

Biological invasions in the Antarctic: extent, impacts and implications

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ABSTRACT

Alien microbes, fungi, plants and animals occur on most of the sub-Antarctic islands and some parts of the Antarctic continent. These have arrived over approximately the last two centuries, coincident with human activity in the region. Introduction routes have varied, but are largely associated with movement of people and cargo in connection with industrial, national scientific program and tourist operations. The large majority of aliens are European in origin. They have both direct and indirect impacts on the functioning of species-poor Antarctic ecosystems, in particular including substantial loss of local biodiversity and changes to ecosystem processes. With rapid climate change occurring in some parts of Antarctica, elevated numbers of introductions and enhanced success of colonization by aliens are likely, with consequent increases in impacts on ecosystems. Mitigation measures that will substantially reduce the risk of introductions to Antarctica and the sub-Antarctic must focus on reducing propagule loads on humans, and their food, cargo, and transport vessels.

Key words: alien species, human impact, tourism, Antarctica, sub-Antarctic, ecosystem consequences, climate change, life history, colonization.

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I. INTRODUCTION

Biological invasions are amongst the most significant threats to biodiversity (McKinney & Lockwood, 1999; Sala *et al.*, 2000; Courchamp, Chapuis & Pascal, 2003), posing both a significant threat to individual species (Case, 1996; Williamson, 1996), and being responsible for major changes to ecosystem structure and functioning (Heywood, 1989; D'Antonio & Dudley, 1995; Mack *et al.*, 2000). Their extent and significance are likely to increase with global environmental change (Dukes & Mooney, 1999; Hughes, 2000; Smith *et al.*, 2000; McKinney, 2001; Prinzig *et al.*, 2002; Walther *et al.*, 2002). Whilst these threats and their economic implications are now well documented for many regions (Vitousek *et al.*, 1996; Pimentel *et al.*, 2000), their sheer pervasiveness is less well appreciated (Gaston *et al.*, 2003).

The Antarctic region includes only small, isolated landmasses – either true islands or fragments of ice-free ground isolated by ice (habitat islands, *sensu* Bergstrom & Selkirk, 1997). Following convention (see Smith, 1984; Longton, 1988), in this review we consider the ‘Antarctic’ to include the main continental landmass, the Antarctic Peninsula and associated archipelagoes (South Shetland, South Orkney, South Sandwich Islands) and a ring of ‘sub-Antarctic’ oceanic islands surrounding the continent at relatively high latitude in the Southern Ocean (Fig. 1, Appendix 1). Three biogeographical zones are recognized – referred to as the continental, maritime and sub-Antarctic. The sub-Antarctic includes islands close to (north or south) the oceanic Polar Frontal Zone, where cold Antarctic waters sink below a warmer surface layer. North of these lie further groups (e.g. the Falkland Islands, Gough Island, Amsterdam Island, New Zealand shelf islands) which some authors have included within the sub-Antarctic. However, they are better termed cold temperate, being distinguished by the presence of woody vegetation, and do not form a key component of this review. Where appropriate, examples are drawn from studies of their biology.

Despite Antarctica's isolation, invasions have taken place, some with profound impacts on indigenous biota. Indeed, invasions are widely recognized to constitute a serious risk to the Antarctic region (Pugh, 1994; Dingwall, 1995; Smith, 1996; Chown *et al.*, 2001; Greenslade, 2002), while rapid climate change in the region, and increases in

human activity will increase their number, extent and significance (Greenslade, 1987; Frenot, Gloaguen & Tréhen, 1997; Chown, Gremmen & Gaston, 1998*b*; Bergstrom & Chown, 1999, Chown & Gaston, 2000; Convey, 2001*b*).

These threats are serious, as the ice-free areas of Antarctica support a large proportion of the world's seabird species (Chown, Gaston & Williams, 1998*a*; Woehler *et al.*, 2001; Kooyman, 2002), and their biotas, though species poor (Gressitt, 1970; Chown *et al.*, 1998*b*; Vernon, Vannier & Tréhen, 1998; Convey, 2001*a*), include a high proportion of endemic taxa (lichens – Øvstedal & Smith, 2001; liverworts – Bednarek-Ochyra *et al.*, 2000; flowering plants – Greene & Walton, 1975; mites – Pugh, 1993; springtails – Greenslade, 1995; insects – Gressitt, 1970; Chown, 1990; nematodes – Andrassy, 1998). Human influence has increased rapidly. Excessive commercial exploitation took place in the sub-Antarctic during the late 18th and 19th Centuries, initially through sealing and subsequently in the onshore and offshore whaling industries. Farming development also occurred. Scientific research started to be emphasized during the ‘heroic age’ of exploration of the early 20th Century, which also marked the start of human impact on the continent itself. The Discovery Expeditions of the 1930s were followed by the International Geophysical Year (1958), and the establishment of research stations across the Antarctic over approximately the last 50 years. Finally, a tourist industry has developed over the last some 25 years, and continues to grow.

Management interventions are required that are likely to lower risks to Antarctic communities in the face of increasing human activity and changing climates, and that are sensitive to the likely variations in risk across the broader Antarctic region. Such interventions rely on knowledge of the groups of organisms that have already invaded the Antarctic region and their likely future performance, understanding of their origin and colonization, and assessment of how environmental change and dynamic patterns of human use might expedite further alien colonization and consequent modification of ecosystem functioning. Our goals are to provide this information.

There has been much recent discussion over the terminology applied to invasive ecology (e.g. Davis & Thompson, 2000; Richardson *et al.*, 2000; Daehler, 2001). Taking note of the warning by Daehler (2001) that terminology in this

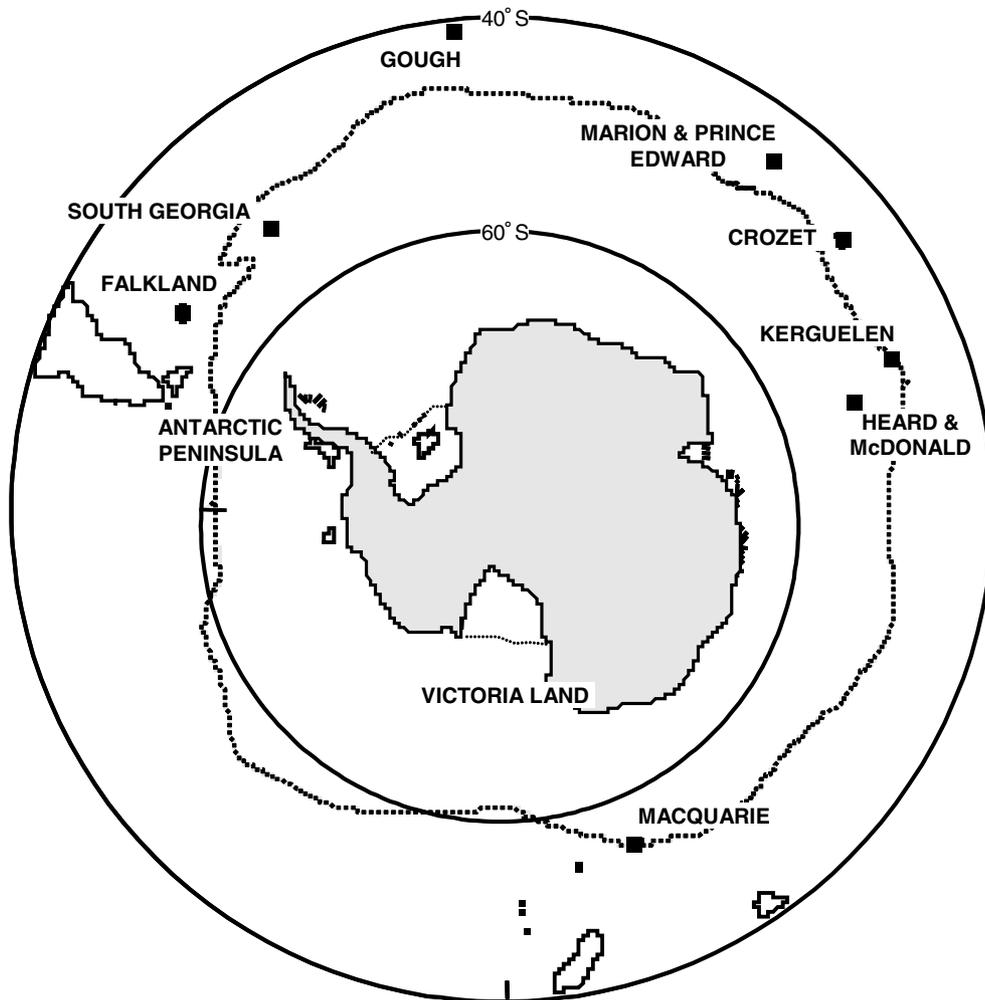


Fig. 1. Map of the Antarctic continent and neighbouring regions of the Southern Ocean, indicating areas referred to throughout the text. Position of the oceanic Polar Frontal Zone indicated by dotted line.

field can be confusing, we have adopted the following definitions based on Greene (1964), Walton & Smith (1973) and Richardson *et al.* (2000), as being appropriate to the current and likely future status of alien species in the Antarctic.

Alien: introduced to an ecosystem as a result of human activity (including species that arrive by natural means to a specific ecosystem but are alien to that biogeographical zone)

Transient alien: survived in small populations for a short time period but either died out naturally or was removed by human intervention

Persistent alien: survived, established and reproduced for many years in a restricted locality, but has not expanded range from that location

Invasive alien: spread into native communities and displaced native species

The expanded definition of the term alien is to account for Northern Hemisphere species that have been introduced through the process of human migration to Southern Hemisphere locations and subsequently arrived by natural colonization means to Antarctic ecosystems.

