio (in 1859), Brown Trout Salmo trutta (in 1892), Rainbow Trout Oncorhynchus mykiss (in 1897) and Largemouth Bass Micropterus salmoides (in 1928) (Ellender and Weyl 2014). Direct escape from fish farms is also an important invasion pathway. For example, the invasion of the Olifants and Limpopo rivers by Silver Carp Hypophthalmichthys molitrix originated from a government fish farm at Marble Hall (Ellender and Weyl 2014) and the escape of Redclaw Crayfish Cherax quadricarinatus from an aquaculture facility in Swaziland was responsible for its naturalisation and subsequent spread into South Africa (Nunes et al. 2017). As was the case with the pet trade, contamination of introduced fishes and subsequent infection of other species on fish farms resulted in the spread of many parasitic organisms together with their fish and crayfish hosts (Smit et al. 2017).

Several releases of biological control agents also resulted in the naturalisation of several alien taxa. The direct release of aquatic insects as biological control agents is associated with stringent testing of host specificity (Hill and Coetzee 2017). In contrast to the careful screening, and consequent impressive safety record of alien plant biological control (van Wilgen et al. 2013), the misguided release of Grass
Carp *Ctenopharyngodon idella* to control aquatic plants, and the Mosquitofish *Gambusia affinis* to control mosquitoes, have resulted in invasions and impact (Ellender and Weyl 2014).

### 6.2 South Africa’s Alien Freshwater Fauna

#### 6.2.1 Protozoa

Current knowledge of alien freshwater protozoa is scant and is restricted to research by fish parasitologists who have recorded one alien flagellate and eight ciliates introduced as contaminants of alien fishes (Smit et al. 2017). Some of these have not been reported from the wild, or information on their distribution is too scant to make any inferences. For example, the ciliates *Trichodina mutabilis*, *T. reticulata* and *T. uniforma* are only known from samples taken from *C. auratus* in captivity (Smit et al. 2017).

Four alien ciliates have been reported from native and alien fish populations in the wild (Table 6.1). *Ichthyophthirius multifiliis*, the causative agent for the disease ichthyophthiriosis or “White-Spot”, is now a common problem in aquaculture and the pet trade that was most likely introduced together with *C. auratus* and spill-over to native Mozambique Tilapia *Oreochromis mossambicus*, Straightfin Barb *Enteromius paludinosus* and African Longfin Eel, *Anguilla mossambica* is reported (Smit et al. 2017). *Apiosoma piscicola* (Fig. 6.2a), a parasite that lives on the gills and body surface of its host, was most likely introduced and spread together with *C. carpio* but has since spread to alien *M. dolomieu*, and to at least eight native fish species in multiple locations (Table 6.1; Smit et al. 2017). Similarly, infestation of the body surface, gills and fins of freshwater fish hosts by the ciliates *Chilodonella piscicola* (Fig. 6.2b) and *Chilodonella hexasticha* (Fig. 6.2c) cause chilodonellosis, a disease that has resulted in death of *O. mossambicus* under culture conditions (Smit et al. 2017).

#### 6.2.2 Platyhelminthes

All 16 known alien flatworms in freshwater ecosystems in South Africa are parasitic organisms, either of fishes (Smit et al. 2017) or of crayfishes (Du Preez and Smit 2013). Although many are widespread, they have strong affinities for the host with which they were introduced. For example, no spillover to native fishes has been reported for the six ancylorhynchid monogeneans found on Black Bass (*Micropterus* spp.), despite the almost ubiquitous presence of its fish hosts in South African ecosystems (Truter et al. 2017). Others, such as the Asian Tapeworm *Schyzocotyle acheilognathi*, are not only widespread, but have also spilled over to several native taxa (Smit et al. 2017).

*Schyzocotyle acheilognathi* (Fig. 6.2d) is a global invader that is known to be capable of infecting more than 300 fish species (Smit et al. 2017). In South Africa, *S. acheilognathi* was introduced in 1975 with infected *C. idella* from Malaysia. Its subsequent spread was facilitated by the release of infected fish into the wild and by
its intermediate bird hosts (Smit et al. 2017). The low specificity of *S. acheilognathi* for intermediate or definitive hosts resulted in its rapid naturalisation and spread to fish populations throughout the country, where it now infects at least ten native fish hosts (Smit et al. 2017).

