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CHAPTER 1

The Prince Edward Islands in a global context

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The history of the planet is one of change. Continental positions have moved, sea-levels have advanced and retreated, mountains have been formed and eroded, climates have varied from warm to cool and back again, and life has responded to and sometimes driven these processes, with species and higher taxa waxing and waning for the last several billion years (Stanley 1989; Behrensmeyer *et al.* 1992). More recently, humans have come to influence these changes. Our recent history has been one of significant effects on the abiotic environment, including elevation of atmospheric greenhouse gas concentrations, depletion of stratospheric ozone, and alterations to the global climate (Watson 2002; Domack *et al.* 2005). In turn, changing climates have had and continue to have profound effects on biodiversity, ranging from population and species loss (Pounds *et al.* 2006) to alterations in species distributions, changes in phenology, and shifts in ecological regimes (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003).

Humans have also had profound direct effects on landscapes, populations and species. Habitat destruction and transformation have been responsible for considerable biodiversity loss, with co-extinctions exacerbating the scale of the problem (e.g. Beier *et al.* 2002; Brooks *et al.* 2002; Koh *et al.* 2004; Dunn 2005; Millennium Ecosystem Assessment 2005). Likewise, direct and indirect

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utilization has meant that many species are critically endangered (Baum *et al.* 2003; Brashares *et al.* 2004; Pauly *et al.* 2005). As a consequence of human activities such as trade and shipping, the movement of species from their indigenous ranges to areas where they have previously not occurred, is also having significant effects on global biodiversity (Mack *et al.* 2000; Bax *et al.* 2001; Grosholz 2002; Blackburn *et al.* 2004; Drake & Lodge 2004; Richardson & Van Wilgen 2004; Cassey *et al.* 2005). The interactive effects of invaders can lead to wholesale ecosystems changes, termed invasional meltdown (O'Dowd *et al.* 2003; Sanders *et al.* 2003; Grosholz 2005), and the extent and pace of invasion globally (e.g. Gaston *et al.* 2003) has led many to suggest that the next period in the earth's history might be one of substantial biotic homogenization (McKinney & Lockwood 1999; Olden *et al.* 2004).

In many instances, the effects of habitat destruction and alteration, climate change, and biological invasions are likely to be interactive. For example, nutrient loading and disturbance often promote biological invasions, increasing the chances for the progress of non-indigenous species from establishment to full invasion (e.g. Dukes & Mooney 1999; Huston 2004). Habitat availability and fragmentation also substantially alter the extent and nature of the response of species to changing climates (Hill *et al.* 1999, 2006). At least in some instances, changing climates might favour introduced over indigenous species as a consequence of substantial differences in the life history and physiological traits of the two sets of organisms (Stachowicz *et al.* 2002; Walther *et al.* 2002; Daehler 2003; Chown *et al.* 2007). In consequence, an understanding of human impacts on the environment must not only involve investigations of direct effects of major processes, such as climate change and habitat transformation, but also their interactive effects (Dukes & Mooney 1999). Indeed, in describing the effects of interactions between global change (of all kinds) and biological invasions, Mooney and Hobbs (2000) have noted that such interactions are becoming an ever more important feature of the world, substantially affecting our capacity to retain biodiversity and the services we derive from it.

1.1 Environmental change in the Antarctic region

Antarctica, its surrounding islands, and the Southern Ocean have changed in concert with global changes, and geological and oceanographic evolution in the region has precipitated large-scale alterations of the global climate (see summaries in Crame 1997; Clarke 2003; Peck *et al.* 2006; Chown & Convey 2007). However, in many ways the region has long been considered comparatively isolated from the rest of the planet. The Southern Ocean is recognized as a particularly well-defined marine ecosystem, especially given that the Antarctic Circumpolar Current has been in evidence for c. 25 million years, endemism of many marine groups is substantial (Longhurst 1998; Clarke & Johnston 2003; Clarke *et al.* 2005), and in several terrestrial taxa endemism is significant too (Chown & Convey 2007). Likewise, and despite their varied histories (LeMasurier & Thompson 1990; Hall 2002), many of the Southern

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Ocean islands are well removed from major landmasses, and show substantial endemism in a range of groups (Gressitt 1970; Chown *et al*. 1998; Greve *et al*. 2005). In terms of direct human influence, the first landing on Antarctica took place only in 1821. Many of the Southern Ocean islands have had similarly short human histories (Headland 1989; Chown *et al*. 2005), and permanent human settlements in the region have remained rare.

