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CHAPTER 14

CONCLUSION: CHANGE IN TERRESTRIAL AND MARINE SYSTEMS

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The modern climate of the Prince Edward Islands has been described as one of the most oceanic and stable on earth (Schulze 1971; Van Zinderen Bakker 1978; le Roux 2008). Indeed, on the basis of the typically low daily amplitude of temperatures and their small variation between summer and winter, this characterization is correct. However, over both longer and shorter timescales, stability is something of a caricature. The islands have changed dramatically over the course of their history. Although much remains to be learned about the sequence of glaciation and volcanism on both islands (Boelhouwers *et al.* 2008), it is clear that they underwent considerable modification as a result of changing global climates and isostatic adjustment that was a consequence thereof.

Modern measurements of climate, which commenced in the late 1940s, have signalled ongoing change in climate too. Not only have mean annual temperatures increased and precipitation declined (Smith 2002; le Roux 2008), but a host of other changes have been effected to local climate. In turn these are thought to be having a variety of biological and geomorphological consequences. The former includes a significant increase in the effect of invasive species on local communities and species (Bergstrom & Chown 1999; Chown & Smith 1993; Chown *et al.* 2002), whilst the latter includes disappearance of Marion Island's ice plateau (Sumner *et al.* 2004), and thermal erosion and subsidence of areas previously underlain by buried glacial ice. Alterations in

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the number of clear sky evenings are also thought to be having significant biological effects (Smith & Steenkamp 1990; Sinclair & Chown 2005).

Recent work on microclimates has also drawn an important distinction between variability in thermal regimes and their predictability. Whilst a system with no variability is clearly predictable over a wide range of timescales, a highly variable system might be either predictable or unpredictable. For example, over a seven-day period, soil temperatures on the coast at Lambert's Bay, South Africa vary between 5°C and 24°C in a predictable fashion (Deere & Chown 2006). From one day to the next it is clear that the hottest time is just after noon, and the coldest about 11-12 hours later. By contrast, at sea level on Marion Island temperature is much less variable, but importantly also much less predictable. Whilst the overall range is 7°C at most, it is never quite clear at what times the highs and lows can be expected. Autocorrelation plots or spectral analyses reveal these substantial differences in predictability, with significant autocorrelation persisting for seven days in the Lambert's Bay data, but disappearing within 11 hours for Marion Island (Deere & Chown 2006). Whilst the importance of understanding both variability and predictability has been appreciated for some time (Kingsolver & Huey 1998), especially when distinguishing marine and terrestrial environments (Vasseur & Yodzis 2004), it is only more recently that the significance of this distinction for understanding climate change responses has come to be appreciated (Ghalambor *et al.* 2006; Chown & Terblanche 2007). Indeed, the unpredictability of thermal regimes in the temperate southern hemisphere (despite a lower overall range than in the north (Bonan 2002)) is thought to be an important driver of north-south differences in biodiversity, from the physiological to the species richness levels (Chown *et al.* 2004). Not only is unpredictability reflected in the responses of the biota on the Prince Edward to local environmental circumstances, but these responses also differ markedly between marine and terrestrial species, as might be expected from differences in the thermal regimes of the two environments (Deere & Chown 2006).

14.1 Historic change and evolutionary responses

How past glaciations and volcanism affected organisms and communities at the Prince Edward Islands is poorly understood. The responses of particular plant species and past vegetation dynamics are at least partly known. Paleoecological studies have demonstrated the absence during glacial maxima of many species typical of the islands' current assemblages, and a clear vegetation succession at other times (Boelhouwers *et al.* 2008). This succession has taken place many times and is typically one from barren fellfield to *Azorella selago*-dominated fellfield to *Agrostis magellanica* and *Acaena magellanica* peatland. What remains much less clear is how glaciation and repeated volcanic events affected evolutionary processes on the island. No studies have examined intra-island evolutionary dynamics of the indigenous plants, and even such basic questions as their current mode of pollination remain largely unanswered.

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Nothing is known about how past geological and climate events might have affected vertebrate populations. No sub-fossils (see Steadman 1995) are known from the islands and basalt is not fossil-bearing for obvious reasons. The 1980 volcanic event at Marion Island closed off a large haul-out area for Elephant Seals in the Kaalkoppie/Swartkop area of the island, but it seems that the seals simply moved to other beaches (M.N. Bester, personal communication). Given the mobility of the pelagic seabirds and seals, and genetic cohesion across the region amongst at least some of them (Burg & Croxall 2001), it seems likely that, despite their philopatry, local geological events would have had little, long-lasting effects on these predators. Nonetheless, even such questions as the likelihood of local population bottlenecks and the extent of migration between Marion and Prince Edward Island have not been addressed, with the exception of occasional reporting from elsewhere of animals tagged on Marion Island (Ryan & Bester 2008).