II. CURRENT KNOWLEDGE OF ALIEN SPECIES IN SUB-ANTARCTIC AND ANTARCTIC ECOSYSTEMS

(1) Plants

In the sub-Antarctic two major islands, Pingouins (Crozet archipelago) and McDonald Islands, remain botanically pristine, with no alien plants (Dreux *et al.*, 1988; Jenkin, 1997; Y. Frenot, personal observations). Elsewhere, alien higher plants belong mainly to common, widely distributed, families (Table 1) that are amongst those considered most invasive at a global scale (Pyšek, 1998), including Poaceae (39 species), Asteraceae (20), Brassicaceae (8) and Juncaceae (7). Little attention has yet been given to detecting alien non-vascular plant species. Among the 108 alien vascular species currently found in the sub-Antarctic, only *Poa annua* occurs on all major islands (Table 1). *Cerastium fontanum*, *Rumex acetosella*, *Stellaria media*, *Sagina procumbens* and *Poa pratensis* also have wide distributions. A few species (e.g. *Plantago lanceolata*, *Taraxacum officinale*, *Agrostis stolonifera*, *Elymus repens*,

Table 1. Species of alien vascular plants on the sub-Antarctic islands, including life cycle classification (a, annual, b, biennial, p, perennial). (a) Dicotyledons; (b) monocotyledons; (c) pteridophytes; (d) summary. Notes: xx, invasive alien; x, persistent alien; (1) only on or in the immediate vicinity of research stations or sites of habitation, (2) only at Port-Couvreux (Iles Kerguelen), (3) only on sites recently influenced by sheep farming (Iles Kerguelen), (2–3) only at Port-Couvreux or on sites recently influenced by sheep farming (Iles Kerguelen). Data sources: South Georgia, McIntosh & Walton (2000); Marion and Prince Edward Islands, Gremmen & Smith (1999); Iles Crozet and Kerguelen, Frenot *et al.* (2001); Heard Island, Scott (1989); MacDonald Island, Jenkin (1997); Macquarie Island, Selkirk *et al.* (1990)

Species	Life cycle	Family	South Georgia	Marion	Prince Edward	Crozet	Kerguelen	Heard	Mac Donald	Macquarie
(a) Dicotyledons										
<i>Achillea millefolium</i> L.	p	Asteraceae	x			x	x (3)			
<i>Achillea ptarmica</i> L.	p	Asteraceae	x			x				
<i>Alchemilla monticola</i> Opiz	p	Asteraceae	x							
<i>Anagallis arvensis</i> L.	a	Primulaceae				x				
<i>Anthemis arvensis</i> L.	a	Asteraceae					x (1)			
<i>Anthemis cotula</i> L.	a	Asteraceae					x (1)			
<i>Anthriscus sylvestris</i> (L.) Hoffm.	p	Apiaceae	x							
<i>Barbarea verna</i> (Miller) Ascherson	b	Brassicaceae					x (1)			
<i>Bellis perennis</i> L.	p	Asteraceae				x				
<i>Brassica napus</i> L.	b	Brassicaceae				x	x (1)			
<i>Brassica oleracea</i> (L.) Koch	b	Brassicaceae				x				
<i>Calluna vulgaris</i> (L.) Hull	p	Ericaceae				x				
<i>Capsella bursa-pastoris</i> (L.) Med.	a	Brassicaceae					x			
<i>Centauria scabiosa</i> L.	p	Asteraceae				x				
<i>Cerastium fontanum</i> Baumg.	p	Caryophyllaceae	xx	xx	x	xx	xx			x
<i>Cerastium glomeratum</i> Thuillard	p	Caryophyllaceae				x	xx			
<i>Chamomilla recutita</i> (L.) Rauschert	a	Asteraceae				x				
<i>Chamomilla suaveolens</i> (Pursh) Rydb.	a	Asteraceae				x				
<i>Chenopodium rubrum</i> L.	a	Chenopodiaceae					x (1)			
<i>Cirsium arvense</i> (L.) Scop.	p	Asteraceae				x	x (3)			
<i>Empetrum rubrum</i> Vahl ex Willd.	p	Ericaceae	x							
<i>Epilobium tetragonum</i> L.	p	Onagraceae				x	x (1)			
<i>Erica scoparia</i> L.	p	Ericaceae				x				
<i>Galium aparine</i> L.	a	Rubiaceae				x				
<i>Galium mollugo</i> L.	p	Rubiaceae				x				
<i>Galium uliginosum</i> L.	p	Rubiaceae				x				
<i>Hieracium</i> sp.	p	Asteraceae	x							
<i>Hypericum humifusum</i> L.	p	Hypericaceae				x				
<i>Hypericum</i> sp.	p	Hypericaceae	x							
<i>Hypochoeris radicata</i> L.	p	Asteraceae		x			x (1)			
<i>Leontodon taraxacoides</i> (Vill.) Merat	p	Asteraceae				x				
<i>Lepidium campestre</i> (L.) R. Br.	ab	Brassicaceae					x (1)			
<i>Leucanthemum vulgare</i> Lam.	p	Asteraceae					x (3)			
<i>Lotus corniculatus</i> L.	p	Fabaceae	x							
<i>Matricaria perforata</i> Merat	a	Asteraceae				x				
<i>Medicago sativa</i> L.	p	Fabaceae				x	x (1)			
<i>Melilotus officinalis</i> (L.) Pallas	p	Fabaceae					x (1)			
<i>Myosotis discolor</i> Pers.	a	Boraginaceae					x (1)			
<i>Oxalis corniculata</i> L.	ab	Oxalidaceae				x	x (1)			
<i>Plantago lanceolata</i> L.	p	Plantaginaceae		x		x	x (1)			
<i>Pratia repens</i> Gaudich.	p	Campanulaceae	x							
<i>Ranunculus acris</i> L.	p	Ranunculaceae	x							
<i>Ranunculus repens</i> L.	p	Ranunculaceae	x			x	x			
<i>Raphanum raphanistrum</i> L.	ab	Brassicaceae				x	x (1)			
<i>Roripa austriaca</i> (Crantz) Besser	a	Brassicaceae					x (1)			
<i>Rumex acetosella</i> L.	p	Polygonaceae	xx	x		xx	x (2–3)			
<i>Rumex conglomeratus</i> Murr.	p	Polygonaceae				x	x			
<i>Rumex crispus</i> L.	p	Polygonaceae				x	x			
<i>Sagina procumbens</i> L.	ab	Caryophyllaceae	x	xx	x	xx	xx			
<i>Senecio jacobaea</i> L.	p	Asteraceae				x				
<i>Senecio vulgaris</i> L.	ab	Asteraceae					x			
<i>Sherardia arvensis</i> L.	a	Rubiaceae				x				
<i>Sinapis arvensis</i> L.	a	Brassicaceae				x	x (1)			
<i>Stellaria alsine</i> Grimm	p	Caryophyllaceae				xx	x (2)			
<i>Stellaria media</i> (L.) Vill.	p	Caryophyllaceae		xx		x	xx			x
<i>Tanacetum vulgare</i> L.	p	Asteraceae					x (3)			
<i>Taraxacum erythrospermum</i> group	p	Asteraceae				x	xx			
<i>Taraxacum officinale</i> group	p	Asteraceae	xx			x	xx			
<i>Trifolium repens</i> L.	p	Fabaceae	x			x	x			

Table 1 (cont.)

Species	Life cycle	Family	South Georgia	Marion	Prince Edward	Crozet	Kerguelen	Heard	Mac Donald	Macquarie
<i>Ulex minor</i> Roth.	p	Fabaceae				x				
<i>Vaccinium vitis-idaea</i> L.	p	Ericaceae	x							
<i>Veronica serpyllifolia</i> L.	p	Scrophulariaceae				x				
Total number of alien Dicotyledons		62	17	6	2	40	34	0	0	2
(b) Monocotyledons										
<i>Carex aquatilis</i> Wahlenb.	p	Cyperaceae	x							
<i>Carex nigra</i> (L.) Reichard	p	Cyperaceae	x							
<i>Juncus acutiflorus</i> E. Hrh. ex Hoffm.	p	Juncaceae				x	x (2)			
<i>Juncus bufonius</i> L.	a	Juncaceae				xx				
<i>Juncus conglomeratus</i> L.	p	Juncaceae				x				
<i>Juncus filiformis</i> L.	p	Juncaceae	x							
<i>Luzula campestris</i> L.	p	Juncaceae					x (2-3)			
<i>Luzula multiflora</i> (Retz.) Lej.	p	Juncaceae					x (3)			
<i>Agrostis canina</i> L.	p	Poaceae	x				x			
<i>Agrostis capillaris</i> L.	p	Poaceae	x			x	x			
<i>Agrostis castellana</i> Boiss. & Reuter	p	Poaceae		xx						
<i>Agrostis gigantea</i> Roth (2)	p	Poaceae					x (3)			
<i>Agrostis stolonifera</i> L.	p	Poaceae		xx		x	x			
<i>Aira praecox</i> L.	a	Poaceae					x (2)			
<i>Alopecurus geniculatus</i> L.	p	Poaceae				x	x			
<i>Alopecurus pratensis</i> L.	p	Poaceae					x (3)			
<i>Anthoxanthum odoratum</i> L.	p	Poaceae	x				x (2-3)			
<i>Arrhenatherum elatius</i> (L.) Beauv. ex J. & C. Presl	p	Poaceae					x			
<i>Arrhenatherum elatius</i> ssp. <i>bulbosum</i> (Willd.) Schübler & Martens	p	Poaceae				x	x			
<i>Bromus hordeaceus</i> L.	a	Poaceae				x				
<i>Dactylis glomerata</i> L.	p	Poaceae				x	x			
<i>Deschampsia caespitosa</i> (L.) P. Beauv.	p	Poaceae	xx							
<i>Deschampsia flexuosa</i> (L.) Trin.	p	Poaceae	x							
<i>Elymus repens</i> (L.) Gould	p	Poaceae	x	x		x	x			
<i>Festuca arundinacea</i> Schreb.	p	Poaceae					x			
<i>Festuca ovina</i> L.	p	Poaceae	x				x (3)			
<i>Festuca rubra</i> cf. <i>commutata</i> Gaudin	p	Poaceae					x (2)			
<i>Festuca rubra</i> L.	p	Poaceae	x	x						
<i>Festuca rubra</i> ssp. <i>rubra</i> L.	p	Poaceae					x			
<i>Gaudinia fragilis</i> (L.) Beauv.	a	Poaceae					x (2)			
<i>Holcus lanatus</i> L.	p	Poaceae				x	x			
<i>Holcus mollis</i> L.	p	Poaceae				x	x (2)			
<i>Hordeum distichon</i> L.	a	Poaceae					x			
<i>Lolium multiflorum</i> Lam.	p	Poaceae				x	x			
<i>Lolium perenne</i> L.	p	Poaceae				x	x			
<i>Nardus stricta</i> L.	p	Poaceae	x							
<i>Phleum pratense</i> L.	p	Poaceae				x	x			
<i>Phleum pratense</i> ssp. <i>bertolonii</i> (D.C.) Bornm.	p	Poaceae					x			
<i>Poa annua</i> L. (1)	ab	Poaceae	xx	xx	x	xx	xx	x		xx
<i>Poa cf. palustris</i> L.	p	Poaceae					x			
<i>Poa nemoralis</i> L.	p	Poaceae					x			
<i>Poa pratensis</i> L.	p	Poaceae	xx	xx		xx	x			
<i>Poa trivialis</i> L.	p	Poaceae	x			x	x			
<i>Trisetum spicatum</i> (L.) Rich.	p	Poaceae					x (2)			
<i>Vulpia bromoides</i> (L.) S.F. Gray	a	Poaceae					x (3)			
Total number of alien monocotyledons		45	15	7	1	18	34	1	0	1
(c) Pteridophytes										
<i>Cystopteris fragilis</i> (L.) Bernhardi	p	Woodsiaceae	x			x	x			
Total number of alien Pteridophytes		1	1	0	0	1	1	0	0	0
(d) Summary										
Total number of alien species		108	33	13	3	59	69	1	0	3
% perennial species	74.1		93.9	84.6	33.3	76.2	72.5	0	0	66.6