This perception of isolation is nonetheless deceptive. Climatic teleconnections between the Antarctic and elsewhere are well-established (Bender *et al*. 1994; Carleton 2003), and many regions, such as the Antarctic Peninsula and several sub-Antarctic islands, are showing evidence of pronounced climate change in step with global events. For example, temperatures have increased by several degrees over the past half century at some sites along the Antarctic Peninsula (King & Harangozo 1998), and rain is falling there for the first time in recorded history. In the sub-Antarctic, temperature increases over similar periods have been lower, but still substantial, whilst precipitation has declined by as much as 600 mm per annum (Bergstrom & Chown 1999). Likewise, despite the late arrival of humans in the region, their impacts on vertebrate populations escalated rapidly, leading to widespread declines in several species (many of which have now recovered) and likely irreversible regime shifts (Laws 1984; Weimerskirch *et al*. 2003). Whilst resource depletion has shifted away from seals, whales and seabirds, fish continue to bear the brunt of exploitation (Brandão *et al*. 2002). More recently, scientific research and its logistic support in the Antarctic, and tourism to a more limited number of sites have increased dramatically (Naveen *et al*. 2001; Frenot *et al*. 2005). In consequence, a wide range of species has been introduced from elsewhere, often having significant impacts on local populations and ecosystem functioning (Frenot *et al*. 2005). Moreover, interactions between climate change and alien species are expected to exacerbate the impacts of these species, and to facilitate additional human-mediated colonization events and invasions (Kennedy 1995; Bergstrom & Chown 1999; Chown & Convey 2007).

Therefore, the Antarctic and Southern Ocean regions are in many ways a microcosm of the situation found elsewhere on the planet. Significant changes in many systems have taken place rapidly (Bergstrom & Chown 1999; Weimerskirch *et al*. 2003; Barnes *et al*. 2006), and major concerns about the conservation of the region and its biodiversity have been raised (e.g. Dingwall 1987, 1995). Nonetheless, the region also differs from others in ways that offer advantages for understanding interactive effects of major environmental changes, their conservation implications, and the ways in which they might be addressed. For example, in terrestrial systems the direct impacts of humans (e.g. habitat destruction as a consequence of agriculture) are less pronounced in the Antarctic than elsewhere, and, because the region is more isolated than many others, immigration can be reasonably well documented and the source of propagules identified (e.g. Crafford & Chown 1987; Marshall & Chalmers 1997; Greenslade *et al*. 1999; Muñoz *et al*. 2004). Thus, the effects

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on biodiversity of rapidly changing climates and biological invasions can be readily comprehended because of the absence of many factors that confound investigations elsewhere (Bergstrom & Chown 1999; Chown *et al.* 2005). Moreover, it has long been appreciated in the region that an understanding of the ecology of coastal, offshore and island ecosystems, and comprehension and prediction of the effects of environmental change on these systems, cannot be achieved without considering interactions between the marine and terrestrial environments (see Smith 1977; Smith & Steenkamp 1990; Pakhomov & Chown 2003). In consequence, research that has been done in the region not only provides a useful perspective on Antarctic biodiversity and ecosystem functioning (Knox 1994; Peck *et al.* 2006), but also provides broader insights into the patterns in and processes underlying biodiversity more generally, and how this diversity will respond to environmental change (Chown *et al.* 2000; Clarke 2003). In this regard, the Prince Edward Islands are a model system.