Evolutionary dynamics in the marine system are also poorly known. Whilst the biogeography of the fauna has been investigated (Chown *et al.* 2008), and regional events such as speciation in the notothenioid fish have been thoroughly examined (Bargelloni *et al.* 2000a, b; Verde *et al.* 2007), little detailed work on the phylogeography and population genetics of any marine taxa has been undertaken.

The situation with the terrestrial arthropods is different. Early work (e.g. Chown 1989, 1990a) suggested that a major evolutionary signal in the insects, both on the Prince Edward Islands and on the other South Indian Ocean Province Islands, is a clear division between the eplithic (coastal, fellfield, rockface) and the vegetated (lowland vegetation communities) biotopes. The former biotope is home to speciose assemblages, which are thought to have survived and in some cases speciated during Quaternary glacial events, and whose species are reasonably habitat specific. The latter is characterized by only a few, more modern species with low habitat specificity (Chown 1994). This signal has subsequently been verified for mites on the islands (Barendse *et al.* 2002) and for arthropods more generally across the Antarctic region (Marshall & Convey 2004).

More recent phylogeographic work has demonstrated that evolutionary dynamics on the islands are substantially more complicated than the above, rather simple scenario suggests. For example, it has long been presumed that amongst the weevils on the Prince Edward Islands, two vegetated biotope species exist which have recently speciated as a consequence of size-based assortative mating (Chown 1990b; Kuschel & Chown 1995). A combined morphological and phylogeographic study has revealed a more complex pattern, that is yet to be fully explained (Grobler *et al.* 2006). On Marion Island only a single, size-variable species apparently exists. By contrast, on Prince Edward Island, two species, which differ both in terms of their mitochondrial cytochrome oxidase I (mtCOI) sequences, and size, co-exist. The larger species has been designated a new one, *Ectemnorhinus kuscheli*, because both of the previously known species,

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E. similis and *E. marioni*, were described from Marion Island. How this situation has arisen is not clear. However, introgression of the previous species found on Marion Island may have been driven by a combination of a warming climate and substantial predation by house mice on larger weevils (Chown & Smith 1993; Grobler *et al.* 2006).

Amongst the terrestrial springtails and mites, substantial evidence of complex evolutionary events is also reflected in their phylogeography. In the indigenous springtails, haplotype diversity is extraordinarily high, especially in species such as *Cryptopygus antarcticus travei* (Myburgh *et al.* 2007), which, given its distinctiveness from other taxa with the same specific name, may represent a new species (Stevens *et al.* 2006). Moreover, this haplotype diversity is highly structured geographically, though not in a simple 'isolation-by-distance" fashion. Rather, disjunctions between localities and haplotypes seem to reflect particular geological events on the island including major glaciations and volcanic sequences. Moreover, some localities, such as Katedraalkrans, host a diverse array of haplotypes, indicating biological evidence for the status of the area as a glacial refugium, which is in keeping with geological evidence. The close match between the timing and spatial pattern of geological events and arthropod phylogeography is intriguing. It also includes other patterns, such as the remarkable dissimilarity of Kildalkey Bay to other localities, both amongst mites (Mortimer & Jansen Van Vuuren 2006) and springtails (Myburgh *et al.* 2007). Why this should be the case is not clear, although Kildalkey Bay has been identified as the likely site of first arrival for natural colonists of Marion Island (Chown & Avenant 1992).

Clearly, the study of past evolutionary dynamics on the island is in its infancy. However, modern techniques and an increasingly sophisticated understanding of the geological and climatological past of the islands suggest that such studies would provide considerable insight into the evolution of the islands' landscapes and biota. Some urgency for so doing also exists. Human activity is widely appreciated to lead to species introductions. More significantly, it has also led directly to changes in species distributions on the island (Chown *et al.* 2002). The longer the ongoing human activity, and the less attention given to quarantine procedures in transiting between one area and another, the more likely the historical signal is to be obscured by an anthropogenic one (Myburgh *et al.* 2007).