Holcus lanatus) occur on several islands, but most others are restricted to one or two islands. Most aliens are found on Crozet and Kerguelen Islands and, to a lesser extent, South Georgia. However, most are persistent rather than invasive, and have restricted distributions on the islands they have colonized. Among the 69 species on Kerguelen Islands, only seven are invasive and widely distributed within the archipelago, while the remaining persistent species are linked with sites that are or have been intensively used by humans. Likewise, on Possession Island, 59 aliens are present near the research station. Of these, only seven are invasive with wider ranges, of which *Stellaria alsine* is the most aggressive. It arrived on the island between 1989 and 1996 and its distribution is expanding rapidly (Frenot *et al.*, 2001), displacing native species. This species is extremely fecund, with abundant seeds easily dispersed by water runoff, wind, or human boots.

On Marion Island, the invasive *Sagina procumbens* has rapidly expanded its distribution in the last decade (Gremmen & Smith, 1999). A second invasive, *Agrostis stolonifera*, dominates various habitats, especially drainage lines, modifying vegetation and associated soil fauna (Gremmen, Chown & Marshall, 1998). These two species represent the most significant threat to communities, although other patchily distributed invasives are also apparently spreading (e.g. *Poa pratensis*, *Cerastium fontanum*, *Stellaria media*). The only invasive alien widely distributed on South Georgia is *Poa annua*, although five others (*Cerastium fontanum*, *Rumex acetosella*, *Taraxacum officinale*, *Deschampsia caespitosa* and *Poa pratensis*) grow up to at least 1 km from former whaling stations (McIntosh & Walton, 2000). On Macquarie Island, the three alien species currently present (*P. annua*, *S. media*, and *C. fontanum*) are widespread, but displacement of native communities by these species is, in general, minor.

Most established alien species are long-lived (Table 1), and about 75% of aliens are perennial. By contrast, about 65% of transient species recorded from Kerguelen and Possession Islands (species cited in the literature but not observed in a detailed survey between 1996 and 2000) are annual or biennial (Frenot *et al.*, 2001). Colonization or establishment abilities may be better developed in alien perennial species in the sub-Antarctic environment. If so, this reflects the pattern also found generally in indigenous Antarctic biota, with poor representation of short annual/biennial or temporally determined life cycles (Convey, 1996).

In comparison with the sub-Antarctic islands, the maritime Antarctic shows much less, and continental Antarctic no evidence, of successful alien introduction. Several studies (Edwards & Greene, 1973; Edwards, 1980; Smith, 1996) have shown that a range of Falkland Island, South Georgian and Arctic vascular plants can survive maritime Antarctic environmental conditions, some over a period of several years, and that some species can also reproduce successfully. Long-distance dispersal and subsequent establishment appear to be more problematic than survival alone. The only examples of persistent aliens becoming established in either region are *Poa pratensis* and *P. annua*, present respectively in small areas at Cierva Point, northern Antarctic Peninsula, and on King George Island (Smith, 1996).

(2) Invertebrates

Knowledge of invertebrate faunas varies considerably between taxonomic groups and locations, with less generally known about the smaller organisms or those living in soil. The largest numbers of alien invertebrates (30) is recorded from Kerguelen Islands and Macquarie Islands (28), but comparable detail is not available for most other islands (Table 2). McDonald, Pingouins and Apôtres Islands remain largely free of aliens while Macquarie, Kerguelen, Possession, Marion Islands and South Georgia are those with the highest numbers. Most tardigrade, rotifer and nematode species known from sub-Antarctic islands have cosmopolitan distributions, but specific studies are few and detailed taxonomic and distributional knowledge lacking. As with plants, there are few confirmed cases of persistent aliens in the maritime Antarctic (single species of dipteran and enchytraeid worm, both linked with the above-mentioned transplant experiments), and no records from the continental Antarctic.

Most known aliens are Diptera, followed by Hemiptera and Coleoptera. The latter group includes some of the few species that have been transferred between Southern Ocean islands. The two most widely distributed alien insects are *Psychoda parthenogenetica* (Diptera, Psychodidae) and *Rhopalosiphum padi* (Hemiptera, Aphididae) (Table 2). All aphids found on sub-Antarctic islands are cosmopolitan and have a large range of host plants. Imported vegetable matter, and glasshouses on islands such as Kerguelen Island, might serve as both a source for these species, and a route via which plant viral diseases can be introduced. Greenslade (1987) reported that hydroponic facilities and imported potplants in the Australian Antarctic stations allowed the survival of alien organisms (mites, springtails, enchytraeid worms). Many of the alien invertebrates recorded in Table 2 are known to have been imported amongst general and food stores, although very few records appear to have been formally published.

The presence of alien earthworms is well documented for some islands (e.g. Possession, Kerguelen and Macquarie), but the group has not been well surveyed elsewhere. Among these, *Dendrodrilus rubidus tenuis* is present on most of the sub-Antarctic islands (Table 2). On Kerguelen, this species is invasive, even being an early coloniser of glacier forelands in the west of the archipelago. Bouché (1982) suggested it was probably introduced by sealers and whalers when they came ashore to fill water barrels. By contrast, on Possession Island, this species is persistent, being restricted to the station area, and has spread slowly (Frenot, 1985). Little is known about the three species of alien terrestrial slugs present in the sub-Antarctic, except that they are rare on Kerguelen Islands and more abundant on Macquarie and Marion Islands.

Among the non-marine Crustacea, one alien is established on Marion Island, where its effect on local ecosystems is poorly understood. By comparison with studies on Gough Island, where it is invasive (Jones, Chown & Gaston, 2003), Slabber & Chown (2002) suggested that, if allowed to spread on Marion Island, it would substantially alter nutrient cycling by reducing the bottleneck currently imposed by lepidopteran larvae and earthworms (Smith & Steenkamp,

1992a, b). Pugh, Dartnall & McInnes (2002; Table 2) list three further alien Crustacea in sub-Antarctic locations, of which the amphipod and isopod on Macquarie Island remain within the vicinity of the station.

Comprehensive monographs of the Antarctic Acari exist, largely based on the literature (e.g. Pugh, 1993). Subsequent surveys of poorly sampled islands (e.g. Marion, Heard) have revealed many additional taxa including possible introductions, making generalizations premature. Nonetheless, the majority of species introduced to the region are likely to have been associated with the import of live vegetation, litter or soil (Pugh, 1994). A new monograph of the spiders of the Southern Ocean islands (Pugh, 2004) lists 14 records of anthropogenic introduction, with none apparently becoming established in Antarctic locations.

The alien component of the springtail fauna varies considerably between islands. On Heard Island there are none, increasing to 10% on South Georgia, >15% on Macquarie, 17% on Kerguelen, 21% on Crozet and 38% on Marion. Several of these species are widespread invasives, especially those in the genus *Hypogastrura* (Table 2). Wise (1971) and Greenslade (1995) also reported the invasive springtail *Hypogastrura viatica* from the maritime Antarctic South Shetland Islands (approximately 63° S) and Léonie Island (approximately 68° S), respectively and Greenslade & Wise (1984) identified *Folsomia candida* and *Protaphorura* sp. on Deception Island.

Pugh (1994) lists Acari thought to have been introduced to maritime and continental Antarctic sites. However, the only invertebrates known to have successfully established in the maritime Antarctic (Signy Island) following accidental introduction are a chironomid midge (*Eretmoptera murphyi*) and an enchytraeid worm (*Christensenidrilus blocki*), both linked with transplant experiments (Block, Burn & Richard, 1984; Dózsa-Farkas & Convey, 1997). At Casey station, in the eastern continental Antarctic, a parthenogenetic *Lycoriella* sp. (Diptera, Sciaridae), initially imported with fresh vegetables, has been established for at least four years within the plumbing associated with the station sewage system (Anon., 2002).

Invasive alien invertebrates can have considerable impacts on native fauna. Ernsting *et al.* (1995, 1999) showed that the introduced predatory carabid beetle *Trechisibus antarcticus* is both spreading in the Husvik area of South Georgia, and having direct and indirect effects on the indigenous perimylopod beetle *Hydromedion sparsutum*, including an increase in body size and decline in abundance. On Kerguelen, *Oopterus soledadinus* is having similar effects on indigenous prey species, whilst the fly *Calliphora vicina* is linked with a decline in the abundance of an indigenous dipteran competitor, *Anatalanta aptera* (Chevrier, Vernon & Frenot, 1997). On Marion Island, the midge *Limnophyes minimus* may contribute substantially to nutrient turnover owing to the very high densities at which it occurs. Indeed, Hänel & Chown (1998) argued that nutrient turnover by this species might rival that of the indigenous *Pringleophaga marioni* (Lepidoptera, Tineidae), the larvae of which make a key contribution to nutrient release. Several other species have potentially major effects on either their host plants or on the wider local ecosystem, but such effects have not yet been investigated.

