

Chapter 8

Biological Invasions in South Africa's Offshore Sub-Antarctic Territories



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Abstract The sub-Antarctic Prince Edward Islands (PEIs) constitute South Africa's most remote territory. Despite this, they have not been spared from biological invasions. Here, we review what is known about invasions to the PEIs for terrestrial taxa (vertebrates, invertebrates, plants and microbes), freshwater taxa and marine taxa. Currently, Marion Island is home to 46 alien species, of which 29 are known to be invasive (i.e. they are alien species that have established and spread on the island). Prince Edward Island, which has no permanent human settlement and is visited only infrequently, has significantly fewer alien species: only eight alien species are known from Prince Edward Island, of which seven are known to be invasive. The House Mouse (*Mus musculus*), which occurs on Marion Island, can be considered the most detrimental invader to the islands; it impacts on plants, insects and seabirds, which result in changes to ecosystem functioning. The impacts of other terrestrial invaders are less well understood. At present, no invasive freshwater or marine taxa are known from the PEIs. We conclude by discussing how invasion threats to the PEIs are changing and how the amelioration of the climate of the islands may increase invasion threats to both terrestrial and marine habitats.

8.1 Introduction

South Africa's southernmost territory, the Prince Edward Islands (PEIs), consists of two islands: the larger Marion (~270 km²), and the smaller Prince Edward (~45 km²) Islands (Fig. 8.1a). The islands lie approximately 2000 km south-east of Cape Town,

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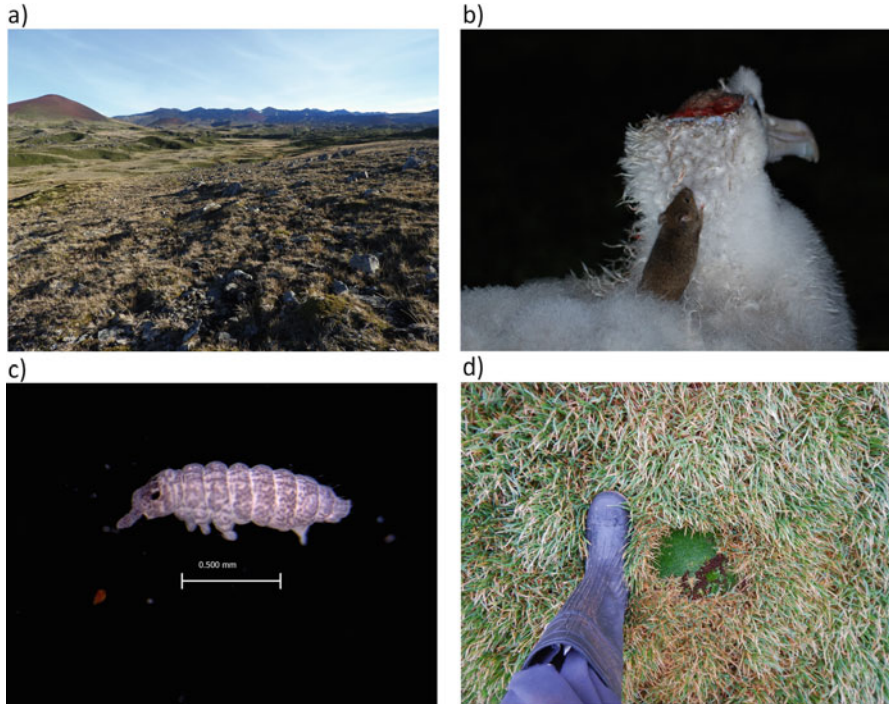


Fig. 8.1 (a) A view towards the interior of Marion Island. (b) A house mouse attacking a wandering albatross chick. Mouse-induced mortality amongst albatross chicks is high. (c) The invasive collembolan *Ceratophysella denticulata*. (d) A nutrient-enriched coastal site dominated by the invasive grass *Poa annua*. Additionally, a native *Azorella selago* cushion is being outcompeted by the invader *Sagina procumbens* (centre). Photographs: (a) M. Greve; (b) S. & J. Schoombie; (c) C. Janion-Scheepers; (d) M. Louw

in the cold, windy and wet Southern Ocean (Fig. 8.2). The PEIs are of volcanic origin (Boelhouwers et al. 2008). They support a variety of habitat types which are largely determined by elevation (cold high elevation areas are devoid of vascular vegetation), the age of volcanic activity and glaciation activity (older volcanic flows have often been exposed to glaciation), and, in the coastal zone, by nutrient inputs due to animal activity and salt spray (Boelhouwers et al. 2008; Gremmen and Smith 2008). The highest points on Marion and Prince Edward Islands are 1242 and 672 m above sea level respectively.