14.2 Modern change across the biological hierarchy

As is the case elsewhere in the world, three elements dominate modern change at the Prince Edward Islands: biological invasions, climate change, and exploitation. The two other significant threats to modern ecosystems, pollution (especially eutrophication) and habitat destruction (Millenium Ecosystem Assessment 2005), are of negligible importance on the islands. Contemporary human activity to date has been restricted to logistic operations and their scientific *raison d'etre* (De Villiers & Cooper 2008), and to long-line fishing (as

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opposed to trawling which is more destructive of the benthos, Watling & Norse 1998). The significance of the three change elements well represented on the islands differs among the terrestrial and the marine ecosystems, although the effects of these impacts cannot be entirely separated because of the close ties between the marine and terrestrial systems (Pakhomov & Chown 2003; McQuaid & Froneman 2008; Smith & Froneman 2008).

14.2.1 Biological invasions

In the terrestrial systems, commercial exploitation is non-existent. Small numbers of terrestrial species are harvested each year for scientific investigations, and typically the impact is considered negligible. By contrast, a wide range of species has been introduced, many of which are invasive and are having substantial effects on terrestrial species and ecosystems. The invasive species that wrought the most damage to terrestrial systems and species at Marion Island was the feral Domestic Cat. Although the introduced population was exterminated by 1991 (Bester *et al.* 2000), it caused substantial damage. Not only were hundreds of thousands of seabirds consumed as prey, but the cats are thought to have altered significantly nutrient dynamics at the island (Gremmen & Smith 2008). The large inland tussock grasslands previously associated with small burrowing seabird species and the manured slope crest communities typical of black lava areas have now both largely disappeared from Marion Island (see Smith 1978, 1987; Crafford & Scholtz 1986, 1987; Gremmen & Smith 2008), with a few notable exceptions in the former case. This may explain the difference in appearance of Marion Island now to what it was at annexation in 1947 when John Marsh (1948: 71) wrote: "Marion was a lovely picture. She rose, a jade jewel, out of the sea. Her lush green coat was fringed with the black lace of the cliffs and her heights draped in scintillating snow." On Prince Edward Island, large inland tussock grasslands and slope crest communities are still common. These differences between the islands, along with the presence of the feral House Mouse (*Mus musculus domesticus* – see Jansen Van Vuuren & Chown 2007 and below) on Marion Island, but not on Prince Edward Island, explain substantial differences in invertebrate assemblages and in ecosystem function, between them (Crafford & Scholtz 1987; Smith & Steenkamp 1990; Chown & Smith 1993). The eradication of cats has seen an increase in breeding success of several seabird species on Marion Island (Ryan & Bester 2008). Were all else equal, this might have spelled the return of the 'jade jewel'. Unfortunately, in modern systems, all else is rarely equal.

The direct impact of the feral House Mouse has been no less dramatic than that of the feral cats, but more controversial. Early studies noted substantial differences in invertebrate population densities between Marion Island and Prince Edward Island (Crafford & Scholtz 1987) and ascribed these partly to the presence of mice on the former. The predilection of mice for invertebrate prey, and especially caterpillars of the keystone, flightless moth, *Pringleophaga*

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marioni (see Smith & Steenkamp 1990, 1992) had been noted previously (Gleeson & Van Rensburg 1982). Subsequent empirical work, employing both temporal and spatial (among island) data, confirmed the direct impact of mice on prey such as weevils and flightless moth caterpillars, and their indirect effect on the distribution and abundance of the sedge *Uncinia compacta* (Chown & Smith 1993; Chown *et al.* 2002). Moreover, temporal studies also indicated that the importance of caterpillars in the diet of mice had declined from the late 1970s to the early 1990s (Smith *et al.* 2002), presumably reflecting a decline in prey abundance.

By contrast, later experimental exclusions of mice from fixed size plots provided no indication of changes in abundance, diversity, biomass or assemblage composition (Van Aarde *et al.* 2004). However, the authors of the work concluded that the statistical power of the experiments might have been too low to detect differences. The short duration of the experiment (four years) relative to the presumed lifespan of some of the key prey species (five years or more for *P. marioni* – Crafford 1990; at least one year for the weevil *E. similis* Chown & Scholtz 1989) may also have precluded detection of an exclusion effect. Further work, designed to test ideas that mice are food limited or are hampered by climate, which form the basis of the hypothesis that climate change is affecting mouse densities, in turn causing elevated impacts on invertebrate prey and substantial ecosystem effects (Smith & Steenkamp 1990), has continued to unveil the complexity of the situation (Van Aarde & Jackson 2007). Food supplementation did not alter overwinter survival or reproduction, although it did enhance survival during summer, suggesting a more important role for low temperatures *per se*. Increasing temperatures at the island are leading to enhanced population densities, but in turn density-dependent regulation suggests that these changes might not be as significant as previously suspected (Ferreira *et al.* 2007). Nonetheless, these studies and others suggest that low winter temperatures are limiting for the mice and that population densities now are higher than they were in the 1970s, probably as a consequence of changing climates, but not as a consequence of reduced cat predation (Ferreira *et al.* 2007).