Within the insects, the higher taxonomic pattern of invasion is highly non-random, with no Hymenoptera, and few Coleoptera and Lepidoptera represented. This taxonomic bias may reflect a preponderance of introductions with livestock feed and in water barrels (Convey & Block, 1996; Chown *et al.*, 1998b), rather than with cultivated plants. Finally, although most insect introductions have been accidental, some have been deliberately planned as part of conservation management. For example European rabbit fleas (and myxomatosis) have been introduced to Macquarie (Copson & Whinam, 2001) and Kerguelen Islands (Chapuis, Chantal & Bijlenga, 1994b; Chekchak *et al.*, 2000) for biological control of rabbits.

(3) Vertebrates

Antarctica has no native fish, amphibians or reptiles. Several salmonid fish have been introduced to Kerguelen and Crozet Islands (Davaine & Beall, 1997) (Table 3), although their current status is poorly known. Little is known about their effects on these sub-Antarctic freshwater ecosystems, although these have probably been substantial on Marion Island (Cooper, Crafford & Hecht, 1992), where the brown trout was introduced and is now extinct.

Few alien birds have established successfully on sub-Antarctic islands and none to the continent. Palearctic mallard (*Anas platyrhynchos*) (first record in 1950s), redpoll (*Carduelis flammea*) (1912) and starling (*Sturnus vulgaris*) (1930) are present on Macquarie Island. These belong to families with the highest success of introduction globally (Lockwood, 1999). Starlings have probably colonized on several separate occasions, without human assistance, following their introduction to New Zealand and Australia (Falla, Sibson & Turbott, 1978; Turbott, 1990; Copson & Whinam, 2001). The line between regular vagrancy and establishment is vague, and the sub-Antarctic islands (and more southerly locations) record vagrant species on a regular basis (e.g. Burger, Williams & Sinclair, 1980; Berruti & Schramm, 1981; Gartshore, 1987; Gauthier-Clerc, Jiguet & Lambert, 2002). Burger *et al.* (1980) estimated that, over the past 10 000 years, at least 80 000 birds might have reached Prince Edward Islands, attributing the failure to establish to low resource availability, severe climate, and high predation of vagrants by sub-Antarctic skuas. Little is known about the biology and impact of alien birds on the sub-Antarctic islands.

By contrast, alien mammals of the sub-Antarctic are well studied, largely through the considerable impacts they have had or are having on indigenous systems (Bonner, 1984; Leader-Williams, 1988; Chapuis, Boussès & Barnaud, 1994a; Bester *et al.*, 2002), naturally devoid of mammalian herbivores or carnivores. Some persistent or invasive mammals have been removed in conservation actions, though these actions themselves have further impacts (Micol & Jouventin, 1995; Myers *et al.*, 2000; Bester *et al.*, 2002; Courchamp *et al.*, 2003). Further eradication programmes are under consideration (the removal of reindeer from South Georgia) or trial (rat eradication on some offshore islets of South Georgia). These activities are incorporated in management plans developed for several sub-Antarctic islands (Anon., 1994, 1996; McIntosh & Walton, 2000).

Table 2. Species of alien terrestrial invertebrate recorded on the sub-Antarctic islands in the published literature. Notes: xx, invasive alien; x, persistent alien; (1) restricted to buildings. Data sourced from: Bouché (1982); Chown *et al.* (1998*b*); Chown & Avenant (1992); Colless (1962, 1970); Convey *et al.* (1999); Crafford (1986); Crafford & Chown (1990); Crafford *et al.* (1986); Dahl (1970*a*, 1970*b*); Darlington (1970); Davies (1973); Deharveng (1981); Deharveng & Travé (1981); Dreux (1965, 1972); Duckhouse (1970); Ernstring *et al.* (1995, 1999); Frenot (1992); Gabriel *et al.* (2001); Greenslade (1986, 1987, 1990); Greenslade (personal communication); Gressitt (1961, 1970, 1971); Hardy (1962); Holdhaus (1931); Hullé *et al.* (2003); Jeannel (1940); Ledoux (1991); Lee (1968); Marshall *et al.* (1999); Marshall & Chown (2002); McQuillan & Marker (1984); Pugh (1993, 1994); Pugh *et al.* (2002); Quate (1962); Séguy (1940, 1971); Slabber & Chown (2002); Travé (1987); Tréhen & Voisin (1984); Usher (1984); Vernon & Voisin (1990); Vogel (1985); Vogel & Nicolai (1983); Vogel & Plassmann (1985); Watson (1967); Womersley (1937)

Higher taxonomy	Species	South		Prince		Mac			
		Georgia	Marion	Edward	Crozet	Kerguelen	Heard	Donald	Macquarie
Annelida									
Naiidae	<i>Nais elinguis</i> Müller								x
Enchytraeidae	<i>Enchytraeus albidus</i> Henle								x
Enchytraeidae	<i>Lumbricillus lineatus</i> Müller								x
Enchytraeidae	<i>Lumbricillus maritimus</i> Ude				x				
Lumbricidae	<i>Dendrodrius rubidus tenuis</i> Eisen		x		x	xx	x		x
Lumbricidae	<i>Dendrodrius rubidus norvegicus</i> Eisen					x			
Lumbricidae	<i>Eiseniella tetraedra</i> Savigny					x			
Mollusca									
Limacidae	<i>Deroceras agreste</i> L.					x			
Limacidae	<i>Deroceras panormitanum</i> Lessona & Pollonera		xx						
Limacidae	<i>Deroceras reticulatum</i> Müller								x
Crustacea									
Amphipoda	<i>Puhuruhuru patersoni</i> Stephensen								x
Isopoda	<i>Porcellio scaber</i> Latreille		x						
Isopoda	<i>Styloniscus otakensis</i> Chilton								x
Acari Astigmata									
Acaridae	<i>Acarus siro</i> Linnaeus								x
Acaridae	<i>Aleurobius farmae</i> De Geer								x
Acaridae	<i>Rhizoglyphus echinopus</i> Fumouze and Robin								x
Acaridae	<i>Tyrophagus longior</i> Gervais								x
Acaridae	<i>Tyrophagus putrescentiae</i> Schrank						x		x
Acaridae	<i>Glycyphagus domesticus</i> de Geer								x
Acaridae	<i>Schwiebia talpa</i> Oudemans								x
Listrophoroidea:	<i>Listrophorus gibbus</i> Pagenstecher								x
Listrophoridae									
Cheyletoidea:	<i>Cheyletus eruditus</i> Schrank								x
Cheyletidae									
Cheyletiellidae	<i>Cheyletiella parasitivorax</i> Mégnin								x
Acari Oribatida									
Brachychthoniidae	<i>Liochthonius muscorum</i> Forsslund					x			
Brachychthoniidae	<i>Paraliochthonius piluliferus</i> Forsslund					x			
Araneidea									
Agelenidae	<i>Tegenaria domestica</i> (Clerck)	x							x (1)
Linyphiidae	<i>Leptyphantes leprosus</i> (Ohlert)								x (1)
Pholcidae	<i>Pholcus phalangoides</i> (Fuesslin)				x (1)				
Theridiidae	<i>Steatoda triangulosa</i> (Walckenaer)								x (1)
Collembola									
Bouletiellidae	<i>Bouletiella hortensis</i> Fitch					x			
Entomobryidae	<i>Lepidocyrtus</i> sp. <i>lignorum</i> (Fabricius) group nr <i>violaceus</i> (Fourcroy)								x
Hypogastruridae	<i>Ceratophysella denticulata</i> Bagnall				x				x
Hypogastruridae	<i>Ceratophysella gibbosa</i> Bagnall				x				
Hypogastruridae	<i>Hypogastrura purpureascens</i> Lubbock	x				x			x
Hypogastruridae	<i>Hypogastrura viatica</i> Tullberg	xx	x		x	x			x
Isotomidae	<i>Desoria tigrina</i> Nicolet								x
Isotomidae	<i>Isotomurus palustris</i> Müller		x			x			

Table 2 (cont.)

Higher taxonomy	Species	South Georgia	Marion	Prince Edward	Crozet	Kerguelen	Heard	Mac Donald	Macquarie
Isotomidae	<i>Parisotoma notabilis</i> Schaeffer		x						
Isotomidae	<i>Parisotoma minutea</i> Tullberg				x				x
Sminthuridae	<i>Jeannenotia stachi</i> Jeannenot					x			
Dyctyoptera									
Blattidae	<i>Blatella germanica</i> L.		x (1)		x (1)	x (1)			
Psocoptera									
Psoquillidae	<i>Rhyopsocus eclipticus</i> Hagen					x			
Thysanoptera									
Thripidae	<i>Apterothrips apteris</i> Esch.						x		
Hemiptera									
Homoptera									
Aphididae	<i>Aulacorthum circumflexum</i> (Buckton)		x						
Aphididae	<i>Aulacorthum solani</i> (Kaltenbach)				x	x			
Aphididae	<i>Brachycaudus helichrysi</i> (Kaltenbach)		x						
Aphididae	<i>Jacksonia papillata</i> Theobald	x							x
Aphididae	<i>Macrosiphum euphorbiae</i> (Thomas)		x		x				
Aphididae	<i>Myzus ascalonicus</i> Doncaster				xx	xx			x
Aphididae	<i>Myzus ornatus</i> Laing					x			
Aphididae	<i>Myzus persicae</i> (Sulzer)					x (1)			
Aphididae	<i>Rhopalosiphum padi</i> (Linnaeus)	x	xx		xx	xx			xx
Coleoptera									
Carabidae	<i>Trechisibus antarcticus</i> (Dejean)	xx							
Ptinidae	<i>Ptinus tectus</i> Boieldieu					x			
Trechidae	<i>Ooapterus soledadinus</i> Guérin-Méneville	xx				xx			
Lepidoptera									
Plutellidae	<i>Plutella xylostella</i> Dugdale		x						
Siphonaptera									
Pulicidae	<i>Spilopsyllus cuniculi</i> Dale								x
Diptera									
Anthomyiidae	<i>Fucellia maritima</i> Haliday					xx			
Calliphoridae	<i>Calliphora vicina</i> Robineau Desvoidy					xx			
Chironomidae	<i>Linnophyes minimus</i> Meigen		xx	xx		xx			
Drosophilidae	<i>Scaptomyza</i> sp.		x						
Muscidae	<i>Fannia canicularis</i> Linné		x						
Mycetophilidae	<i>Mycomia bifida</i> Freeman	xx							
Psychodidae	<i>Psychoda parthenogenetica</i> Tonnoir	x	x		x	x			x
Psychodidae	<i>Telmatoprocus albipunctatus</i> Willirton		x						
Scatopsidae	<i>Scatrope notata</i> Linné	x							
Sciaridae	<i>Bradysia aubertii</i> Séguy		x			x			
Sciaridae	<i>Lycoriella caesar</i> Johansenn	x							
Sciaridae	<i>Lycoriella solani</i> Winnertz				x (1)				
Sphaeroceridae	<i>Leptocera curvinervis</i> Stenb					x			
Trichoceridae	<i>Trichocera maculipennis</i> Edwards					x			
Trichoceridae	<i>Trichocera regelationis</i> Linné	x							
Total number of introduced and naturalized species		12	18	1	14	30	3	0	28