The PEIs are two of a group of sub-Antarctic islands, which are collectively considered to be some of the most isolated places on Earth. Much of the importance of the sub-Antarctic islands lies in the fact that they are the only pieces of land at high latitudes in the Southern Hemisphere. They are thus essential breeding grounds for several top oceanic predators (e.g. Reisinger et al. 2018), and are home to many unique organisms that occur nowhere else. Some species are endemic to one or few islands, while others are shared amongst several islands of the region (Greve et al. 2005; Griffiths et al. 2009; Shaw et al. 2010; Griffiths and Waller 2016).



Fig. 8.2 Position of the sub-Antarctic Prince Edward Islands in the Southern Ocean

Despite their isolation and their harsh climates, sub-Antarctic islands, including the PEIs, have not remained unaffected by humans, and biological invasions have had a major impact on their ecology. Indeed, it has been established that whereas sub-Antarctic islands with milder temperatures tend to support more invasive species (Chown et al. 1998; Leihey et al. 2018), the harsh climate of these islands does not provide a barrier to the survival of a significant number of global invaders (Steyn 2017; Duffy et al. 2017).

8.2 Human Activities at the Prince Edward Islands

The introduction of alien species is closely linked to the human history of the PEIs. The earliest recorded human landings of the PEIs were in the early nineteenth century, when exploitation of seals for commercial gain commenced (Cooper 2008). For the next 50 years, sealing activities on the islands were fairly intense. The presence of one of the first invasive species, *Mus musculus* (House Mouse), was recorded in writings from this time (Cooper 2008), and several plant species were also introduced during this period (le Roux et al. 2013b). By the middle of the nineteenth century, however, seal populations had been greatly reduced, which

Table 8.1 Numbers of known alien species currently present on Marion Island and Prince Edward Island by taxonomic group

Taxon	Marion Island	Prince Edward Island
Mammals	1 (1)	0
Crustaceans	1 (0)	0
Arachnids	6 (1)	1 (0)
Collembolans	5 (5)	1 (1)
Insects	14 (12)	3 (3)
Mollusca	1 (1)	0
Vascular plants	15 (7)	3 (3)
Bryophytes	2 (0)	0
Fungi	1 (0)	0

The numbers of alien species which are also known to be invasive (i.e. are known to have spread beyond the point of first introduction) are indicated in parentheses. These species include species classified as D1-E by Blackburn et al. (2011). Adapted from Greve et al. (2017) and van der Merwe et al. (2019)

meant that sealing became unprofitable and that human traffic to the islands became infrequent (Cooper 2008). In the austral summer of 1947/1948, the PEIs were annexed by the South African Government, and a meteorological station, which, in subsequent years was replaced by larger research stations, were established on Marion Island. A permanent human presence has been maintained on the island since then (Cooper 2008). The PEIs are currently designated as a Special Nature Reserve, which means that it is reserved for research and conservation management activities under permit only; tourist activities are not permitted on either of the islands (Republic of South Africa 2004). Marion Island currently has a permanent contingent of about 20–25 people living on the island for 13 months at a time. Island stocks are usually replenished once a year during April/May, when annual teams are replaced. During this time, additional personnel and scientists visit the island, so that the number of people on the island increases to approximately 80. In contrast, visits to Prince Edward Island are allowed only once every 4 years in terms of the islands' management plan (Department of Environmental Affairs Directorate: Antarctica and Islands 2010). As a consequence, Prince Edward Island supports significantly fewer alien species than Marion Island (Table 8.1, Greve et al. 2017).

8.3 Terrestrial Invasions

Invasive species are, along with climate change, considered to be the greatest threat to the terrestrial ecosystems of sub-Antarctic islands (Frenot et al. 2005).

Terrestrial invasions have led to population declines of several species and even local extinctions, and have impacted ecosystem processes and functioning (Frenot et al. 2005; McGeoch et al. 2015). Invasions have also led to greater taxonomic homogeneity amongst the islands, as many of the same species have become invasive across several of the islands (Greve et al. 2005; Shaw et al. 2010). The PEIs, and especially Marion Island, have not been spared this fate (Greve et al. 2017).

8.3.1 Vertebrates

Only one mammalian invader is currently present on the PEIs, namely *M. musculus*. The rodent occurs only on Marion Island, where it was introduced by sealers during the 1800s (Cooper 2008). *Mus musculus* is absent from Prince Edward Island.

Mus musculus on Marion Island has shown an increase in population density by about 430% over 20 years (McClelland et al. 2018), ostensibly due in part to the eradication of the feral cats (*Felis catus*) on Marion island (see below), but also because of an earlier onset of breeding season brought about by a reduction in winter rainfall (McClelland et al. 2018).