### 6.2.3 Cnidaria

The Freshwater Jellyfish *Craspedacusta sowerbiyi*, most likely introduced into South Africa as a stowaway with aquatic plants, was first reported from Midmar Dam in KwaZulu-Natal in the late 1970s (Rayner 1988). This species is now widespread in South Africa, occurring in large impoundments and ponds in KwaZulu-Natal and the Western Cape (Griffiths et al. 2015). Although no impacts have been documented, freshwater jellyfish are predators on other zooplankton, and so
invasions may impact on zooplankton communities and thereby influence food webs. Its impacts on, and interactions with, native biota have not been researched in South Africa.

6.2.4 Nematoda

The only documented alien freshwater nematode is the recently-discovered *Camallanus cotti*, a generalist fish parasite native to Asia, and was found on guppies (*P. reticulata*) sampled from the Inkomati basin (Tavakol et al. 2017).

6.2.5 Annelida

The aquatic earthworm *Eukerria saltensis* inhabits the roots of aquatic vegetation, and is thought to have been introduced from South America, It has been spread globally and is naturalised throughout the southern hemisphere (Christoffersen 2008). In South Africa, it occurs in variety of moist biotopes along rivers and impoundments in most of the country.

6.2.6 Mollusca

Molluscs are one of the largest invertebrate groups in South Africa with >5000 species in freshwater, marine and terrestrial environments (Hebert et al. 2011). Thirteen alien freshwater snails are known to be present in South African fresh waters, ten of which were introduced via the aquarium and/or ornamental plant trade (Appleton and Miranda 2015; Lawton et al. 2018). Seven of these species have naturalised and four—Quilted Melania *Tarebia granifera* (Fig. 6.3a), Reticulate Pond Snail *Lymnea columella*, Sharp Spired Bladder Snail *Physa acuta* (Fig. 6.3b) and Slender Bladder Snail *Aplexa marmorata*—are increasing their ranges (Appleton and Miranda 2015).

*Terebia granifera* invasions are a particular concern. This freshwater prosobranch gastropod is native to Southeast Asia, and has invaded aquatic ecosystems in North America, South America and Africa (Appleton et al. 2009). In South Africa, it was most likely introduced as a stowaway in aquarium plants. It can reproduce parthenogenically and its ovoviviparous reproductive strategy allows it to deposit live young directly into recipient environments (Appleton et al. 2009). This reproductive strategy, coupled with a high salinity tolerance and its competitive feeding strategy have allowed this species to establish populations in several South African estuaries (Appleton et al. 2009). In its native range, *T. granifera* harbours a diverse and prevalent fauna of trematodes (Appleton et al. 2009) that, as parasitic castrators,
play an important role in the regulation of snail populations. No such trematodes have yet been recorded in this mollusc species in South Africa, presumably giving *T. granifera* the advantage of parasite-release over native species. As a result, population densities in South Africa can attain several thousand individuals per square metre (Appleton et al. 2009; Miranda and Perissinotto 2014; Jones et al. 2017); it is often the dominant component of local invertebrate macrofauna communities (Fig. 6.3c).

Impacts of mollusc invasions on South African ecosystems are not well understood. Research on the trophic niche of these snails has, for example, found minimal evidence for direct food resource competition with native benthic macroinvertebrates (Miranda and Perissinotto 2014; Hill et al. 2015). However, the exceptionally high densities reported from invaded environments may indirectly limit energy transfers within a food web (Hill et al. 2015), and can result in decreased benthic macroinvertebrate biodiversity (Facon and David 2006; Perissinotto et al. 2014). Native predators of gastropods may also be impacted through the replacement of native snail species as they may be unable to feed on the invader as they lack the ability to break the harder shell of *T. granifera* (Miranda et al. 2016).

### 6.2.7 Crustacea

Eight alien freshwater crustaceans have been documented in South Africa. These include a brine shrimp (Order: Anostraca), a freshwater prawn (Decapoda), four crayfishes (Decapoda), a parasitic fish louse (Arguloida), and an anchor worm (Cyclopoida).

The vector(s) and pathway(s) of San Francisco Brine Shrimp *Artemia fransiscana* introduction into South Africa are not known (Kaiser et al. 2006). It is possible that it was introduced by migratory birds, as salt pans in Kenya have been seeded with this species to facilitate commercial harvesting of cysts, which are a valuable product used for rearing larval and juvenile fishes in aquaculture (Kaiser et al. 2006). This
species is currently naturalised in several salt pans in the country where it might replace native *Artemia* species (Kaiser et al. 2006).

The shrimp *Atyoida serrata* was first sampled from the Vungu River in KwaZulu-Natal in 1987, and has subsequently been reported from several other rivers in that province (Coke 2018). It is native to Madagascar and, although listed as alien in South Africa, its introduction history and pathway are not known.