These increases in population density are likely responsible for the substantial decline in biomass of *P. marioni* caterpillars and of weevil larvae in *Poa cookii* tussock grasslands on Marion Island (*P. marioni*: 802 to 47 mg. m^{-2}; *E. similis*: 375 to 45 mg. m^{-2}), and a similar decline in *Crassula moschata*-dominated plant communities (*P. marioni*: 683 to 20 mg. m^{-2}; *E. similis*: 305 to 56 mg. m^{-2}) (Chown *et al.* 2002). Moreover, a more detailed comparison of weevil body sizes among both islands, and including samples taken at various intervals over 20 years, and 4 000 year old samples retrieved from peat cores, supported previous conclusions (Janse Van Rensburg 2006). Thus, whilst adult weevil body sizes have been declining overall in step with increasing temperatures (see Chown & Klok 2003; Kozłowski *et al.* 2004 for a discussion of the likely mechanistic basis of this decline), a strong signal of the indirect impact of

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mice on weevils is nonetheless present. That is, adult weevils of a given species on Prince Edward Island are typically larger than those on Marion Island, presumably owing to the preference of mice for larger-bodied prey (Chown & Smith 1993). This size-selective predation is also thought to be responsible for genetic introgression of two weevil species that once co-existed on Marion Island (Grobler *et al.* 2006).

More recently, mice have been documented feeding directly on seabird chicks, including those of large species such as albatrosses. Early reports were confined to Gough Island (Jones *et al.* 2003; Cuthbert & Hilton 2004). However, it now appears that mice may be having similar effects on seabirds at Marion Island. Thus they constitute a direct and very real threat to seabird populations, possibly throughout the region (Wanless *et al.* 2007).

The impacts of other invasive species have been no less extensive. Plants such as the Procumbent Pearlwort (*Sagina procumbens*) and the grass *Agrostis stolonifera* have substantially altered terrestrial systems (Gremmen *et al.* 1998; Gremmen & Smith 1999). In the latter case, the grass displaces *Acaena magellanica* herbfield from river banks and can lead to a 50% reduction in plant species richness, and a substantial change in invertebrate assemblages in these areas (Gremmen *et al.* 1998). Other vascular plant invaders are having similar impacts (Gremmen & Smith 2008). In addition, some species, such as *Cerastium fontanum*, previously thought to be of little importance, are steadily increasing their abundance and distributional range on Marion Island (N.J.M. Gremmen, personal communication) with little known about the likely effects thereof. On Prince Edward Island, both *S. procumbens* and *C. fontanum* are increasing their ranges, and it seems likely that at least the former species will substantially alter ecosystem functioning at the island, in much the same way it has done on Marion Island (Ryan *et al.* 2003). The recent colonization of Marion Island by a cosmopolitan rush, *Luzula cf. multiflora*, near Sealers Cave, by an unknown thorny shrub (close to Johnny's Hill), and by *Agrostis gigantea* at the scientific station, are all testimony to ongoing colonization processes, either with or without human assistance.

What the impacts are of the introduced invertebrates is more difficult to gauge. Earthworms contribute substantially to nutrient cycling (Smith & Steenkamp 1992, 1993) and it is thought that at least one species is introduced. The very high densities of small introduced species, such as larvae of the midge *Limnophyes minimus*, are also thought to have substantially altered nutrient cycling (Hänel & Chown 1998), and this must be true also of invasive springtails, which often reach densities of tens of thousands of individuals per square metre in mire and other communities (Gabriel *et al.* 2001). In this regard, the recent introduction of the woodlouse *Porcellio scaber* (Slabber & Chown 2002) is concerning, given the total absence of large terrestrial crustaceans from the terrestrial ecosystem throughout its history. Likewise, although the recently introduced wasp *Aphidius matricariae* is a parasitoid of an introduced aphid species (*Rhopalosiphum padi*), its presence has substantially increased ecosystem

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complexity on the island (Lee *et al.* 2007). Previously, insect parasitism was unknown in the vegetated biotope, although in the eplithic biotope parasitism of the fly *Apetaenus littoralis* by the wasp *Kleidotoma icarus* has long been known (Crafford *et al.* 1986). Phylogeographic investigations both of this wasp and of several introduced springtail species (Myburgh *et al.* 2007) have revealed that each species is characterized by a single haplotype. Such low haplotype diversity suggests that successful colonization requires only a few individuals, as has been suggested for arthropod biological invasions on other Southern Ocean islands and elsewhere (Gaston *et al.* 2003). Therefore, propagule pressure, which is thought to be a significant factor explaining introduction success (Lockwood *et al.* 2005), is perhaps not as important in small arthropods as it is in other groups such as plants and birds.