Of all invaders on the PEIs, *M. musculus* has the most severe, and best-studied, impacts (Zengeya et al. 2020, Chap. 17, Sect. 17.3). Several impacts on individual taxa have been recorded. These include impacts on a number of native plant species. The seeds of at least six native vascular plant species are consumed by *M. musculus* (Smith et al. 2002), with some species' seeds being taken at almost 100%, resulting in reduced reproductive output of these species (Chown and Smith 1993). *Mus musculus* also show a preference for creating the entrances to their burrows in the cushion-shaped keystone plant, *Azorella selago* (Avenant and Smith 2003). Such burrows can cause extensive damage to, and in some cases lead to mortality of, *A. selago* cushions (Phiri et al. 2009). Although mouse damage to *A. selago* cushions decreases with altitude, damage has been observed at relatively high altitudes (548 m) within almost 100 m of the altitudinal limit of *A. selago* on Marion Island (Phiri et al. 2009).

Invertebrates constitute the majority of *M. musculus*' diet on Marion Island (Smith et al. 2002; McClelland et al. 2018). It has been estimated that *M. musculus* has reduced total invertebrate biomass by more than 85% (McClelland et al. 2018). Although limited comparisons with mouse-free Prince Edward Island have shown no evidence of lower invertebrate populations on Marion Island (Hugo et al. 2006), it is thought that preferential consumption of large individuals by *M. musculus* has resulted in the body size of weevils on Prince Edward being significantly larger than on Marion Island (Chown and Smith 1993; Treasure and Chown 2014).

Most recently, *M. musculus* has been observed feeding on the live chicks of surface-nesting (Dilley et al. 2016) and on burrowing (Dilley et al. 2018) seabirds on Marion Island (Fig. 8.1b). The first such occurrence on Marion Island was only observed in 2003, where attacks on surface-nesting seabirds started, seemingly independently, at different sites simultaneously across the island (Dilley et al. 2016). The incidence of *M. musculus* attacks on affected populations of four seabird species was recorded to be high, with up to 9% chick mortality (once an attack has taken place) in surface-nesting species, and up to 100% mortality in burrowing species (Dilley et al. 2016, 2018) because chicks do not defend themselves against *M. musculus* attacks (Wanless et al. 2007). However, the occurrence of feathers in the gut content of *M. musculus* was recorded as early as the early 1990s and was initially put down to scavenging (Smith et al. 2002); it may well have been an earlier indication of active predation of seabirds by *M. musculus* (Smith 2008)—perhaps of the burrowing petrels.

Beyond affecting individual species, *M. musculus* also has impacts on ecosystem processes. It has been suggested that, especially due to their heavy predation on

invertebrates, decomposition and peat formation have changed on Marion Island (Smith 2008). More specifically, the reduction in decomposer invertebrates has resulted in lower breakdown of plant litter, lowering the availability of nutrients and slowing the growth rates of plants. This, in turn, is thought to result in slower accumulation of peats (Smith 2008).

Additionally, the burrowing activities of *M. musculus* affect geomorphic processes on Marion Island: soils are destabilised, erosion around burrows increases and temperatures around and in burrows increases (Eriksson and Eldridge 2014).

Rodents have been successfully eradicated from a number of islands (Howald et al. 2007), including several sub-Antarctic islands (Townes and Broome 2003; Martin and Richardson 2017; Springer 2018; <http://milliondollarmouse.org.nz/>). Given the wide-reaching, and seemingly increasing impacts of *M. musculus* on the terrestrial ecosystems of Marion Island, it is encouraging that a House Mouse (*M. musculus*) eradication programme for Marion Island is planned to be undertaken in 2021.

A second invasive mammal that had significant impacts on the island ecosystem did, for some years, occur on Marion Island: *Felis catus* (the Domestic Cat) (Zengeya et al. 2020, Chap. 17, Sect. 17.3). *Felis catus* were intentionally introduced in 1948 to control *M. musculus* populations in the meteorological station, but soon became feral. The diet of *F. catus* consisted mainly of burrowing petrels (*M. musculus* made up only app. 16% of their diet, van Aarde 1980), and it was therefore responsible for causing major declines in burrowing seabird populations, and the local extinction of at least one species (Bester et al. 2002). *Felis catus* was successfully eradicated from Marion Island in 1991 through a combination of hunting, trapping, poisoning, and biological control with a feline virus (Bester et al. 2002).