The Japanese fish louse *Argulus japonicus* (Fig. 6.2e) is a branchiuran species that has very low host specificity and was most likely introduced together with either *C. auratus* or *C. carpio*. This parasite was first reported on common carp in 1983 and has spread to at least nine native host species (Smit et al. 2017; Table 6.1).

The anchor worm *Lernaea cyprinacea* (Fig. 6.2f) is an invasive ectoparasite of fishes. This copepod anchors itself in the muscles of the host fish. This increases their susceptibility to secondary infections due to haemorrhagic ulcers that form at the attachment sites and can result in the reduced condition, growth, fecundity and sometimes the mortality of affected fish (Smit et al. 2017). Since its introduction into South Africa in the 1960s, this parasite is known to have infested 12 native fishes (Smit et al. 2017), including a Critically Endangered species, the Eastern Cape Rocky *Sandelia bainsii* (Fig. 6.4) (Chakona et al. 2019).

Freshwater crayfish invasions in South Africa are a cause for concern because there are no native freshwater crayfishes. Aquaculture and the pet trade have resulted in the introduction of four crayfish species into the country: Smooth Crayfish *Cherax cainii*, Common Yabby *Cherax destructor*, Redclaw Crayfish *Cherax quadricarinatus* and Red Swamp Crayfish *Procambarus clarkii*. A notable absence from this list is the parthenogenetic Marbled Crayfish *Procambrus fallax* which, as a result of spread via the pet trade, has become a global problem species (Jones et al. 2009). While *C. cainii* and *C. destructor* have not been reported from the wild, *C. quadricarinatus* and *P. clarkii* are naturalised in several localities (Nunes et al. 2017).

*Procambarus clarkii*, a small (12 cm), typically dark-red species, is a global invader that was illegally imported into South Africa through the aquarium trade (Nunes et al. 2017). It can reproduce rapidly as it matures at a young age (8 weeks).
and can reproduce several times a year as eggs and larvae remain attached to the female for only 3 weeks. They occupy burrows during the day but emerge at night to forage. *Procambrus clarkii* can disperse over long distances, with reported movements of 17 km over 4 days (Gherardi et al. 2000). Currently, the only populations of *P. clarkii* recorded in the wild in South Africa was reported in 1988 from Dullstroom in Mpumalanga (Nunes et al. 2017) and from a small dam near Welkom in the Free State (L. Barkhuizen, unpubl data).

*Cherax quadricarinatus* is a large, mottled blue and beige crayfish with a red patch located on the propodus (Fig. 6.5). The first record of a *C. quadricarinatus* introduction in South Africa was for aquaculture research in 1988, but permits for its use have not been issued due to concerns about its invasiveness (Nunes et al. 2017). Its reproductive biology is similar to that of *P. clarkii* with maturity attained in its first year of life. It is a non-burrowing species that is tolerant of a wide variety of habitats in rivers, lakes and impoundments. These concerns were warranted as its escape from aquaculture facilities in Swaziland have resulted in its downstream invasion of the Komati, Lomati, Mbuluzi, Usutu and Crocodile rivers in Mpumalanga, and the Phongolo River in South Africa (Nunes et al. 2017).

Further north, this species has invaded considerable reaches of the Zambezi system (Nunes et al. 2017), where observed impacts include predation by *C. quadricarinatus* on fishes entangled in gill nets, which affects catch quality and profits in small-scale fisheries in Zambia (Weyl et al. 2017a, b). While the impacts of crayfishes on South African ecosystems are not well understood, they are likely to include predation on invertebrates, competition with functionally similar decapod

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Fig. 6.5  (a) Redclaw Crayfish *Cherax quadricaricatus* from the Phongolo River infected with (b, c) *Diceratocephala boschmai*. (d) Micrograph of *Diceratocephala boschmai* stained with acetocarmine. Photographs courtesy of Nico Smit
species (freshwater crabs or prawns), disturbance of reproductive activity and
nesting success of substrate-spawning fishes and broad influences on food-web
structure (Nunes et al. 2017). The currently known parasites of crayfishes, such as
*D. boschmai* (Fig. 6.5b–d), are not known to have spread to native biota.