The nature and extent of marine invasions at the Prince Edward Islands is not clear, largely owing to a lack of work on this topic. Recent studies have demonstrated that potentially invasive species such as the Mediterranean Mussel, *Mytilus galloprovincialis*, are regularly transported to the Prince Edward Islands by the research and supply vessel *S.A. Agulhas* (Lee & Chown 2007). It seems likely that other vessels have similarly transported organisms to the islands in their sea chests, as hull fouling, and in ballast water. Indeed, such transport is typical of Antarctic shipping in general, especially for vessels that might have long port layovers before proceeding south (Lewis *et al.* 2003, 2006). Offshore ecological surveys have not identified invasive species to date (Beckley & Branch 1992), although species previously thought to be cosmopolitan may in fact have a local history dating back to the arrival of the earliest sealing vessels (Lewis 2006). Ballast water exchange is also typically not in the right direction, given that cargo is mostly discharged at the islands. Nonetheless, ongoing increases in sea temperature (Mélice *et al.* 2003; le Roux 2008) and a change in zooplankton assemblages to more temperate than Antarctic (Pakhomov & Chown 2003), suggest that the potential for colonization by accidentally introduced marine species is increasing. The need for further work to clarify the pathways for and extent of marine introductions (if any) at the islands, and to identify the ways in which the pathways may be narrowed or closed, is therefore urgent.

14.2.2 Climate change and terrestrial systems

Substantial and ongoing change in the climate of the Prince Edward islands, associated with global climate change, has now been recorded in a variety of studies (summarized in le Roux 2008). From a biological perspective, it is not only the general trend of warming, and in terrestrial systems of drying, that is of significance, but also an increase in the incidence of additional solar radiation and clear-sky days, and increase in wind strength and a change in its direction.

Changing temperature regimes are unlikely to have a major direct effect on terrestrial invertebrates, at least as far as absolute temperature tolerances are

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concerned. These traits have been studied in a wide variety of species found on the island from several perspectives (e.g. Van der Merwe *et al.* 1997; Klok & Chown 1997, 1998, 2000, 2001, 2003; Sinclair & Chown 2003; Sinclair *et al.* 2004; Slabber & Chown 2004, 2005; Deere *et al.* 2006; Deere & Chown 2006; Slabber *et al.* 2007; Terblanche *et al.* 2007). Consideration of absolute thermal tolerances in the context of microclimate temperatures has shown that few species are likely to be unable to survive several degrees increase in temperature (Slabber 2005), although where this is the case it is clear that invasive species are more tolerant of high temperatures than their indigenous counterparts. The converse is also true, with indigenous species tending to be more tolerant of low temperatures than the invasives (Slabber *et al.* 2007). For example, the invasive slug *Deroceras panormitanum* is unable to survive more than a few degrees below 0°C, following which individuals freeze and die. The slug is typically restricted to altitudes below about 300 m, above which winter temperatures regularly decline below its lower lethal temperature of the slug. Only on the western coast, where winter temperatures tend to be higher (McGeoch *et al.* 2008), does this species occur above 300 m. Although this close fit between tolerance and altitudinal distribution would seem to militate against rapid spread of the slug around the island, given several high altitude barriers such as Long Ridge, this has not happened. Rather, humans have spread the slug by helicopter operations to hut sites around the island and the species has spread from these foci (Smith 1992; Chown *et al.* 2002).

Phenotypic plasticity is also thought to be a way in which organisms respond rapidly to environmental change (reviewed in Chown & Terblanche 2007), and indeed it has been suggested that invasive species should be more plastic than indigenous ones (Daehler 2003; Duncan *et al.* 2003). At least in the isotomid springtails this does seem to be the case for certain thermal tolerance traits (Slabber *et al.* 2007). However, in the case of temperature effects on desiccation resistance (Chown *et al.* 2007), a major factor influencing responses to global change type drought (Easterling *et al.* 2000) of the kind happening on and forecast for Marion Island, responses are more complex. Rather than differences in plasticity *per se*, it is the direction of this plasticity that differs. Thus, invasive species show an improvement in desiccation resistance when exposed to high temperatures, whereas the converse is true of the indigenous species. This may account for the substantial declines in abundance of most of the indigenous species, but little change in the abundance of the invasives, in response to simulated warming and drying (McGeoch *et al.* 2006).