Eight invasive mammals, several deliberately introduced, are present on islands in the region (Table 3). The house mouse (*Mus musculus*, *sensu lato*) is the most widespread, occurring on five islands, while the mouflon (*Ovis gmelini*) is restricted to Kerguelen, the island group with the highest number of alien species (7). Cats have had the greatest impacts, being responsible for drastic reductions in some

seabird populations and local extinctions of several species (Pascal, 1980; van Aarde, 1980; Bonner, 1984; Brothers, 1984). At Kerguelen, Pascal (1980) estimated that cats killed 1.2–1.3 million birds per year. The population of cats on the main island is currently estimated at about 7000 individuals (Say, Gaillard & Pontier, 2002). Estimates of the effects of cat predation on Marion Island in the 1970s–1980s were equally

Table 3. Species of terrestrial vertebrate introduced and naturalized on the sub-Antarctic islands (see text for references). x, persistent alien; xx, invasive alien; (1) restricted to Ile Longue; (2) restricted to Ile Haute; (3) last sighting, following eradication programme, in 1991; (4) last sighting, following eradication programme, in June 2000; (5) introduced in 1990, becoming naturalized; (6) becoming rare

Species	South Georgia	Marion	Prince Edward	Crozet				Kerguelen	Heard	MacDonald	Macquarie
				Possession	Est	Cochons					
<i>Rattus rattus</i>				xx				xx			xx
<i>Rattus norvegicus</i>	xx										
<i>Mus musculus</i>	x	xx				xx	xx	xx			xx
<i>Oryctolagus cuniculus</i>					xx	xx	xx	xx			xx
<i>Ovis aries</i>							xx (1)				
<i>Ovis gmelini</i>							xx (2)				
<i>Rangifer tarandus</i>	xx						xx				
<i>Felis catus</i>		(3)				xx	xx				(4)
<i>Salmo trutta</i>				x			x				
<i>Salmo alpinus</i>							xx (5)				
<i>Salmo salar</i>							x (6)				
<i>Salvelinus fontinalis</i>				x			x				
<i>Oncorhynchus kisutch</i>							x				
<i>Anas platyrhynchos</i>											x
<i>Sturnus vulgaris</i>											x
<i>Carduelis flammea</i>											x
Total alien vertebrates	3	1	0	3	1	3	12	0	0		6

dramatic but, by 1991, the population had been eliminated by an eradication programme utilizing a combination of feline panleucopaenia, trapping, hunting and poisoning (Bester *et al.*, 2002). Control of feral cats on Macquarie Island commenced in 1985, eventually leading to eradication (Scott, 1996), and there have been no sightings or evidence of cats since June 2000 (G. Copson, pers. comm.).

Both rats and mice are also significant predators. Ship rats (*Rattus rattus*) are present (probably introduced by sealers and whalers) on Kerguelen, Possession and Macquarie Islands (Cumpston, 1968; Chapuis *et al.*, 1994a; Pye, Swain & Seppelt, 1999), and have drastically reduced the number of petrel species on Possession (8 species *cf.* 17 species on neighbouring Est Island where rats are absent) (Jouventin *et al.*, 1984). On both Macquarie and Possession Islands, rats are common in tall tussock grassland (Copson & Whinam, 2001) where they impact the reproductive dynamics of the megaherbs *Pleurophyllum hookeri* (Shaw, Bergstrom & Hovenden, in press) and *Pringlea antiscorbutica* (Y. Frenot, personal observations), respectively. Brown rats (*Rattus norvegicus*), invasive on South Georgia, have had a deleterious effect on the endemic South Georgia pipit (the only passerine resident in the Antarctic), now virtually absent from all areas of the island colonised by rats. Healthy pipit populations remain only in rat-free areas, largely on smaller offshore islets (Pye & Bonner, 1980). This rat utilises several different sources of food through the year, including plant material (tussock grass), invertebrates (largely the endemic perimylopod beetles) and vertebrates (birds and carrion) (Pye & Bonner, 1980). The risk of further rodent introductions through shipping operations is ever-present.

The impacts of house mice on sub-Antarctic plants and invertebrates are well documented (Gleeson & van

Rensburg, 1982; Copson, 1986; Chown & Smith, 1993; Le Roux *et al.*, 2002; Smith, Avenant & Chown, 2002), including direct reductions in population sizes and effects on the life-history traits (Crafford & Scholtz, 1987; Chown & Smith, 1993; Le Roux *et al.*, 2002). Huyser, Ryan & Cooper (2000) suggested that, on Marion Island, house mice indirectly affect lesser sheathbills (*Chionis minor*) by reducing the numbers of invertebrates available to them (their major prey during winter). On the nearby, mouse-free, Prince Edward Island sheathbill numbers have remained unchanged between 1977 and 1997, whereas there has been an almost 20% decline in abundance at Marion Island (Huyser *et al.*, 2000).

Amongst the herbivores, reindeer and rabbits have had major impacts on the vegetation of the sub-Antarctic islands. Ten reindeer from Sweden were introduced to Kerguelen in 1955 (Lesel, 1967), becoming established on the mainland, and had increased to a population of *c.* 2000 individuals by 1972 (Pascal, 1982), since when numbers have remained fairly stable (J.-L. Chapuis, personal communication). The consequences of three separate introductions of reindeer to South Georgia in the early 20th century have been documented in greater detail (Leader-Williams, Smith & Rothery, 1987; Leader-Williams, 1988; Leader-Williams, Walton & Prince, 1989). With no predators, populations are regulated by resource availability (as with mouflon on Kerguelen; Chapuis *et al.*, 1994a), and are particularly vulnerable to starvation during winters with heavy snowfall, which may lead to the death of 60% or more of individuals (Réale, 1996). Of the three introductions, one population has become extinct and two remain, with their geographical ranges limited by their inability to cross large tidewater glaciers. With most glaciers on South

Georgia in rapid retreat, this limitation is likely to be relaxed. Population densities are much greater than those found in their natural northern range, and these reindeer have considerably modified or totally destroyed native vegetation, both directly through trampling and grazing, and indirectly, through encouraging the dispersal and establishment of the more resilient invasive grass, *Poa annua*. By causing the spread of this indigestible species, reindeer are also indirectly affecting the body size of the indigenous herbivorous perimylopod beetles (Chown & Block, 1997).

Rabbits have also caused major changes to indigenous biota. On the eastern Kerguelen, they have eliminated most of the native plant species, leaving *Acaena magellanica* to become dominant in nearly monospecific communities (Chapuis *et al.*, 1994*a*). They also have direct impacts on the avifauna, especially Procellariidae, through their burrowing activity. However, their main impact is indirect: rabbits form the main prey of cats in winter, whose survival rate is thereby improved and hence their impact on bird populations is greater during the following summer (Chapuis *et al.*, 1994*a*; Courchamp, Langlais & Sugihara, 1999). To rehabilitate islands degraded by rabbits, a program of eradication by poisoning has been implemented since 1992 on three islands of the Kerguelen archipelago, each 145 to 165 ha (Chapuis *et al.*, 2001). Subsequent changes in plant, invertebrate and bird communities are currently being assessed (Chapuis, Frenot & Lebouvier, 2004). Rabbits introduced to Macquarie Island have had similar major effects on vegetation (Copson & Whinam, 1998). Here, control using the myxoma virus (*Myxomatosis cuniculi*) with the European rabbit flea (*Spilopsyllus cuniculi*) as a vector began in 1978 (Brothers *et al.*, 1982), when the rabbit population was estimated at 150 000 (Copson, Brothers & Skira, 1981). Again, a secondary consequence of rabbit control was to increase feral cat predation on burrow-nesting seabirds and other species leading, *inter alia*, to eradication from the island of the alien weka (*Gallirallus australis*) (Brothers & Skira, 1984; Copson & Whinam, 2001). By 2002, the rabbit population had decreased to 14 000–16 000 (G. R. Copson, personal communication). A further indirect impact of this control programme was a decline in sub-Antarctic skua breeding sites inland (54%), whereas those in coastal areas increased (17%), suggesting that skua numbers had increased after the introduction of rabbits due to the additional prey availability (Copson & Whinam, 2001).

(4) Microbial groups and diseases

The classically described algal flora appears to contain a large cosmopolitan element (Broady, 1996), and introductions associated with human activity have been recorded (Broady & Smith, 1994). Kashyap & Shukla (2001) briefly describe the detection of six species of algae in soil attached to vegetables taken to the Schirmacher Oasis with the 15th Indian Antarctic expedition, one of which, *Phormidium uncinatum*, was not found amongst the indigenous flora of the local lakes.

Otherwise, very little is known about either levels of endemicity in the various microbial groups present in Antarctica, or of the presence or population trends of alien species

(see Wynn-Williams, 1996*a*). Assessments of microbial diversity, using either classical or molecular techniques, are complicated by the paucity of detailed Antarctic studies, and/or the lack of comparable data from elsewhere. Thus, while it appears that the Antarctic prokaryote (Franzmann, 1996) and eukaryote microbial floras may be distinct (B. Lawley and collaborators, unpublished data) this may simply result from the lack of non-Antarctic sequence data.