### 6.2.8 Insecta

Several insects have been introduced either purposefully for biological control, or
accidentally as stowaways (Table 6.1). In this chapter we consider only insects that
are dependent on the aquatic environment for parts of their life cycle. The
intentionally-introduced insects include mostly biological control agents for invasive
aquatic plants (Janion-Scheepers and Griffiths 2020, Chap. 7; Hill et al. 2020a, b,
Chap 19). Before introduction, candidate biological control agents are subject to
intensive testing to ensure that they do not impact on non-target taxa. While these
organisms fulfill the criteria of being fully invasive *sensu* Blackburn et al. (2011),
their impacts are beneficial as they are confined to the control of the relevant aquatic
plant species, with no evidence of spread to native species.

Knowledge of the introduction history of other insects not introduced for biolog-
ical control is scant, because they generally arrive as stowaways and, as is the case
for many other invertebrates, reports of their presence in the wild are often dependent
on their discovery by specialists in unrelated surveys, rather than on arrival dates.
The Asian tiger mosquito *Aedes albopictus*, which was first reported in Cape Town
in 1990, was most likely a stowaway in imports from Asia (Picker and Griffiths
2011). For other species, such as the water boatman *Trichocorixa verticalis*, current
knowledge is limited to occurrence records.

### 6.2.9 Teleostei

Fishes are among the most commonly intentionally introduced organisms in the
world (Gozlan et al. 2010). The origins, vectors, and invasion status of naturalised
alien fishes are summarised in Table 6.1, and their current distributions are illustrated
in Fig. 6.6.

**Centrarchidae**
The fish family Centrarchidae includes popular North American fishes of the genus
*Micropterus* that were introduced to develop opportunities for angling. Four species,
Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*,
Spotted Bass *Micropterus punctulatus* and Florida Bass *Micropterus floridanus* have
naturalised and most river basins in the country contain at least one of these species
(Hargrove et al. 2019; Weyl et al. 2017a, b). These are the focus of a large
Fig. 6.6 Established alien fishes and their distributions in South Africa. (a) *Salmo trutta*; (b) *Oncorhynchus mykiss*; (c) *Lepomis macrochirus*; (d) *Micropterus salmoides* and hybrids; (e) *Micropterus dolomieu*; (f) *Micropterus punctulatus*; (g) *Carassius auratus*; (h) *Cyprinus carpio*; (i) *Ctenopharyngodon idella*; (j) *Hypophthalmichthys molitrix*; (k) *Tinca tinca*;
recreational fishery that makes considerable economic contributions through equipment and tourism-related expenditure (Weyl and Cowley 2015).

Most widespread is *M. salmoides*, which can attain weights of more than 4 kg in South Africa (Weyl et al. 2017a, b). As is the case with other members of the genus, *M. salmoides* is an aggressive predator, first on invertebrates as juveniles, becoming more piscivorous as adults (de Moor and Bruton 1988). Its reproduction includes the construction and defence of shallow-water nests in spring with males guarding eggs, larvae and fry. As a result of its affinity for vegetated still waters, it is common in slower sections of all larger rivers and in impoundments (Khosa et al. 2019).

*Micropterus floridanus* was until relatively recently, considered a subspecies of *M. salmoides* because the two species are difficult to distinguish morphologically and because they hybridise when their ranges overlap (Hargrove et al. 2019). *Micropterus floridanus* is better adapted to warmer climates than *M. salmoides* (Philipp and Whitt 1991), where it has a longer spawning season (Rogers et al. 2006), lives longer and attains larger sizes than Largemouth Bass (Neal and Noble 2002). Its introduction into southern Africa in 1980, resulted in the increase of the angling record for “Largemouth Bass” that had remained stable at ca. 4.2 kg for more than 50 years, to 8.3 kg in Zimbabwe in 2004 (Weyl et al. 2017a, b) and 7.1 kg in South Africa in 2018 (O. Weyl, unpubl. data). Morphological similarity to *M. salmoides* and the generally unreported nature of introductions following the cessation of government support to stocking programmes in the early 1990s (Ellender et al. 2014) have resulted in a paucity of knowledge on the extent of spread of this species (Weyl et al. 2017a, b). Recent genetic assessments of *Micropterus* species sampled from 20 South African reservoirs demonstrated that *M. floridanus* is not only widespread, but is also expanding its distribution (Weyl et al. 2017a, b; Hargrove et al. 2019).

Two other *Micropterus* species were imported to fill gaps between the high-altitude trout waters and the slow-flowing, lower-lying *M. salmoides* zone. *Micropterus dolomieu*, which have an affinity for flowing water, were introduced from the USA in 1937 and *M. punctulatus* in 1939 for stocking in rivers too turbid to suit *M. dolomieu* (see Ellender et al. 2014). Although not as widespread as *M. salmoides* and *M. floridanus*, *M. dolomieu* and *M. punctulatus* have invaded parts of many river systems in the Eastern and Western Cape (Khosa et al. 2019).