An increase in the number of clear sky nights may also have a profound effect on invertebrates because of an increase in the frequency of freeze-thaw events (Smith & Steenkamp 1990). For example, caterpillars of the flightless moth *P. marioni* can tolerate freezing as long as temperatures do not decline below about -6°C (Klok & Chown 1997). In addition, they can also survive (to pupation) several successive bouts of freezing and thawing (Sinclair & Chown 2005). However, the effects of repeated exposure to low temperature (not

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necessarily accompanied by freezing) is deleterious, with caterpillars showing substantial declines in gut mass and a reduction in growth rates. An increase in the frequency of freeze-thaw cycles is therefore likely to have a marked influence on the population dynamics of this significant keystone species.

Likewise, if the cold hardiness strategy of freeze tolerance is typical of species found in unpredictable environments where temperatures remain close to zero (Sinclair *et al.* 2003; Chown *et al.* 2004), then species which do not utilize this strategy might well find themselves at a disadvantage compared with those that do, as freeze-thaw cycles increase in frequency. On Marion Island freeze tolerance is common among the insect species, but both mites and springtails are constrained to a strategy of freeze intolerance (Sinclair *et al.* 2003). Whether such relative differences in advantage will be detected by selection, above the direct effects of climate change on biological rates and its indirect effects on interactions between invasive and indigenous species, is difficult to tell.

Although physiological tolerances set the limits to performance, within these limits temperature nonetheless has a strong effect on performance in ectotherms because of its effect on physiological processes. Whilst individuals are not at the mercy of the temperature effect (the tyranny of Boltzmann, *sensu* Clarke & Fraser 2004), and can indeed respond over the short term to changes in thermal regimes (Hochachka & Somero 2002; Chown & Terblanche 2007), population responses may be constrained in various ways. Several studies have suggested that indigenous insect species may have shallower rate-temperature curves than their introduced counterparts (summarized in Chown *et al.* 2002), and this also appears to be the case in several species of springtails (C. Janion, H.P. Leinaas & S.L. Chown, unpublished data). What the long-term consequences of these changes in relative advantage of the indigenous and invasive species are likely to be, is not known. However, indigenous springtails are typically rare in lowland areas, whilst invasive species are absent from the highlands (Gabriel *et al.* 2001). Moreover, it has been suggested that at the sub-Antarctic island of South Georgia, invasive springtails have displaced their indigenous counterparts in low elevation communities (Convey *et al.* 1999). If the manipulative experiments undertaken in an *A. selago*-dominated fellfield (McGeoch *et al.* 2006) prove to be an accurate reflection of responses to change, then such displacement can also be expected at the Prince Edward Islands. Nonetheless, the effects on Prince Edward Island may be less pronounced given the absence of many invasive species there (Crafford *et al.* 1986; Hugo *et al.* 2006).

Curiously, despite substantial understanding of plant community structure and productivity (summarized in Gremmen & Smith 2008; Smith 2008; Smith & Froneman 2008), little is known about the likely direct responses of individual species to climate change. Some early work demonstrated that the sedge *U. compacta* is increasing its range on Prince Edward Island as a consequence of warming and drying, but is being prevented from doing so on Marion Island because of seed harvesting by mice (Chown & Smith 1993).

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It has also been suggested that climate change may be enhancing the rate of spread of some alien vascular plant species at the island (Chown *et al.* 2000). However, increasing human traffic (owing to the cat eradication programme – see Bester *et al.* 2000) over the same period that the plants showed range expansion confounds interpretation to some extent. Only more recently have investigations commenced to understand changes in the altitudinal distributions of species, based on comparisons of modern data with that from careful studies made in the 1960s (Huntley 1970). This work is being accompanied by detailed investigations of the keystone cushion plant *A. selago* (le Roux *et al.* 2005; McGeoch *et al.* 2008), and interactions between the plant and the local landscape on the Marion Island. Not only is ongoing warming and drying likely to see increases in the upper elevational range of this species, but overtopping and dieback at low altitudes will probably lead to a decline in abundance at low altitudes (le Roux *et al.* 2005).