1.2 The Prince Edward Islands

Marion Island and Prince Edward Island form the Prince Edward Islands. Together with a small number of other islands and archipelagos, such as South Georgia, Bouvetøya, Crozet, Kerguelen, Heard, Auckland and Campbell, they represent the only land in the vast Southern Ocean, which occupies half of the area between 30° and 60° South (as opposed to the 7% of area that ocean occupies in the same northern latitudes) (Chown *et al.* 2004). The nearest landfall to both of the islands is Île aux Cochons of the French Crozet Island Group, which lies 950 km to the east. The two islands lie close to each other, with the more southerly and larger island, Marion (46° 54´S, 37° 45´E), separated from the smaller Prince Edward Island (46° 38´S, 37° 57´E) by 19 km.

The islands are young in geological terms. The oldest recorded date for lavas on Marion Island is 450 000 years, and it seems likely that the islands are less than one million years old (McDougall *et al.* 2001). Local climates and the extent of glaciation have varied substantially since the islands became sub aerial (McDougall *et al.* 2001; Hall 2002), in keeping with global climatic fluctuations (Augustin *et al.* 2004). It seems likely that Marion Island was subjected to at least five, though possibly more, glaciations during the Quaternary, whereas there is no evidence for glaciation on Prince Edward Island. The glacial cycles on Marion Island had a major effect on the vegetation. Glacial maxima generally caused the local extirpation of vascular plants, with the possible exception of species such as the cushion-forming *Azorella selago* (Scott 1985). During the more recent interglacials the vegetation resembled that currently found on the island, although in some cases it included species, such as the brassica *Cardamine*, that are not present in the modern flora (Scott & Hall 1983). The glacial cycles are also thought to have had a substantial influence on the invertebrate fauna, reflected in low habitat specificity and species richness in the vegetated biotope, but much higher richness and greater habitat specificity

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in the epilithic biotope (rock faces, fellfield, polar desert) (Chown 1989, 1990; Barendse *et al*. 2002). This pattern seems to be repeated across most of the sub-Antarctic islands and in Antarctica (Chown 1994; Chown & Klok 2001; Marshall & Convey 2004).

More recent changes have included historical decimation of seal populations (Cooper & Headland 1991) and modern over-exploitation of marine resources (specifically the Patagonian toothfish, *Dissostichus eleginoides*) (Brandão *et al*. 2002). The latter has had substantial indirect impacts on several seabird species as a consequence of long-line fishing-associated mortality (Nel & Nel 1999; Nel *et al*. 2000). Climates have also been changing rapidly at the islands. Sea surface temperatures and Stevenson Screen temperatures have increased by more than 1°C over the past 50 years, and on land mean annual precipitation has declined by ≈ 600 mm (Smith 2002; Mélice *et al*. 2003; le Roux & McGeoch 2007). These changes in climate have had or seem set to have major impacts on assemblage structure and ecosystem functioning in both marine and terrestrial environments (Smith & Steenkamp 1990; Chown & Smith 1993; Smith 2002; Pakhomov & Chown 2003).

Many of the impacts of climate change are being mediated through interactions between indigenous and invasive species (Chown & Smith 1993; Frenot *et al*. 2005). Since the discovery of the islands and their exploitation by sealers, but particularly since their annexation by South Africa in 1947 and the establishment of a scientific station, a steady stream of non-indigenous species has colonized the island (Watkins & Cooper 1986; Cooper & Condy 1988; Chown *et al*. 2002). Some of them have become highly invasive, and have caused local extinctions and/or major changes to the local ecosystem. Amongst the most damaging invaders have been feral cats (now extirpated) (Bester *et al*. 2002), house mice (Crafford 1990; Chown & Smith 1993), the grass *Agrostis stolonifera*, and the forb *Sagina procumbens* (Gremmen *et al*. 1998; Gremmen & Smith 1999). Some evidence now exists that house mice are starting to attack procellariiform chicks (including those of albatrosses), as is the case on Gough Island (Jones *et al*. 2003; Cuthbert & Hilton 2004). What the effects are of other alien species, such as aphids, mosses and isopods (Crafford *et al*. 1986; Slabber & Chown 2002) is not known, nor is the extent of marine invasions. Hull fouling is known to be a significant concern elsewhere in the region (Lewis *et al*. 2003, 2006), and recent studies have recorded both hull fouling and invasive alien species in the sea chests of the research and supply vessel, the *SA Agulhas* (Lee & Chown 2007).