Other vertebrate species that were intentionally introduced to Marion Island to provide fresh food for sealers, or, more recently, for overwinterers after the establishment of the South African meteorological station, include *Sus scrofa domesticus* (Domestic Pig), *Ovis aries* (Sheep), *Capra hircus* (Goat) and *Gallus gallus domesticus* (Chicken) (Watkins and Cooper 1986; Greve et al. 2017). Additionally, *Canis lupus familiaris* (Domestic Dog) and two parrots were kept on Marion Island for companionship in the 1960s (Watkins and Cooper 1986). All these species either did not establish in the wild, or were subsequently removed from the island (Watkins and Cooper 1986; de Villiers and Cooper 2008; Greve et al. 2017). Based on evidence from other islands, it is highly likely that some of these species could have caused significant damage, had they persisted as self-sustaining populations (Frenot et al. 2001; Courchamp et al. 2003; Lecomte et al. 2013).

8.3.2 *Free-living Invertebrates*

The first summary of invasive insects of Marion Island was made by Crafford et al. (1986); this account listed nine species that were classified as alien and ‘naturalised’. Currently, a total of 27 invasive terrestrial invertebrate species is known from the PEIs (Greve et al. 2017). As with the continental areas of South Africa (Janion-

Scheepers and Griffiths 2020, Chap. 7, Sect. 7.2), the Lepidoptera are the invertebrate group with the highest number of invasive species, followed by the Diptera. An additional 15 species that have been recorded from the PEIs have not become naturalised on the islands. The number of invasive species is probably an underestimate, as the earthworms, nematodes and tardigrades have not been adequately sampled. As with other invasive taxa, Marion Island has more invasive terrestrial invertebrate species than neighbouring Prince Edward Island due to the strict regulations for visiting the latter island. Nevertheless, the potential for invasive invertebrates to be introduced to Prince Edward Island from Marion Island by means of birds or wind exists (Ryan et al. 2003).

Known pathways for introductions of invertebrates to the PEIs include as contaminants in fresh fruit and vegetables (no longer allowed ashore at either island), in dry-food stores, and in packing containers and building material (Smith 1992; Hänel et al. 1998; Slabber and Chown 2002). Evidence from invasive springtails (Fig. 8.1c) suggests that only a few individuals of a species are required for introductions to be successful (Myburgh et al. 2007).

The spread of invasive terrestrial invertebrates can vary substantially. For example, the Parasitic Wasp (*Aphidius matriciae*), first introduced in about 2001, spread at a rate of 3–5 km year⁻¹ and currently occurs across the island. Within 5 years, abundances of adults doubled whilst the percentage of parasitism in its host, *Rhopalosiphum padi* (Bird Cherry-oat Aphid), increased from about 7% to 30% (Lee and Chown 2016). On the other hand, it has been estimated that *Pogonognathellus flavescens* (Springtail), first recorded in 1993, will take centuries to spread around the island (Treasure and Chown 2013), and it is currently only known from a few localities.

The impacts of invasive terrestrial invertebrates are difficult to measure, but examples on other sub-Antarctic islands suggest that the high abundance of an invasive species can result in the displacement of native species (Convey et al. 1999; Terauds et al. 2011). On Marion Island, for example, the midge *Limnophyes minimus* significantly alters nutrient cycling in areas where it is very abundant (Hänel and Chown 1998). New interactions can also form among invasive species. For example, *A. matriciae* became a parasitoid of *R. padi* (Lee and Chown 2016).

The distribution of many invasive invertebrate species seems to be restricted to lower altitudes (Gabriel et al. 2001; Lee et al. 2007). This may be due to physiological or microclimate restrictions. For example, *Deroceras panormitanum* only occurs at altitudes up to 300 m, above which it is physiologically limited by low temperatures (Lee et al. 2007). However, as temperatures continue to increase on the PEIs (le Roux and McGeoch 2008), invasive invertebrate species are expected to expand to higher altitudes, either because they are able to cope physiologically, or because their host plants are also expanding their ranges in response to a milder climate.

Due to their size, abundance and wide distribution, the eradication of widespread invasive terrestrial invertebrates on the PEIs is not currently considered feasible. However, *Porcellio scaber* (Common Rough Woodlouse), which was restricted to the immediate vicinity of the old meteorological station, has been controlled with an insecticide since it was first discovered on Marion Island in 2012 (D. Muir, pers. comm). Ongoing monitoring will be needed to confirm its eradication.

8.3.3 Plants

Seventeen alien plant species are currently established on the Prince Edward Islands, of which all occur on Marion Island, and only three on Prince Edward Island. The first alien plants are thought to have been introduced to the PEIs by sealers. However, most introductions were probably associated with the importation of building material to Marion Island for the construction of the station and other infrastructure, and with fodder imported for sheep and chickens between the late 1940s and early 1970s (Gremmen and Smith 1999; Greve et al. 2017, Cooper et al., pers. comm.), though propagules of some alien species may well have been introduced with clothing and other outdoor equipment (Lee and Chown 2009).