The dangers of importation of microorganisms into the Antarctic, and movement of these organisms between different parts of the continent, have been recognized (Smith, 1996; Wynn-Williams, 1996*b*), but there have been few attempts to quantify or minimise the risk or assess the impact on native microbial floras. One specific exception to this generalisation relates to operations to drill into the subglacial Lake Vostok, where the danger of inadvertent introduction of microbes to an otherwise pristine environment is clear (Gavaghan, 2002). On land, Wynn-Williams (1996*b*) described the release and subsequent discovery of spores of a *Penicillium* species at Mt. Howe, and the presence of human pathogens in soil close to McMurdo station. Fungal species recently isolated from huts at historic sites on Ross Island (Cape Evans, Cape Royds, Discovery Point and Cape Crozier) are presumed to originate either with the early explorers or with more recent scientific or tourist visitors to the sites (Minasaki *et al.*, 2001). Likewise, there are several documented introductions to the sub-Antarctic. Kloppers & Smith (1998) suggested that *Botryotinia fuckeliana* (conidial state: *Botrytis cinerea*), the cause of grey mould rot in vegetables and now infecting entire stands of *Pringlea antiscorbutica* on Marion Island, was probably transferred to the island on fresh vegetables (no longer brought ashore).

Azmi & Seppelt (1998) reported a total of 35 taxa of fungi from the Windmill Islands, of which 12 were restricted to soils in the vicinity of Casey Station, suggesting their introduction was associated with human activities. Similarly, Kerry (1990) reported 20 fungal taxa from the Vestfold Hills and MacRobertson Land, of which 10 were most common in sites affected by human activities, and were interpreted as human introductions. A toadstool was found growing in the ruins of Atlas Cove station (Heard Island) and removed (Smith, 1986). Glasshouses, hydroponic rooms and other artificial means to grow vegetables may also be avenues for the propagation of alien fungi.

Not all plant pathogens known from the sub-Antarctic are human introductions. The recently identified Stilbocarpa Bacilliform Mosaic Virus (SBMV), a badnavirus causing bright yellow mosaic symptoms on leaves of the megaherb *Stilbocarpa polaris* (Skotnicki *et al.*, 2003), is only known to infect *S. polaris* and is recorded only from Macquarie Island, where it is widespread. Badnaviruses are most often found associated with tropical and subtropical plants and are usually transmitted between plants by sucking insects. On Macquarie Island, it is likely that occasional transfer between plants could now be undertaken by aphids, although the natural vector is unknown.

Human activity in Antarctica has been identified as a potential source of disease in wildlife, either by translocating pathogens or acting as a source of stress, leading to a reduction of immunity and creating the opportunity for

expression of dormant diseases (Kerry, Riddle & Clarke, 1999). A clear link between Antarctic wildlife disease and human activity has yet to be documented. There is, however, substantial evidence of exposure to disease-causing agents. For example, avian paramyxoviruses (APMV) and antibodies to Newcastle Disease (NDV) have been found in Macquarie Island royal penguins (*Eudyptes chrysolophus*) (Morgan & Westbury, 1981). APMVs, NDV antibodies and five species of *Salmonella* have been isolated from Adélie penguins (*Pygoscelis adeliae*) (Oekle & Steiniger, 1973; Morgan *et al.*, 1978), and *Salmonella enteritidis* phage type 4, the most common clinical isolate in affluent countries (Olsen *et al.*, 1996), has been isolated from a gentoo penguin (*Pygoscelis papua*) at Bird Island, South Georgia. On Crozet Islands, antibodies to Lyme disease have been found in king penguins (*Aptenodytes patagonicus*), and the Lyme Disease spirochete, *Borrelia burgdorferi*, has been found in the cosmopolitan tick *Ixodes uriae* (Gauthier-Clerc *et al.*, 1999). Substantial reviews of disease in penguins and other Antarctic wildlife are presented by Clarke & Kerry (1993) and Kerry *et al.* (1999). However, it should also be recognized that many Antarctic bird species come into contact with humans well outside the Antarctic region, especially during the winter months. For instance, brown skuas (*Catharacta lonnbergi*) and Dominican gulls (*Larus dominicanus*) migrate to the nearest continent (South America, Australia), often foraging around ports and human waste dumps, while wintering south polar skuas (*Catharacta maccormicki*) are regularly observed in the northern Pacific Ocean.

Human microorganisms discharged within raw sewage from Antarctica's largest station, the U.S. McMurdo Station (around 1000 summer inhabitants) have been located in the surrounding marine environment and sea-ice (Edwards, McFeters & Venkatesan, 1998; Smith & McFeters, 1999). The latter authors traced the distribution of *Clostridium perfringens*, an indicator bacterial species of human faecal contamination, to just beyond 400 m from the station's sewage outfall, noting that the concentration of bacteria decreased with sediment depth and distance from the outfall. This bacteria was also found in the intestines of sea urchins, tunicates, clams and starfish within the 400 m zone. Similarly, Hughes (2003 *a, b*) quantified dispersal and survival of sewage-derived faecal coliforms near the U.K. Rothera Station (Adelaide Island). Enteric bacteria [the pathogenic *Yersinia enterocolitica*, *Salmonella typhimurium*, enterotoxigenic *Escherichia coli* and conjugative/antibiotic resistance plasmid-harboring (pUC19, pFamp) bacteria] grown in chilled McMurdo sea water can survive significantly longer than in temperate environments (Smith, Howington & McFeters, 1994). Smith & McFeters (1999) concluded that these results 'indicate the potential for transfer of virulence, and/or antibiotic resistance genes from pathogenic microorganisms which may be present in untreated sewage, to indigenous microbiota with unknown effects on susceptible wildlife' and applied the term 'genetic pollution' (the introduction of new genetic material to an environment as a result of anthropogenic activities) to this situation. While sewage discharges are permitted under the Antarctic Treaty, there are relatively simple engineering means by which to minimize release of such microorganisms (Hughes & Blenkarn, 2003).

(5) Marine introductions

The potential for introduction of alien marine taxa to the Antarctic region is largely unstudied. The green alga *Enteromorpha intestinalis* grows in dense mats in the intertidal zone at Half Moon Island (62° 37' W 59° 57' S), and may have been introduced via the hulls of visiting vessels (Clayton, Wiencke & Klöser 1997). A single recent study (Lewis *et al.*, 2003) investigated the potential for transport of marine organisms between Tasmania, Macquarie Island and the Antarctic continent by ships used to support Antarctic science and tourism. The study identified three pathways enabling the transport of (i) planktonic organisms from the Southern Ocean and Tasmanian waters, (ii) epibenthic organisms from Tasmania, and (iii) fouling assemblages. Finally, the potential exists for transfer of organisms on anthropogenic marine debris (Barnes, 2002; Barnes & Fraser, 2003), with many sites in the sub- and maritime Antarctic accumulating substantial quantities of marine debris annually (Ryan, 1987; Gregory & Ryan, 1997, Convey, Barnes & Morton, 2002 *a*).

(6) Concluding remarks on status and patterns

The number of species introduced to an area is much greater than those that eventually establish, while only 10% of the latter then become 'invasive' (Williamson, 1996; Williamson & Fitter, 1996). Most alien plants in the Antarctic are currently persistent, with only a few species highly invasive and causing significant change to the ecosystems (Table 1), although the impact of these few species can be large. The same generalization holds for alien invertebrates, with a few insect species again having pronounced effects on local ecosystems (Table 2). Most vertebrates (Table 3) are invasive and have had substantial impacts although, in part, this difference may be explained by some being selective and deliberate introductions. Despite the technical difficulties in detection and previous lack of research effort there is already evidence of introduction of microorganisms to the region. However, a clear link between humans and disease in wildlife has yet to be established.

Aliens can have pronounced indirect effects on local species and ecosystems (e.g. Bergstrom & Chown, 1999; Courchamp *et al.*, 1999; Crooks & Soulé, 1999), which need to be considered carefully prior to any management actions. The massive, and often unpredictable, indirect effects of control programmes have now been widely documented in other regions (see Zavaleta, Hobbs & Mooney, 2001), and there is every reason to expect them to be important in the broader Antarctic region too.

III. ORIGINS AND CORRELATES OF INVASION

(1) Origins

Most alien plants introduced to the sub-Antarctic are European and usually show a large ecological range. Many alien invertebrates (e.g. the springtail *Hypogastrura viatica*, the fly *Fannia canicularis*, the isopod *Porcellio scaber*, the slug *Deroceras*

panormitanum (= *caruanae*) and the earthworm *Dendrilus rubidus*) and birds (e.g. mallard, redpoll, starling) are also of European origin, although now cosmopolitan. This is partly because colonization by humans in the Antarctic was largely from Europe (Headland, 1989). European species, however, are also very successful invaders of other temperate areas (e.g. Pyšek, 1998; Prinzig *et al.*, 2002). di Castri (1989) has ascribed this to the long association of European species with human disturbance, and Prinzig *et al.* (2002) also emphasise the importance of disturbance in allowing European species to colonize sites in Argentina. The absence of significant numbers of Southern-Hemisphere-origin introduced species in the Antarctic may also be a consequence of loading supplies from either the Northern Hemisphere, or from disturbed Southern Hemisphere sites (farms, ports, holding areas in cities), where both the abundance and diversity of European invasives is high (Slabber & Chown, 2002).

Exceptions to the pattern of introductions from Europe do exist, including the plants *Empetrum rubrum* and *Pratia repens* to South Georgia. Among the carabid beetles native to the Falkland Islands (Smith, 1996; McIntosh & Walton, 2000), *Trechisibus antarcticus* was probably transferred to South Georgia, and *Oopterus soledadinus* to Kerguelen Islands and South Georgia (Tréhen & Voisin, 1984; Ernsting, 1993). On the site of the beetle's introduction to Kerguelen Islands, *Trisetum spicatum*, a bipolar plant species also growing in the Falkland Islands (Moore, 1968) was recently recorded. The plant was probably introduced at this site with sheep imported from the Falkland Islands in 1907 (Frenot *et al.*, 2001).

Separating indigenous species from Southern Hemisphere regional introductions may be problematic. For example, the winged chironomid midge, *Parochlus steinenii*, is found on South Georgia and the South Shetland archipelago and is widely distributed in southern South America. Although regarded as being indigenous, it is plausible that the species might have been introduced in water barrels of whaling and sealing ships (Convey & Block, 1996). The diving beetle *Lancetes angusticollis* is also found on South Georgia and in South America. This species has well-developed wings and flight musculature but has not been observed in flight or away from water on South Georgia, suggesting that it might also have been transferred in water containers.