Understanding of the assemblage level effects of climate change on plants is equally poorly developed. However, this owes nothing to a lack of appreciation for the importance of doing so, and everything to the difficulty of disentangling short-term variability from long-term climate change-related effects. Many studies have made clear the substantial small-scale variability in plant assemblages at the Prince Edward Islands, associated with minor changes in topography, water availability, manuring and salt spray (Gremmen 1981; Smith *et al.* 2001; Gremmen & Smith 2008). Year to year variation in these factors has to be distinguished from long-term trends if change at the plot scale is to be correctly interpreted. Doing so requires observations over decades or, especially in the case of interactions between indigenous and invasive species, the kind of experimental work that is often frowned upon in an IUCN category I reserve. Given that few studies have been set up to do the former (and even these may fail given inappropriate time scales – see above), and the difficulty of overcoming the latter, understanding of climate change effects at this level are some way away. Nonetheless, judicious mesocosm-type studies and ethical manipulative field experiments (le Roux *et al.* 2005; McGeoch *et al.* 2006) may provide the required insights.

14.2.3 Climate change and marine systems

The impact of global climate change on the marine ecosystem of the Prince Edward Islands is only now receiving attention (Pakhomov & Chown 2003; McQuaid & Froneman 2008). Global climate change in the Southern Ocean is causing shifts in the position and intensity of the major frontal systems and changes in oceanic circulation patterns within the region of the islands. The change in ocean circulation patterns will influence the generation of far field eddies upstream of the islands resulting from the interaction of the Antarctic Circumpolar Current with the southwest Indian ridge (Lutjeharms & Ansorge 2008). Preliminary data suggest that these eddies represent important foraging grounds for several top predators found on the islands, due to the elevated

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macrozooplankton stocks within these features (McQuaid & Froneman 2008). Global climate change will therefore be associated with a change in the offshore food delivery to the island top predators.

The most direct effect of a meridional shift in position of the SAF has been on the species composition of the zooplankton. Over the past two decades the contribution of Antarctic species has decreased by some 20%, while at the same time, the contribution of subtropical species has increased from 6% to 26% (McQuaid & Froneman 2008). The more frequent intrusion of sub-Antarctic surface waters into the polar frontal zone will likely also result in a decrease in the total zooplankton biomass in the vicinity of the Prince Edward Islands because sub-Antarctic surface waters typically show low productivity.

Less direct than the effects of long-term changes on species composition, but perhaps more significant, are changes in hydrodynamics around the islands. These are resulting in less frequent retention of water over the island, and more common through-flow conditions (McQuaid & Froneman 2008). These changes in turn have resulted in less frequent diatom blooms over the plateau, and changes in foraging distances for land-based predators on the islands. Thus, $\delta^{13}C$ values of the swimming prawn *Nauticaris marionis* have undergone a significant decrease over the period 1984 to 2000 suggesting a shift in the primary carbon sources utilised by the shrimp. In addition, the period over which the SAF has shifted south has seen medium- to long-term increases in populations of offshore feeding birds such as Grey-headed Albatrosses and Northern Giant Petrels, that are likely to feed at the front, and a simultaneous decline in inshore feeders such as Rockhopper Penguins (Pakhomov & Chown 2003). Interestingly, species with mixed diets, like the Macaroni Penguin, have shown relatively more stable populations over the corresponding period. Patterns for smaller petrel species are difficult to gauge because they are not so readily monitored (Ryan & Bester 2008). Interactions between climate-induced changes in population size, the short-term impacts of incidental mortality (Ryan & Bester 2008), and the measures taken to reduce this mortality make forecasts of future trends complex.

14.2.4 Exploitation

With the exception of the use of lowland areas on the island for grazing by a small flock of sheep, a practise abandoned in the 1970s, no exploitation of the terrestrial environment has taken place at the islands (Cooper & Condy 1988). Habitat destruction has been limited to the small area of the scientific station (though recently the area has more than doubled owing to the construction of a new facility), to the immediate areas occupied by field huts, and to a small, dysfunctional hydroelectric plant and dam on the Van den Boogaard River, which has now been decommissioned (the Hydro Shack and Dam remain). Each year, relatively small numbers of samples are taken for scientific purposes, but the impact of this sampling is considered minor or transitory, and is regulated by South African law (see De Villiers & Cooper 2008). Past

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removal of geological and archaeological souvenirs has substantially depleted the numbers of 'volcanic bombs' found on the island, and has affected several sites of historical significance. Such practices are now prohibited.