*Micropterus* spp. have had deleterious impacts on native fish and invertebrate species (see Ellender and Weyl 2014; Ellender et al. 2014 for reviews). Most severe are the impacts on native minnows that have not coevolved with native predatory fishes (Ellender et al. 2018). For example, in the Olifants River system in the Western Cape, predation has fragmented native minnow populations to such an

![Fig. 6.6](continued) (l) *Oreochromis niloticus*; (m) *Oreochromis aureus*; (n) *Perca fluviatilis*; (o) *Gambusia affinis*; (p) *Poecilia reticulata*; (q) *Xiphophorus hellerii*; (r) *Pterygoplichthys disjunctivus* (adapted from Skelton and Weyl 2011; Marr et al. 2018; Khosa et al. 2019)
extent that most species now only persist in headwater refugia that are isolated from black bass invasion by the presence of waterfalls (van der Walt et al. 2016). This has reduced the available habitat for native fishes in the Olifants-Doring River system by more than 700 km of river (van der Walt et al. 2016). As a result, Micropterus spp. are typical conflict species that require management interventions that consider both, economic value and harm to biodiversity (Zengeya et al. 2017).

Bluegill Lepomis macrochirus is a relatively small (maximum mass 1 kg) centrarchid species often co-introduced as prey for Micropterus spp. Imported from the USA in 1938, this species has been stocked widely, both through formal stocking initiatives and illegally by anglers. While this species has established populations in parts of many major South African River systems, published information about this species in South Africa is limited to a description of its diet (Ndaleni et al. 2018) and experimental comparisons of its predation efficiency relative to that of native predatory fishes (Wassermann et al. 2016).

**Cyprinidae**

Carp-like fishes of the family Cyprinidae in South Africa include Goldfish *C. auratus* and the Asian carps: Common Carp *C. carpio*, Silver Carp *H. molitrix* and Grass Carp *C. idella*, that are among the most invasive fishes globally (Lowe et al. 2000). Although invasive cyprinids have been associated with a variety of impacts, including the co-introduction of alien parasites and diseases (e.g. Smit et al. 2017), habitat modifications and competition with native fishes (Ellender and Weyl 2014), surprisingly little research has been conducted on their impacts in southern Africa (Table 6.1). As cyprinid fishes are well represented in African native fish faunas, the introduction of novel parasites and diseases by alien cyprinids is a concern as there are already several examples of spillover to native species (Smit et al. 2017).

The first documented introduction of a freshwater taxon into South Africa was *C. auratus* in 1726 (de Moor and Bruton 1988). This ornamental fish was most likely introduced from Asia on Dutch trading vessels (de Moor and Bruton 1988). As it is a popular aquarium fish, *C. auratus* continues to be imported via the pet trade and fish are occasionally introduced into the wild by aquarists when they outgrow aquaria, or accidentally during flooding of ornamental ponds. Although this fish is highly invasive elsewhere, in South Africa feral populations are rare and generally associated with urban areas. With regard to impacts, *C. auratus* is associated with the spread of protozoan, monogenean, branchiuran and nematode parasites around the world, but because these parasites are often associated with other alien fishes, the direct impact of *C. auratus* cannot be determined (Smit et al. 2017).

*C. carpio* is a large (>1 m in length and 24 kg in mass), brazen gold or brown fish that is native to Europe and Asia, but has been domesticated as a food fish for more than 2000 years (Winker et al. 2011). Wild forms are fully-scaled, but domestic forms include mirror (few scales) and leather (no-scales) variants that were developed to improve their appeal as a table fish. *C. carpio* was first introduced to South Africa from England in 1859 and, as a result of releases into the wild, now occurs in dams and mainstream rivers of all major river basins in the country. It
is the most popular recreational angling species in the country and is important in small-scale and subsistence fisheries (Weyl and Cowley 2015). Impacts on recipient ecosystems are mainly associated with its impacts on water quality because bottom-grubbing during feeding suspends sediments, increasing nutrient availability and turbidity (Lougheed et al. 1998). In addition, this species is responsible for introducing the most parasitic species into South Africa. Interestingly, while *C. carpio* is also considered as the host fish that co-introduced the anchorworm *L. cyprinacea*, to date no *C. carpio* has been reported to be infected by this parasite.