Thus, just like other areas in the region, the Prince Edward Islands have been subject to considerable past geological and climatological variability, are experiencing rapid modern changes owing to climate change and biological invasions, and have been at the receiving end of historical resource exploitation and continue to experience it today. However, unlike many other areas, a considerable body of scientific research has been undertaken to understand these changes and how they have affected interactions between marine and

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terrestrial systems of the islands, and to determine and demonstrate, what lessons they hold for other areas of the planet.

1.3 Research at the Prince Edward Islands

1.3.1 Early terrestrial work

Although the Prince Edward Islands were probably discovered in the mid 1600s, it was not until the early 1800s that the first landing was effected. By the early 1900s most of the fur seals and elephant seals on the two islands had been exterminated (Cooper & Headland 1991). The early history of the islands was thus one of considerable exploitation, as was the case for most other Southern Ocean islands (Headland 1989; Downes 2002). Although a variety of scientific expeditions visited the Prince Edward Islands from the late 1800s onwards (Cooper & Headland 1991), it was only in 1965/66 that the first formal geological and biological research was conducted. This resulted in a substantial volume providing comprehensive baseline information on the climatology, geology, glacial and vegetation histories, and biodiversity of the islands (Van Zinderen Bakker *et al.* 1971). It also set the stage for a large and comprehensive terrestrial research programme.

In essence, the programme addressed four major sets of goals from the early 1970s through to the end of the century, and can therefore be divided into four phases, named by Smith (1991): the reconnaissance, whole island systems, national priorities, and climate change phases. The reconnaissance phase was just that, focussing largely, but not exclusively, on cataloguing the biota. In the next phase, the emphasis switched to understanding the whole island ecosystem, a goal that was influenced to a large degree by the contemporaneous International Biological Programme's Biome Project. This work also involved detailed investigations of nutrient inputs by vertebrates to the terrestrial environment, so forming the first investigations of land-sea interactions. The whole systems approach continued to dominate in the national priorities phase, but by then research also came to include a variety of topics that did not directly address the whole systems model, but were concerned with national significance or especially suited to the opportunities provided by the island system and its biota. Investigations of the impacts of alien species, especially feral cats and house mice had already been established as important avenues of conservation research (Bester & Skinner 1991; Smith 1991). The late 1980s and early 1990s saw a switch in emphasis to studies of the impacts of climate change on the islands. Shortly thereafter a change in administration of research of the islands led to a focus on conservation and monitoring issues identified by the Prince Edward Islands Management Plan (Anonymous 1996), precipitated largely by the declaration of the islands as Special Nature Reserves in 1995. Whilst some other work took place, the emphasis of terrestrial studies was largely on conservation-related science.

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Much of this research was essentially land-based, even though large projects were concerned with marine vertebrate predators and their diets. What these predators were doing at sea was more poorly known, mostly as a consequence of an early, negligible oceanographic capacity, and a later oceanographic focus on other significant questions and regions of the Southern Ocean (Lutjeharms 1991). Although much work was done on the nearshore and intertidal zones (see de Villiers 1976; Beckley & Branch 1992), only a single programme (the Marion Offshore Ecosystem Study) focussed on deeper waters.

1.3.2 Marine investigations

The study of the marine environment in the vicinity of the Prince Edward Islands can be traced to the late nineteen century when the *HMS Challenger* briefly visited the islands in 1873. Nearly a hundred years later (1976), the first comprehensive investigation of the biology of the marine environment was undertaken when the *MS Marion Dufresne* visited the islands (Grindley & Lane 1979; Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). This study provided the first scientific information on plankton community structure and distribution within the vicinity of the Prince Edward Islands (Grindley & Lane 1979).