Of the alien plants that have been introduced to Marion Island, some never naturalised, i.e. they were casual invaders and no longer occur on the island (Gremmen and Smith 1999). Other species remain localised in their distribution, despite the fact that several have been on the island for more than 50 years (le Roux et al. 2013b). It could be that these localised species are poorly suited to the sub-Antarctic environment; indeed, non-invasive and invasive alien species show consistent differences in their traits, which could support this explanation (Mathakutha et al. 2019). However, the possibility that these species are still in the lag phase of the invasion process (Crooks and Soulé 1999), and may spread in future, cannot be ruled out. Several of these localised alien species [e.g. *Festuca rubra* (Creeping Red Fescue) and *Rumex acetosella* (Sheep Sorrel)] are widespread across the sub-Antarctic islands (Shaw 2013). Given their success across the region, these species could spread more widely on Marion Island if control measures are not carried out (four populations of localised species on Marion Island are now regularly controlled with herbicides; Department of Environmental Affairs Directorate: Antarctica and Islands 2010). A single shrub of *Ochetophila trinervis* (Floating-heart), native to the South American Andes, is thought to have been introduced on Marion Island through natural dispersal by vagrant birds (and should thus be considered a native species) (Kalwij et al. 2019).

Of the 17 introduced plant species on the PEIs, 8 of the species on Marion Island and three on Prince Edward Island have become established and spread over substantial distances from likely sites of introduction (Greve et al. 2017), and are considered invasive (sensu Richardson et al. 2000). The invasive plants of the PEIs are of European origin and widespread across the sub-Antarctic region, occurring on several other islands (Shaw 2013). The invasive plants of Marion Island include three species in the Poaceae [*Agrostis stolonifera* (Creeping Bent Grass), *Poa annua* (Annual Meadow Grass, also present on Prince Edward Island, Fig. 8.1d) and *Poa pratensis* (Kentucky Bluegrass)], and three in the Caryophyllaceae [*Cerastium fontanum* (Common Mouse-ear Chickweed), also on Prince Edward Island], *Sagina procumbens* (Birdeye Pearlwort, also on Prince Edward Island, Fig. 8.1d) and *Stellaria media* (Common Chickweed)] (Greve et al. 2017).

The spread rates of invasive plant species on the PEIs have been estimated to vary between 0.13 and a fairly rapid 2.36 km² year⁻¹ (le Roux et al. 2013b). The spread of invasive plants on the PEIs is enhanced by a number of factors. On Marion Island,

humans have played an important role. Patterns of spatial occupancy of invaders suggest that invasions radiate out from human structures (*viz.* the research base and the field huts) (le Roux et al. 2013b). Additionally, disturbance caused by human trampling provides an opportunity for invaders to establish, increasing their cover and abundance (Gremmen et al. 2003). Disturbances along with nutrient addition that are associated with seal colonies further increase suitability for invasion (Haussmann et al. 2013). Coastal vegetation thus tends to be more invaded than inland vegetation (Greve et al. 2017). Birds also play a role: some invading plants, such as the grass *P. annua*, are associated with the burrows and nests of seabirds (Ryan et al. 2003), and it is thought that two (*S. procumbens* and *C. fontanum*) of the three invasive plants on Prince Edward Island were introduced from Marion Island with natural vectors—either by seabirds or by wind (Ryan et al. 2003).

Little is known about the impacts of plant invaders on Marion Island. Only the impact of *A. stolonifera* has been rigorously assessed (Gremmen et al. 1998). This grass species especially dominates drainage lines and slopes, where it is outcompeting native species, although it is not thought to threaten any native species with extinction (Gremmen et al. 1998). A more recent study that compared the plant and springtail communities associated with *S. procumbens* with those associated with two native plants that were being overgrown by *S. procumbens*, showed that epiphytic plant communities did not differ between the native and invasive host species. However, *S. procumbens* appeared to facilitate a higher richness and biomass (though not abundance) of invasive Collembola than did the native plant species (Twala 2018).

8.3.4 Microbes

Although microbes are some of the most readily transported, and thus most frequently introduced, group of organisms (Mallon et al. 2015), not much is known about their invasion ecology in the Antarctic region (Hughes et al. 2015). The microbiology of the PEIs has received little attention (Sanyika et al. 2012), and to date only one fungus, which is presumed to be invasive, has been recorded from Marion Island. *Botryotinia fuckeliana* is a fungal pathogen that attacks the leaves of the native *Pringlea antiscorbutica* (Kerguelen Cabbage), and is thought to have been introduced to Marion Island in fresh produce (Kloppers and Smith 1998).