(2) Correlates

Quantitative investigation of the correlates of invasion has been limited to the Southern Ocean islands. Earlier investigations suggested that parthenogenesis is a characteristic of many of the successful invaders (Crafford, Scholtz & Chown, 1986). Later, Chown *et al.* (1998b) investigated the relationships between several abiotic and biotic variables and the richness of alien vascular plants, insects, birds and mammals for all of the Southern Ocean islands. For vascular plants, larger islands have more aliens because of both elevated habitat heterogeneity and higher numbers of human occupants. However, cold islands are less susceptible to invasions than warm ones. For insects a similar relationship holds, although indigenous vascular plant richness is also an

important correlate of the richness of alien insects. The level of human occupancy and the temperature of an island are important correlates of the species richness of alien mammals. For birds, distance to the nearest continent and indigenous plant and insect species richness were the most important explanatory variables, especially given that many of these mostly passerine species were self-introduced. A subsequent re-analysis of these data incorporating the effects of spatial autocorrelation supported most of these conclusions, excepting the influence of distance on alien bird establishment (Selmi & Boulinier, 2001).

The association between levels of human occupancy and numbers of alien species clearly reflects propagule pressure (see Williamson, 1996) associated with more frequent and/or larger visits by resupply vessels. For instance, between 1675 and 1956 approximately 51 landings were made at Gough Island (South Atlantic) (Gaston *et al.*, 2003), and an invertebrate survey in 1955/6 revealed 25 alien insect species (Holdgate *et al.*, 1956). Between 1957 and 2000 (following the construction of a permanent scientific station in 1955/56) approximately 182 landings were made, and a further 43 species were introduced. Much colonization occurred during the construction and maintenance of the scientific station, associated with sand, wood and other imported material. Major infrastructure programmes at research stations on sub-Antarctic islands are likely to carry a particularly high risk of alien introduction owing to the enforced use of large amounts of imported materials.

Using springtail abundance and distributions on Marion Island, Gabriel *et al.* (2001) tested the hypothesis that temperature is an important correlate of alien species richness (Chown *et al.*, 1998b). They demonstrated that alien species prefer warmer, moister and more nutrient-enriched sites, while indigenous species tended to prefer cooler, drier sites, and suggested that interactions between alien and indigenous species were less important than climate in determining the distribution and abundance of the former. In a study relating the occurrence of the cosmopolitan necrophagous fly, *Calliphora vicina*, with available meteorological data (1951–2001) at Kerguelen Islands, Y. Frenot, P. Saccone and P. Vernon (unpublished data) have found that establishment was possible only after the early 1980s and that its continued absence in West Kerguelen is explained by the current climatic conditions there. These findings support studies suggesting that climate matching, or the ability to adapt quickly to local climates (Lee, 2002), are important determinants of invasion success (e.g. Lodge, 1993; Pyšek, 1998; Blackburn & Duncan, 2001), with biotic resistance being less significant (but see Mack, 1996; Williamson, 1996; Tilman, 1999 for contrary views).

Low species richness and the absence of many functional groups might make islands, and the island-like exposed land of Antarctica, more susceptible to alien invasion (Bergstrom & Chown, 1999; Chown, Gaston & Gremmen, 2000). Islands are generally considered to be more susceptible to invasion than other terrestrial systems, mainly because indigenous species lack mechanisms to buffer themselves against associated change (D'Antonio & Dudley, 1995; Vermeij, 1996; Williamson, 1996; Bowen & Van Vuren, 1997). Lonsdale (1999) demonstrated that, at least for plants,

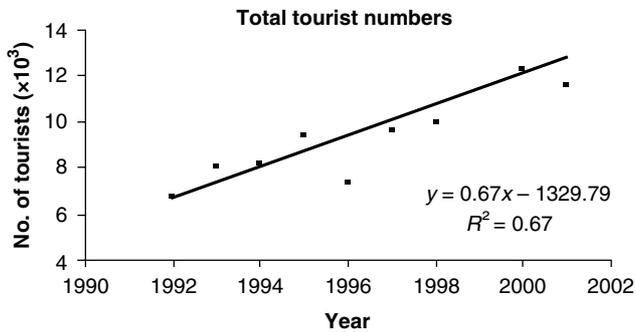


Fig. 2. Trend in total numbers of tourists visiting Antarctica between 1992 and 2001.

once area is accounted for, islands tend to support more aliens than do continents. In the Antarctic, for example, the absence of terrestrial mammalian predators could be responsible for a higher susceptibility of native fauna to the introduction of carnivorous species.

Many ecophysiological studies demonstrate that a wide range of terrestrial organisms can survive in the extreme conditions of the maritime and continental Antarctic (Convey, 1996). Rather, long-distance dispersal limits their range expansion (Pugh, 1994; Pugh *et al.*, 2002). Although a major problem, this limit is not insurmountable. Aerobiological studies (Marshall, 1996) have demonstrated low-frequency input of airspora from lower latitudes to the region. Studies of the biota of geothermally heated ground at various locations in Antarctica (the South Sandwich Islands, Deception Island and Victoria Land) have found natural colonization by a range of sub-Antarctic and lower latitude bryophyte and arthropod taxa (Convey, Greenslade & Pugh, 2000*a*; Convey *et al.*, 2000*b*; Skotnicki *et al.*, 2001). Some of these taxa are found only in the close vicinity of areas of heated ground that are transient on a timescale of decades. Repeated surveys indicate both that some taxa persist in the locality and that new species are recorded. It is likely that local colonization of new areas of heated ground and repeated long-distance colonization events are both involved. Other taxa, however, have expanded distributions away from the likely initial colonization site and can clearly survive the ambient conditions. These findings suggest that it is not only climate, but also opportunity for dispersal that keep the numbers of alien plant and invertebrate species low in the broader Antarctic region.

IV. CHANGING PATTERNS OF USE

The overriding influences on levels of introduction of alien biota are human patterns of use and climate matching. Changes in these variables are likely to have the largest impacts on the likelihood of further establishment and impact of alien species in the Antarctic (Chown & Language, 1994; Kennedy, 1995*a*; Chown & Gaston, 2000). Changes in both climate and patterns of human use are taking place rapidly, although somewhat differently, throughout the region.

(1) Tourism

Tourism began in Antarctica in 1956 with a Chilean flight over the continent. This was soon followed by cruises to the South Shetland Islands (1957), and commercial tours (1958) (Stonehouse, 1994). There has since been an initially erratic but later rapid increase in tourism and, in the last decade, tourist numbers have doubled (Fig. 2). Tourism is overwhelmingly based around the Scotia Arc and Antarctic Peninsula, due to their easy accessibility from southern South America. In the 2001/02 austral summer season 96% of the approximately 13 600 tourists who visited Antarctica were active in this region. The majority departed by small ship from Ushuaia, Argentina, or Punta Arenas, Chile, and participated in multi-site tours, generally island-hopping between the Falkland Islands, South Georgia, the Scotia Arc islands and locations on the Antarctic Peninsula (IAATO, 2002). The sequence of sites visited over a short time period (2–4 weeks) is often from warmer, higher biodiversity areas to cooler, lower biodiversity areas. Examining trends over 10 years (1989–1999), Navareen *et al.* (2001) reported that the majority of landings were in the South Shetland Islands (43%) followed by north-western areas of the Peninsula. In the 2001/02 summer landings occurred at 118 sites with a maximum of nearly 7000 people visiting Whalers Bay, Deception Island. Recently, there appear to be trends towards larger rather than smaller tours and the use of larger ships (Moser & Betts, 2002).

The remaining tourism in the Antarctic region is based around the New Zealand cold temperate islands, Macquarie Island and the Ross Sea sector (see Heritage Expeditions, 2002). In the 2001/02 season, visits occurred at 23 sites in this sector, including approximately 300 people landing sequentially on Campbell, Auckland and Macquarie Islands, during expeditions leaving from southern New Zealand or southern Australia. A small number of operators offer longer tours, combining visits to the Ross Sea sector and Antarctic Peninsula.

In 2001/02 most tourists were from seven countries: United States of America (41%), United Kingdom (13%), Germany (12%), Australia (7%), Japan (5%), Canada (3%) and Switzerland (2%). All have cold temperate, alpine or tundra environments supporting taxa that, if transported on human vectors, could establish in some areas of the Antarctic. Furthermore, Antarctic ecotourists are well travelled (J. Whinam, D. Bergstrom & N. Chilcott, unpublished data), commonly visiting other high-latitude or high-altitude regions within six months before departing for Antarctica.

Four trends in tourism patterns are of significance to the potential for the introduction and spread of alien organisms to and in the Antarctic region:

(1) Tourists are disproportionately attracted to sites of high/medium diversity (Navareen *et al.*, 2001) (high diversity ≥ 10 faunal species or major floral groups, medium diversity 5–9 faunal species or major floral groups). Of 85 sites visited during 1998/99, only 23.5% were high to medium diversity. These sites, however, received approximately 50% of vessels and visitors. Because numbers of alien and indigenous species tend to be strongly related across sites both in the

sub-Antarctic and elsewhere (Chown *et al.*, 1998*b*; Sax, Gaines & Brown, 2002) impacts of aliens are likely to be more pronounced on high-diversity sites. Indeed, sites where the two species of native vascular plants occur on the Antarctic Peninsula (see Smith, 1994) are likely to be those most at risk of introductions.

(2) The intensity of visitor use is increasing. Reviewing data from 165 sites in the Antarctic Peninsula region, Navareen *et al.* (2001) reported increases of 425% in inflatable boat landings between 1989/90 and 1998/99, and 321% in the total number of people participating in these landings (from 17 759 to 74 772). Greater numbers of ships and tourists lead to greater chances of introductions.

(3) Sites of high popularity are not consistent over time. The 25 most visited sites in the Antarctic Peninsula region have changed over the last 10 years (Navareen *et al.*, 2001), meaning that the potential for human impact is not contained to a number of specific sites but varies as tourist trends/fashions change.