*Hypophthalmichthys molitrix* and *C. idella* were considered unable to reproduce outside of captivity because they need to migrate up large rivers to spawn in flowing water to allow eggs to float downstream and hatch prior to larvae settling in floodplains (Skelton and Weyl 2011). Grass Carp *Ctenopharyngodon idella*, introduced from Malaysia in 1967, was stocked into ponds throughout South Africa for the control of invasive aquatic plants. After its naturalisation and invasion of the Vaal River system, this aggressive feeder on aquatic plants, has been demonstrated to decrease the richness and abundance of native aquatic plants (Weyl and Martin 2016). *Ctenopharyngodon idella* was also responsible for the introduction and spread of the tapeworm *S. acheilognathi* (Smit et al. 2017).

Similarly, *H. molitrix* imported in 1975 from Germany to the Marble Hall experimental fish farm on the Olifants River, escaped, naturalised and spread into the Limpopo River system (Lübcker et al. 2014; Ellender and Weyl 2014). As there has been little ecological research directed at this species in South Africa (Lübcker et al. 2016), their impact potential has yet to be determined. In North America however, they have altered ecosystem structure and negatively affected commercial and recreational fisheries and human safety (Kolar et al. 2007).

Tench *Tinca tinca*, a European fish species that can attain a weight of 5 kg was introduced into the Western Cape in 1910 for angling but although widely stocked, it currently only persists in the Breede River system in the Western Cape (Ellender and Weyl 2014). Adults are omnivorous bottom feeders that grub through soft sediments for insect larvae, worms, crustaceans and molluscs. There has not been any research into the ecology of this species in South Africa which, as a result of dietary overlap, has the potential to compete with native fishes and is likely to prey on native snails. As its feeding behaviour is similar to that of common carp, it is also likely to contribute to increased turbidity and nutrient cycling.

**Cichlidae**

Although several cichlid species have been introduced into the country, there is currently only evidence for the establishment of the Blue Tilapia *Oreochromis aureus* (Marr et al. 2018) and the Nile Tilapia *Oreochromis niloticus* (Ellender and Weyl 2014).

*Oreochromis niloticus* is a medium-sized fish (max 4 kg) that, as a result of its global importance in warm-water aquaculture, is one of the most introduced species in the world (Ellender et al. 2014). It was widely spread in neighbouring Zimbabwe and Mozambique for aquaculture in the 1980s, and its subsequent escape from captivity and direct releases by anglers facilitated its invasion of the Inkomati and
Limpopo River systems in South Africa. Impacts of invasions include decreased abundance of native congeners resulting from habitat and trophic overlaps, competition for spawning sites, and hybridisation (Ellender et al. 2014). In South Africa, hybridisation and potential loss of genetic integrity with native Mozambique tilapia Oreochromis mossambicus are the main concerns regarding its invasions (Ellender and Weyl 2014).

Oreochromis aureus was imported (as “Tilapia nilotica”) for experimental purposes from Israel to the Jonkershoek Hatchery near Stellenbosch in 1959 and released into farm dams in the Lourens and Eerste River catchments in 1961 and 1962 to evaluate its potential to survive the Western Cape winter (Marr et al. 2018). Its persistence in the Eerste River catchment was recently confirmed using morphological and genetic identification methods (Marr et al. 2018). Impacts on native biota are likely to be similar to those reported for O. niloticus, including hybridisation with, and loss of genetic integrity by, native O. mossambicus (Marr et al. 2018). The case of the O. aureus is interesting because it demonstrates the potential for the persistence of other introduced fish species that are presumed to have failed. These include the Red-bellied Tilapia Tilapia zilli, Threespot Tilapia Oreochromis andersonii and Nembwe Serranochromis robustus (Ellender and Weyl 2014).

Percidae
European Perch Perca fluviatilis was introduced in 1915 from England for angling in impoundments. Although this species favours slow flowing parts of rivers and still-water habitats in lakes and dams and can tolerate brackish water environments, naturalised populations are limited to a few small dams around the country (Ellender and Weyl 2014). It is not considered as an invasive threat.

Poeciliidae
The fish family Poeciliidae includes Mosquitofish Gambusia affinis, Guppy Poecilia reticulata, Southern Platfish Xiphophorus maculatus and Green Swordtail Xiphophorus helleri. Poecilids are small (<10 cm), live-bearing fishes that mature within months of birth. Early maturity together with an ability for females to “store” sperm and produce multiple broods in a season, results in rapidly growing population sizes (Sloterdijk et al. 2015; Howell et al. 2013). This, coupled with aggressive behaviour and generalist diet, has resulted in G. affinis and P. reticulata being considered among the world’s worst invasive species (Lowe et al. 2000).