Records of direct marine exploitation prior to the 1990s are scant, although anecdotal evidence exists that fishing vessels, especially from the Soviet fleet, visited the area (Cooper 2008). Very much earlier, during the 18th and early 19th centuries, commercial sealing severely reduced fur seal populations in the Southern Ocean, resulting in local extinctions at some sites. Populations at the Prince Edward Islands did not escape the effects of sealing (Cooper & Headland 1991), although the islands supported one of only three remnant populations of sub-Antarctic Fur Seals (Ryan & Bester 2008).

A legal fishery for Patagonian Toothfish *Dissostichus eleginoides* began in the islands' Exclusive Economic Zone in 1996, but illegal vessels had already been operating in the area for several years, ultimately leading to near-collapse of the fishery (Pakhomov & Chown 2003). The intense exploitation of this top predator is likely to have far reaching effects on the marine ecosystem community structure and functioning in the immediate vicinity of the islands. The extent of this impact, however, remains unclear. The illegal fishery was also responsible for substantial incidental seabird mortality (Ryan & Bester 2008). For example, it is estimated that over the four peak years of the fishery 6 000-14 000 White-Chinned Petrels and 1 000-2 500 Grey-Headed Albatrosses were killed. Several seabird species continue to suffer the effects of incidental mortality associated with various fisheries, given that their large foraging ranges overlap with these fisheries (De Villiers & Cooper 2008; Ryan & Bester 2008). Substantial efforts are underway by international organizations and via the Agreement on the Conservation of Albatrosses and Petrels to reduce the incidental impacts of fishing on pelagic seabirds, though Illegal, Unreported and Unregulated fishing continues to pose considerable problems (De Villiers & Cooper 2008). Recently, steps have been taken to declare a large Marine Protected Area (MPA) around the Prince Edward Islands, including nearby seamounts (Lombard *et al.* 2007). This MPA should substantially reduce threats to commercially significant species, and improve the conservation prospects for several of the pelagic predators nesting on the islands.

14.3 Land-sea interactions in a changing ecosystem

Marsh's (1948) 'jade jewel' and 'scintillating snow' description of Marion Island has become iconic. This is not because the island's modern appearance can be accurately captured by Marsh's phrase, but rather because the opposite is true. The permanent snow and ice have largely melted and the island is more brown now than green. These differences reflect the impacts humans are having on the Prince Edward Islands, as a consequence of their global, industrial activities, their local habit of accidentally or intentionally introducing species to places from which they were previously absent, and their need for resources to fuel a growing population, segments of which have an increasingly

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sophisticated desire for rare resources. This triumvirate of impacts has altered the Prince Edward Islands in a wide variety of ways, and in so doing has demonstrated that conservation of one component of the system cannot hope to succeed without attention being given to all others. A final example clearly illustrates this point.

Caterpillars of the flightless moth, *P. marioni*, are keystone species, representing a major conduit for nutrient cycling in terrestrial systems (Smith & Steenkamp 1990, 1992). They are also the preferred prey species of introduced House Mice (Smith *et al.* 2002), and are susceptible to frequent low temperature events (Sinclair & Chown 2005). Recent work has shown that the caterpillars have much higher and considerably less variable populations in recently abandoned Wandering Albatross nests (and presumably also in occupied nests) than in old nests and in other plant communities (Sinclair & Chown 2006). The reasons for this pattern are simple. Wandering Albatross nests are occupied for close to a year and have temperatures elevated by at least 5°C above ambient. Caterpillars are likely to show higher survival and growth rates in nests than elsewhere because of the elevated temperatures. Indeed, these nests may serve as a source for the population. Thus, a pelagic predator not only contributes nutrients to the system, with direct effects on the dynamics of vegetation and some of the invertebrates dependent on it (Smith 1978; Crafford & Scholtz 1986), but acts as a thermal ecosystem engineer for a species crucial to nutrient recycling in all communities. A closer and more complex interaction between the land and sea environments is difficult to envisage.

Future work will have to explore these interactions more closely. In this regard, the declaration of a large marine protected area around the islands (Lombard *et al.* 2007) is timely. This book has also made it clear that comparisons of the relative merits of Marion and Prince Edward Island from a conservation perspective, as is often done (Chown *et al.* 2001), are helpful more from a theoretical than a practical perspective. The islands and the marine environment within which they are embedded simply cannot be managed separately. Therefore, if, to use Marsh's words, there is anything in the region of 'little charm of appearance', it is lack of appreciation for the integrated nature of the Prince Edward Islands ecosystems.

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