8.4 Freshwater Invaders

Two species of trout, the Rainbow Trout (*Oncorhynchus mykiss*) and the Brown Trout (*Salmo trutta*), are the only non-native freshwater species that are known to have been introduced, and survived, on the PEIs (Watkins and Cooper 1986; Cooper et al. 1992). Both species were introduced to Marion Island, *O. mykiss* in 1959, and *S. trutta* in 1964. Neither are thought to have reproduced and both species are now extinct on the island (Watkins and Cooper 1986; Cooper et al. 1992). Stomach contents of the Brown Trout (*S. trutta*) revealed that the species had a fairly

impoverished diet, consisting mainly of terrestrial invertebrates; it is thus unlikely that the species had a major impact on the river system (Cooper et al. 1992).

Some algal surveys have been conducted on the PEIs (van de Vijver et al. 2008; van Staden 2011) but no alien species have been detected (Greve et al. 2017).

8.5 Marine Invaders

For the Southern Ocean, invasion of marine habitats by alien species is a widely-held concern (Barnes 2005; Frenot et al. 2005; Aronson et al. 2007). However, there are currently no known cases of alien marine species establishing anywhere in the region, including the Prince Edward Islands and surrounds (Barnes 2005). Nevertheless, the concern is well-founded as there have been several documented occurrences of alien marine species from the Southern Ocean (Ralph et al. 1976; Thatje and Fuentes 2003; Tavares and De Melo 2004).

At Marion Island, intertidal and subtidal shelf habitats have been periodically sampled over the past five decades, allowing a reasonable degree of confidence of the absence of marine alien species. The earliest descriptions of the subtidal macrobenthos and fishes come from the Challenger (1873) and Discovery II (1935) expeditions, while the intertidal habitats of Marion Island were first surveyed by Fuller (1967), with more detailed work following in the 1970s and 1980s (de Villiers 1976; Blankley and Grindley 1985). The shores were re-surveyed in 2017, and no alien species were recorded (M. Pfaff pers. comm.). Likewise, subtidal habitats on the north-eastern coast of Marion Island were surveyed by SCUBA divers to a depth of 15 m in 1988 (Beckley and Branch 1992). Extensive dredge and photographic surveys of the deeper benthos of the island plateau and shelf edge (35–750 m) were completed over the same period (Branch et al. 1993). This resulted in the production of detailed taxonomic keys and the description of several new species (e.g. Arnaud and Branch 1991; Branch et al. 1991; Branch 1994, 1998; Branch and Hayward 2007). These stations are now the subject of long-term monitoring by the South African Environmental Observation Network, with photographic resampling undertaken in 2013, 2015 and 2017. Although this work has identified shifts in the relative composition of benthic assemblages, no alien species have yet been recorded (von der Meden et al. 2017). A major caveat here, of course, is that the deep-sea (>800 m) benthic ecosystems surrounding the PEIs remain almost entirely unsampled, leaving the status of biological invasions in these environments unknown.

8.6 Changes to the Likelihood of Introductions and Spread of Invasive Alien Species

8.6.1 *Terrestrial Invasions*

As the role of the PEIs has changed from being mainly of commercial/exploitation interest (pre-annexation), to being a politically strategic outpost (post-annexation), to

becoming a sentinel for research and conservation (most recently) (de Villiers and Cooper 2008), the probability of introducing new invasive alien species to the islands has changed (Fig. 8.3). The islands were probably most vulnerable following annexation in 1948, when voyages to the islands were more common than prior to annexation (Cooper 2008), but when there was little awareness of invasions (de Villiers and Cooper 2008). During this period, several species were intentionally introduced, and others arrived accidentally (de Villiers and Cooper 2008; Greve et al. 2017). In the 1970s, concerns were raised about the threats posed by invasive species, and since then, policy governing movements to and from, and activities on, the islands has increasingly focussed on reducing the possibility of introducing new species to the PEIs (de Villiers et al. 2006; de Villiers and Cooper 2008; Department of Environmental Affairs Directorate: Antarctica and Islands 2010). Policies related to biological invasions focus mainly on preventing new introductions to the islands (Department of Environmental Affairs Directorate: Antarctica and Islands 2010); the introduction phase is the easiest and most effective stage at which to control invasions (Blackburn et al. 2011). Indeed, given the fact that introduction pathways to the PEIs are few and generally well-understood, and because the islands are highly isolated, the management of these pathways is much simpler than those associated with the South African mainland (Faulkner et al. 2016).