Gambusia affinis was introduced into South Africa in 1936 to control mosquitoes; and was subsequently released into many watersheds for this purpose and as prey for introduced gamefishes (de Moor and Bruton 1988). Current distribution includes most of the southern drainages from the Great Fish River to the Berg River, as well as parts of the Limpopo and Mvoti River systems. Gambusia affinis are omnivorous, feeding on a variety of prey that includes small invertebrates, fish eggs and larvae, including cannibalism, as well as on vegetative material and detritus. There has been no research into the impacts of G. affinis on native biota in South Africa, but their diet often overlaps with that of native fishes and there is potential for competition with native fishes when resources are limited (Pyke 2008). Experimental work by Cuthbert et al. (2018), however, also highlighted that G. affinis select non-mosquito
crustacean prey over mosquitos, highlighting their potential for impact on a broad range of invertebrate taxa.

*Poecilia reticulata* and *X. helleri* are popular aquarium fishes native to freshwater and brackish water habitats in Central America. *Poecilia reticulata* was first introduced to the Western Cape from Barbados in 1912 for mosquito control but failed to establish as it is intolerant of temperatures below 15 °C (de Moor and Bruton 1988). Subsequent imports by the pet trade of *P. reticulata* continue because they are popular aquarium fishes. All naturalised populations in the wild occur warmer coastal regions of the country and are likely to be a result of direct releases by aquarists (Ellender and Weyl 2014). Impacts of established populations have not been studied in South Africa, but evidence from around the globe has shown that *P. reticulata* invasions deplete native fauna and alter ecosystems (El-Sabaawi et al. 2016).

*Xiphophorus helleri* and *X. maculatus* were likely introduced into the wild by aquarists releasing unwanted fish, and naturalised populations are restricted to urban environments in sub-tropical parts of KwaZulu-Natal (Ellender and Weyl 2014). Impacts, although poorly explored, are likely to be similar to those observed for *G. affinis* and *P. reticulata*.

**Salmonidae**

The family Salmonidae includes trouts and salmons, which are popular table and sport fishes. As popular angling species, they are among the earliest intentionally introduced fishes in the country. Atlantic Salmon *Salmo salar*, Brown Trout *Salmo trutta*, Brook Trout *Salvelinus fontinalis* and Rainbow Trout *Oncorhynchus mykiss* were introduced into the country in the late 1800s, and were released into the wild to develop angling opportunities for species familiar to European settlers (Ellender and Weyl 2014). *Salmo salar* and *S. fontinalis* failed to establish in the wild, but *S. trutta* and *O. mykiss* naturalised and are popular with recreational anglers (Weyl et al. 2017a, b).

*Oncorhynchus mykiss*, characterised by an iridescent pinkish lateral band, is native to North America but was introduced to South Africa for sport fishing in 1897. This species was subsequently released in many localities to sustain recreational angling (Ellender et al. 2014). In impoundments these fish can attain weights of 6 kg but fishes from naturalised populations in rivers seldom attain weights greater than 1 kg (Skelton and Weyl 2011). Naturalised populations are limited to cool, clear mountain streams, where their downstream spread is mediated by temperature (Shelton et al. 2018).

*Salmo trutta* is distinguished from *O. mykiss* by its brown colour and the presence of large reddish brown spots on its flanks. *Salmo trutta* were imported into South Africa from their native range in Europe in 1890. As is the case with *O. mykiss*, *S. trutta* were released into streams in mountainous regions. *Salmo trutta* has established in some mountain streams where maximum temperatures seldom exceed 17 °C and, because of their lower tolerance to high temperature, they are not as widespread as *O. mykiss* (Weyl et al. 2017a, b).