The systematic study of the link between the marine and terrestrial environment only began in the late 1980s. The Marion Offshore Ecosystem Study (MOES) addressed the problem of how the Prince Edward Islands, located within the relatively unproductive Polar Frontal Zone waters (PFZ), could seasonally sustain enormous numbers of top predators including seals, penguins and flying seabirds. The initial target of investigation was the existence of an island mass effect at the archipelago, a phenomenon of greatly enhanced primary production in a low productivity part of the ocean, and how, or whether this production fed through to the top predators (Boden 1983; Allanson *et al*. 1985; Pakhomov & Froneman 1999a). The programme was unique in that it placed equal emphasis on the availability of food and the importance of its physical supply to consumers. By the end of the programme an understanding of trophic relationships between autochthonous or allochthonous food sources and the top predators was developed as what became known as the "life support system" of the islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

The subsequent research programmes conducted in the 1990s and early 21st century, the Marion Islands Offshore Variability Study (MIOS), the Marion Offshore Variability Study (MOVES) and Dynamics of Eddies Impact on Marion's Ecosystem (DEIMEC), modified or refined the concept of the "life support system of the islands" (Pakhomov & Froneman 1999b; Pakhomov & Chown 2003; McQuaid & Froneman 2004). These investigations have focused on the upstream region (west) of the islands. The main finding thereof was that plankton distribution and species composition was closely linked to mesoscale variability in the oceanographic environment, including meanders in fronts

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that delimit the Polar Frontal Zone and the presence of both warm and cold core features. More significantly, these studies highlighted the importance of the interaction of the Antarctic Circumpolar Current (ACC) with prominent topographic features, and its effects on zooplankton community composition and the delivery of food to pelagic predators on the islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

1.3.3 Recent developments

Over the last decade, research at the islands has focussed mostly on the terrestrial system, although considerable advances were made in understanding marine processes around the islands. Unfortunately, the marine research has been restricted to the autumn months, and investigations of seabirds and seals have been land-based, with limited work on at-sea distributions. Despite proposals for detailed work on understanding the marine system and the resource base it provides, especially during the months when the majority of seabirds and seals reproduce, such work was much delayed (Cooper & Ryan 2001), or scaled-down (Nel *et al.* 2001), and has only recently become the focus of attention. Therefore, whilst understanding of the terrestrial system and its inhabitants is becoming ever more sophisticated, insights into the surrounding marine systems and the ways in which they influence terrestrial processes has lagged behind. One of the major consequences of the limited marine work is that the development of a major Marine Protected Area for the islands has had to be based largely on surrogate environmental information, rather than spatially comprehensive biological data (Lombard *et al.* 2007).

In the mid 2000s, another administrative change saw the research component of the South African National Antarctic Programme transferred from the Department of Environmental Affairs and Tourism to the relatively new Department of Science and Technology, with management thereof being undertaken by the National Research Foundation. A new science policy for the region (the Antarctic Research Strategy for South Africa) was articulated, with major themes including, *inter alia*, climatic variability and the responses of biodiversity to earth system variability. Since then, research has largely been required to address these goals and those of various international polar programmes, such as the International Polar Year. At the Prince Edward Islands, several new projects have started to build on the past work, including joint marine and terrestrial work on seabirds and seals and their foraging areas, investigations of microbial diversity using molecular techniques, and studies of the interactions between biodiversity and geomorphological processes.

1.4 This book

The period from the mid 1960s to the present has been an exceptionally productive one scientifically (Hänel & Chown 1999). Substantial knowledge of the geology and biodiversity of the islands now exists, much is known about how the marine and terrestrial systems of the islands function, and comprehension

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of the nature of the interactions between the marine and terrestrial systems is well advanced. However, not since the landmark volume by Van Zinderen Bakker *et al*. (1971) has a review and synthesis of scientific knowledge of the islands and their biodiversity been presented. This book does just that in the context of the contribution this research has made to our understanding of environmental change in a system dominated by land-sea interactions.

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