Not only the nature of human activities, but also the amount of human traffic to the islands affects the dynamics of invasions (McGeoch et al. 2015). The number of voyages to the PEIs has not increased recently. Only during the construction phase of a new research base on Marion Island (2003–2011) did the numbers of voyages undertaken increase from one per year to several per year. However, since the completion of the base, the number of research voyages is back one annually. (Some exceptions have occurred; for example, in December 2016, the Antarctic Circumnavigation Expedition stopped at Marion Island, and in the two subsequent

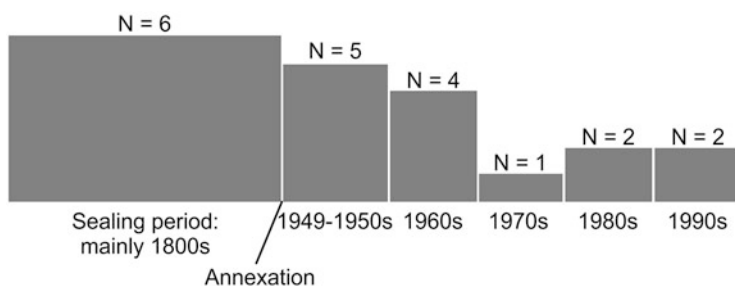


Fig. 8.3 The number of introductions of alien plants per time period to Marion Island since the island was first inhabited by people. Some dates of introductions are estimates, as it is difficult to determine exact dates of first introductions (le Roux et al. 2013b). Dates are taken from Greve et al. (2017). Two species listed in Greve et al. (2017) were not incorporated into this graphic: *Ochetophila trinervis* (first discovered in 2004) is thought to have been introduced through natural means (Kalwij et al. 2019). The “Unidentified plant” (first discovered in 2016) is a woody plant with a well-developed stem. It is thought that the plant has been growing on the island for some years, possibly decades; it is thus difficult to determine its date of introduction

years, an additional resupply voyage was required to supply the base). While visits to Prince Edward Island are permitted only every 4 years (Department of Environmental Affairs Directorate: Antarctica and Islands 2010), more than 4 years may pass without a visit.

The new base, and the new research and supply vessel, the *S.A. Agulhas II* (completed in 2012), house more people than did the old base and research vessel. Therefore, the numbers of people that arrive at, and overwinter on, the island annually has increased, which is likely to increase the opportunities for the introduction of new species (McGeoch et al. 2015).

Improved policy brought about by better awareness of the problem of invasions has resulted in lowered rates of introduction of terrestrial species to the islands, especially to the more frequently visited and inhabited Marion Island (Greve et al. 2017), and the eradication of some invasive species (Cooper et al. 1992; Bester et al. 2002), with efforts for the eradication of four localised alien plant species ongoing (DEA: Natural Resources Management Programme et al. 2012). However, despite strict biosecurity regulations, which include, amongst others, no tourism, a ban on fresh food or other biological material such as untreated wood, regulated checks on field equipment and containers, and the disinfection of footwear (Department of Environmental Affairs Directorate: Antarctica and Islands 2010), the success of these policies depend on awareness, buy-in and cooperation from the community that travels to the islands, and the effectiveness of policy implementation (McGeoch et al. 2015).

It has long been suggested that climate change will exacerbate the extent and impact of biological invasions (Dukes and Mooney 1999; Walther et al. 2002; Daehler 2003). This is also evident on the PEIs, where rapid climate change has been shown to benefit a number of invasive terrestrial taxa, including *M. musculus*, which have shown range expansions and increases in density over the past 20 years (McClelland et al. 2018), and several alien plant species, which have expanded their ranges up altitudinal slopes (Chown et al. 2012; le Roux et al. 2013a).

There is also evidence that climate change may benefit invaders into the future, often more so than native species. Physiological experiments on invertebrates such as springtails have shown that, for certain thermal traits, invasive alien species have higher phenotypic plasticity than the native species (Chown et al. 2007; Slabber et al. 2007; Janion et al. 2010). Also, invasive species survive longer under drier conditions when acclimated at warmer temperatures, whilst native species do not. Manipulative field experiments corroborate these findings: the abundance of alien species is higher under drier, warmer conditions (McGeoch et al. 2006). This could result in the displacement of native species by the abundant invasive species (Terauds et al. 2011), although the impacts on functional roles remains poorly understood. Finally, an increase in the frequency of low temperature events due to an increase in freeze-thaw cycles as a result of less snow and more clear-sky nights (Smith and Steenkamp 1990), are expected to alter the abundances and distribution of invertebrates species (Chown and Froneman 2008); this could indirectly affect assemblage-level function (Janion et al. 2009).

For plants, trait studies indicate that the leaves of invasive species on Marion Island have poorer defence mechanisms (including lower frost tolerance) than native

species; this suggests that invasive plants too will benefit more from a milder climate than native plants (Mathakutha et al. 2019).