*Oncorhynchus mykiss* and *S. trutta* are generalist predators that through dietary interactions can impact on recipient ecosystems at numerous trophic levels (Weyl...
et al. 2017a, b). In South Africa, the two species have been linked to the decline, and in some cases local extinction, of native invertebrates, frogs and fishes (Karssing et al. 2012; Rivers-Moore et al. 2013; Shelton et al. 2015a; Jackson et al. 2016; Avidon et al. 2018). Shelton et al. (2015a) for example, demonstrated that the mean densities and biomass of the native Breede River Redfin *Pseudobarbus burchelli*, Cape Kurper *Sandelia capensis* and Cape Galaxias *Galaxias zebratus*, were 5–40 times higher in streams where *O. mykiss* were absent. Based on comparisons of insect communities, Shelton et al. (2015b) also demonstrated that, in the Breede River, *O. mykiss* do not functionally compensate for the native fishes that it has replaced, being weaker regulators of herbivorous invertebrates than native fishes. As a result, algal biomass is significantly higher at sites containing trout than at sites without (Shelton et al. 2015b). On a broader scale, Jackson et al. (2016) working on *S. trutta* invaded streams in the Drakensberg and Amathole mountains, demonstrated that emerging aquatic insects were less important in the diet of populations of terrestrial spiders alongside streams that were invaded by *S. trutta* than in those that were not. As emerging aquatic insects are an important source of energy and nutrient transfer from aquatic to terrestrial environments, the loss of this trophic subsidy is likely to have further reaching consequences than the reduced spider abundance reported by Jackson et al. (2016).

**Siluridae**

There is evidence for the introduction of two catfish species, the Highfin Pangasius (*Pangasius sanitwongsei*) and the Vermiculated Sailfin *Pterygoplichthys disjunctivus*. The occurrence of the *P. sanitwongsei* in the Breede River is considered incidental, based on the lack of evidence for reproduction (Mäkinen et al. 2013). *Pterygoplichthys disjunctivus*, an armoured catfish native to the Amazon River in Bolivia and Brazil is an important species in the pet trade that has colonised the Mthlatuze and Nseleni Rivers in KwaZulu-Natal after escaping from captivity (Jones et al. 2013). Its impacts are yet to be evaluated in South Africa, but elsewhere include siltation and shoreline instability resulting from the burrows constructed by breeding males into which females lay eggs; and potential displacement of native fishes (Jones et al. 2013; Hill et al. 2015).

### 6.3 Conclusion

South Africa’s geographic position and diverse landscape provides opportunities for establishment of both temperate and tropical freshwater species. This is illustrated in Fig. 6.7, which shows the extent of suitable habitat for *S. trutta*, a typical cold-water fish, a warm-water tilapia *O. niloticus*, and *M. salmoides*, which has a wide temperature tolerance (Fig. 6.7). Consequently, few introductions have failed and most of the freshwater biota that have naturalised have also become invasive (Table 6.1).

While many taxa are considered to have the potential for high impacts (e.g. Nunes et al. 2017; Marr et al. 2017), evidence for actual impacts in South Africa is scant
Fig. 6.7 Results of niche models fitted to the distributions of Brown Trout *Salmo trutta* which require cold (<9 °C) winter temperatures for spawning and do not establish in rivers where temperatures exceed 22 °C for more than a few days, Nile Tilapia *Oreochromis niloticus* which is a warm-water species that is intolerant of temperatures cooler than 14 °C, and Largemouth Bass *Micropterus salmoides* which have a wide temperature tolerance ranging from just above freezing to 34 °C.
(Ellender and Weyl 2014). This is problematic, as reported impacts cover all aspects of biological organisation from loss of genetic diversity resulting from hybridisation to native species extirpations resulting from direct predation by alien predatory fishes (Ellender and Weyl 2014). Preventing new invasions and containing existing ones is therefore important.

An examination of the current invasion status of freshwater biota and an analysis of the pathways associated with them (Fig. 6.8) provides some important insights

![Fig. 6.8](image-url) (a) Number of naturalised aquatic biota in South African freshwaters by decade, and (b) the pathway associated with their introduction into the country. Decade refers to the date that a taxon was shown to be present in the country.
into the future of freshwater invasions in the country. As management of invasive alien species is a legislated priority in South Africa, the likelihood of the importation of alien freshwater biota, such as fishes, for intentional release is limited. Indeed the number of naturalised fishes has been stable for several decades (Fig. 6.8). It is also likely that the trend in discovery of new alien invertebrate taxa will continue. This will be either the result of new invasions by contaminants or stowaways in the international trade or, as was the case with the crayfish *P. clarkii*, the result of discovery with increasing research effort. This is also true for alien molluscs, most of which have been identified in KwaZulu-Natal due to the greater search effort by the freshwater mollusc specialist Christopher Appleton, who is based in this region.

Knowledge requirements for the management of invasive alien biota in freshwater environments include data on their taxonomic diversity, distribution and impact. In South Africa, such knowledge is often limited to isolated case studies that lack the geographic coverage required for effective decision-making. As a result, greater investment in research securing contemporary data on all aspects of the invasion process is an urgent requirement.

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