More generally, climate matching approaches conducted across the sub-Antarctic islands suggest that these islands, including the PEIs, will become more vulnerable to invasions under climate change (Steyn 2017; Duffy et al. 2017).

8.6.2 Marine Invasions

The threat of marine invasions at the PEIs, and how these are changing, has received relatively little attention. Nevertheless, increasing vessel traffic in the Southern Ocean has been highlighted as a substantial factor promoting marine introductions (Barnes et al. 2006; Lee and Chown 2007; Hughes and Ashton 2017). Prolonged survival of hull-fouling marine taxa, including the highly invasive bivalve *Mytilus galloprovincialis* (Mediterranean Mussel), has been demonstrated on research vessels travelling to the Prince Edward Islands (Lee and Chown 2007). There is some consolation in the notion that the predominant direction of transport of any alien species via ship's ballast water is likely to be from the Southern Ocean northwards due to intake of ballast at destinations within the Southern Ocean. Conversely however, transport of hull-fouling communities is predominantly expected to be southwards following winter docking in mainland ports (Lewis et al. 2003).

There is an increasing likelihood that regions of the Southern Ocean will receive introductions of new marine species stemming from weakening or disrupted climatic and oceanographic barriers, and long-distance transport via kelp and plastic debris (Aronson et al. 2007; Fraser et al. 2018; Waters et al. 2018). This is particularly true with respect to the location of the PEIs relative to southward variations in the position of the sub-Antarctic Front and associated oceanographic eddies which, for example, are known to facilitate cross-frontal transport of zooplankton within the PEI region (Pakhomov and Chown 2003; Bernard et al. 2007). Technically, new introductions associated with kelp rafting would be considered natural range expansions, as they are not assisted by humans (Blackburn et al. 2011); however, new introductions associated with floating waste are considered to be invasion events (Gregory 2009). Indeed, the rise in anthropogenic debris (mostly plastic) globally means there is much more material on which marine species can raft (Barnes 2002; Eriksen et al. 2014). Despite the lowest colonisation rates for anthropogenic debris occurring at high latitudes ($>50^\circ$) globally, it is estimated that such material has tripled the transmission of fauna in these latitudes (Barnes 2002).

Targeted systematic long-term sampling of marine habitats, and meaningful oversight of ballast water and hull-fouling are essential to ongoing information gathering and prevention of marine invasions to the PEI. Although detection is difficult given the very large and inaccessible environment, including oceanic and deep benthos across the 500,000 km² exclusive economic zone, focused sampling efforts will provide some chance of early detection. Efforts should include well-defined sentinel areas such as intertidal shores and leeward anchorages, and opportunistic observations of benthic fauna brought up as bycatch from long-line fishing activities.

As is the case for the Southern Ocean generally, the risk of successful introductions at the PEIs are increasing as global climates are changing: due to the weakening and disruption of thermal and oceanographic barriers the islands become less isolated (Aronson et al. 2007; Fraser et al. 2018; Waters et al. 2018). The warming Southern Ocean and southward shifts in the Antarctic Circumpolar Current and associated Sub-Antarctic Front illustrate this, with the PEIs located directly in the path of southerly movements of the Sub-Antarctic Front and experiencing biological changes in benthic and zooplankton communities (Pakhomov et al. 2000; Hunt et al. 2001; Gille 2002; Mélice et al. 2003; Allan et al. 2013).

8.7 Conclusions

Recent decades have seen an increased interest in the invasion biology of the sub-Antarctic islands, including the PEIs (Greve et al. 2017). This has come with improved awareness and policies governing activities on, and movement to and from, the islands (See Department of Environmental Affairs Directorate: Antarctica and Islands 2010), and decreased rates of invasion (Fig. 8.3).

Some gaps in knowledge remain. These include taxonomic gaps: some groups have received little to no attention (Greve et al. 2017). Impacts of invaders other than *M. musculus* are also mostly poorly quantified. However, new opportunities also exist. The planned eradication of *M. musculus* from Marion Island in 2021 could bring about drastic changes in the abundance and composition of native species, species traits (e.g. body size of insects) (Treasure and Chown 2014), and in ecosystem processes and function. Additionally, Prince Edward Island, which is free from *M. musculus*, provides an excellent study system to understand whether Marion Island recovers to a “natural” state, or whether its ecology will take a trajectory different to what it would have been had *M. musculus* never been on the island; making this an interesting study system.

Although the PEIs have some of the strictest policies among sub-Antarctic islands regarding biosecurity (McGeoch et al. 2015), buy-in and enforcement of the policies are, at times, lacking. It therefore remains imperative that the policies for the PEIs are strictly adhered to and enforced, and that improvements in the policies are made when and where needed.

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