(4) The range of tourist activities is expanding. The standard pattern of visits during the 1980s and early 1990s was simply to land on beaches and observe immediately accessible wildlife, but options now include extensive walks, kayaking trips and even a marathon on King George Island (South Shetland Islands) (<http://www.marathontour.com/antarctica/index.shtml>). In both 2002 and 2003 'grand tours' by commercial operators, visiting multiple sub-Antarctic islands in the Kerguelen sector, have either occurred or been planned. For example, a tour in November 2002 travelled from Mauritius, sequentially landing on Possession, Heard, Kerguelen, Amsterdam and St Paul Islands (Heritage Expeditions, 2002). By moving through larger areas or visiting more islands the chances of spreading alien species increases.

(2) Scientific research activities

There are considerably fewer people involved in national scientific programs in Antarctica than in the tourism industry. Data collected under Antarctic Treaty obligations (COMNAP, 2003) showed that, in the 2001/02 season, Treaty signatory nations had 4390 personnel in Antarctica and the sub-Antarctic islands at any one time, across 67 stations or field camps. This number underestimates the total number of personnel, as many stations have a partially revolving population. The largest numbers were deployed at stations in the Scotia Arc and Antarctic Peninsula sector (1361) and the single McMurdo Station in the Ross Sea sector (1200). Over 60 ships were used by national programs in 2001/02 to transport personnel and cargo to Antarctica. Table 4 lists the main ports of origin used by national scientific programs and other operators. As many of the national programs are run by European and Asian countries, and the USA, large numbers of ships inevitably travel from the Northern Hemisphere, with some working consecutive Antarctic/Arctic summers to take advantage of ice-strengthened or ice-breaking capabilities. Many ships used in tourist operations also work at high northern latitudes during the austral winter, in particular the ice-breakers and larger liners.

Table 4. Summary of shipping ports used by national scientific programs and other operators working in Antarctica

Port	Country	Main operators
Buenos Aires	Argentina	Argentina
El Palomar	Argentina	Argentina
Mar del Plata	Argentina	Argentina
Ushuaia	Argentina	Argentina, Germany, Spain, various tourist operators
Fremantle	Australia	Australia
Hobart	Australia	Australia, France
Rio de Janeiro	Brazil	Brazil, UK
Punta Arenas	Chile	Chile, Germany, Spain, Poland, USA, most operators with stations in the South Shetland Islands, various tourist operators
Valparaiso	Chile	Chile, USA
Shanghai	China	China
Stanley, East Cove	Falkland Islands	UK, various tourist operators
St Denis de la Réunion	France	France
Bremerhaven	Germany	Germany
Ravenna	Italy	Italy
Tokyo	Japan	Japan
Ulsan	Korea	Korea
Bluff	New Zealand	New Zealand and tourist operators
Christchurch	New Zealand	New Zealand
Lyttelton	New Zealand	New Zealand, USA
Otago	New Zealand	New Zealand
Wellington	New Zealand	New Zealand
Oslo	Norway	Norway
Gdynia	Poland	Poland
St Petersburg	Russia	Russia
Cape Town	South Africa	South Africa, Germany, India, UK
Durban	South Africa	France
Malmö	Sweden	Sweden
Seattle	U.S.A.	USA
Sebastopol	Ukraine	Ukraine
Grimsby	United Kingdom	UK
Immingham	United Kingdom	UK
Portsmouth	United Kingdom	UK
Montevideo	Uruguay	Uruguay, UK

(3) The specific case of South Georgia

While the number of tourist visitors and landings made along the Antarctic Peninsula has increased dramatically over the last decade, thereby increasing the risk of transfer of aliens into this region, there is a strong case that parts of the sub-Antarctic remain the most vulnerable. This is, first, because existing patterns of alien occurrence in the sub- and maritime Antarctic highlight the ease with which the former may be colonized and, second, at least some islands in the sub-Antarctic have experienced a comparable surge in visitor numbers to the Antarctic Peninsula. South Georgia is under the greatest pressure by far, being relatively accessible

from South America and the Falkland Islands, and including an administrative centre (King Edward Point), which is the immigration port of entry and point of registration for vessel movements in the British territory of South Georgia and the South Sandwich Islands.

Data on shipping visits to South Georgia are summarised in Fig. 3. The majority of passenger landings on South Georgia are made from cruise ships and yachts (14 and 11%, respectively, of vessels visiting in 2001). The number of landings in summer 2002/03 was a 50% increase over the total in 2001/02, and almost 1000 more than in 1999/2000 when the previous record was set. Of that number, approximately 97% arrived on 45 voyages made by 16 different tour ships, with capacities ranging from 24 to 550 passengers. The remainder arrived on 14 yachts or small expedition vessels, some commercially operated (Moser & Betts, 2003). Tourist landings take place both at the administrative centre and at a range of other sites of historical and wildlife interest (McIntosh & Walton, 2000). South Georgia is also the focus of some of the largest Southern Ocean fisheries but, although fisheries-related vessels make up the largest proportion (55% in 2001) of ships visiting the island (a requirement of obtaining their licences), it is rare for personnel from these ships to land, other than for the exchange of fishery observers. Personnel also regularly land from military (warships and supply vessels, 8%), fishery patrol (7%) and scientific research (4%) vessels. Precise numbers landing are not recorded in these cases, but the ships typically carry 20–100 personnel, the majority of which spend time ashore. Thus, in comparison with all other sub-Antarctic islands, and most sites in the Antarctic Peninsula region, South Georgia receives a much larger number of vessels, from a wider range of operations. The high density of shipping around South Georgia, combined with typically poor sea conditions, leads to an increased risk of accidents (and introductions *via* debris), exemplified by the recent (April 2003) groundings of three fishing vessels near King Edward Point, two of which have not been refloated.

(4) Accessibility by air

In addition to the use of ships for transport to Antarctic locations, several national operators and a small number of non-governmental organisations use air transport. This gives faster, more efficient, exchange of personnel and equipment, but also allows rapid transfer of propagules, allowing even short-lived life stages to arrive alive. For example, a house fly (probable) noticed on the British airlink from the Falkland Islands to Rothera Point, Adelaide Island in mid-January 2003 is possibly the same individual as noted on the nearby (approximately 1 km) Killingbeck Island several days later (S. Ott, personal communication), indicating that both local short-term survival and dispersal are possible.

There are currently five points of departure for flights of tourists or research staff – southern Chile, southern Argentina, Falklands Islands, South Africa and New Zealand; flights will soon begin from Tasmania. The aircraft used originate from several South American countries, Australia and New Zealand as well as others transiting from the USA, Canada, United Kingdom, Germany, Russia and

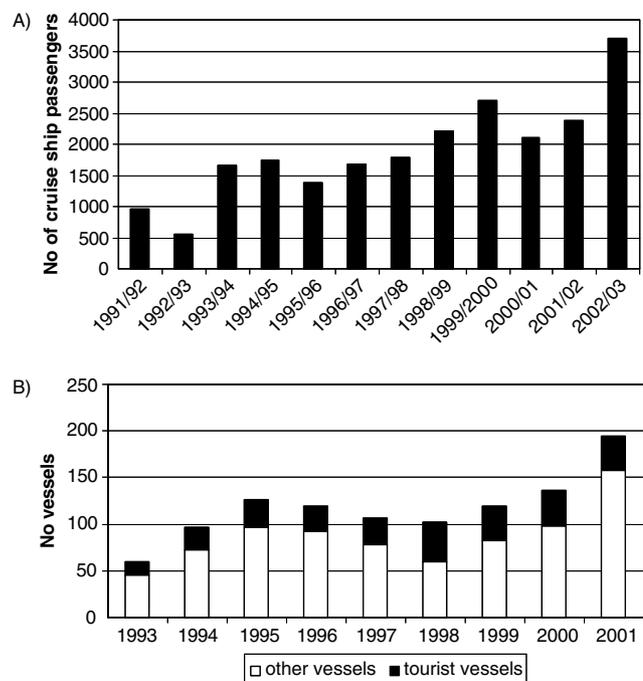


Fig. 3. Trends in numbers of tourists visiting the sub-Antarctic island of South Georgia. (A) Numbers of cruise ship passengers landing each austral summer between the 1991/92 and 2002/03 seasons. (B) Total number of vessels, and number of tourist vessels, visiting the administrative centre at King Edward Point each calendar year between 1993 and 2001.

Kazakhstan, and include both governmental and commercial operators. Some of these flights travel *via* King George Island (South Shetland Islands), and may go onwards to Patriot Hills and other parts of Antarctica.

In terms of personnel and cargo transport, by far the largest operation is that mounted from Christchurch (New Zealand) to the Ross Sea stations of McMurdo (USA) and Scott (New Zealand), utilising US Hercules and Starlifter aircraft, and New Zealand Hercules. Flights commenced from Cape Town, South Africa, to Dronning Maud Land during the 2001/02 season, but at much lower frequency than those from South America or New Zealand. When fully operational, the Australian Antarctic Division plans for flights from Tasmania to have a maximum transporting capacity of up to 400 personnel in a season (Clarke, 2003). Without effective quarantine measures, alien organisms could be transported from all Southern Hemisphere continents to Antarctica within a 3–9 h period.

While intercontinental flights provide potentially rapid transfer into Antarctica, intracontinental flights raise a further, and largely unrecognized, risk of transporting indigenous biota between the different regions of the continent. The potential implications of this may be appreciated when it is realised that much of the terrestrial biota present is endemic to either the continental or maritime biogeographical zones (Pugh, 1993; Greenslade, 1995; Andrassy, 1998; Convey, 2001 *b*; Øvstedal & Smith, 2001). It is likely that biota transferred between zones will have a high chance

of survival, as analogous communities and stresses exist in each, and the likelihood of appropriate adaptations being present is high. There is a similar risk, also rarely highlighted, of accidental movement of indigenous biota within each zone (see Convey *et al.*, 2000*c*), which would compromise scientific studies of molecular adaptation, regional evolution and biogeography.

V. IMPLICATIONS OF CLIMATE CHANGE

(1) Climate trends

Temperature increases amongst the most rapid worldwide are well documented in the maritime Antarctic (Smith, 1990; Fowbert & Smith, 1994; King & Harangozo, 1998; Skvarca *et al.*, 1998; Quayle *et al.*, 2002), with increases in annual air temperatures of at least 1 °C over the last 30–50 years reported at several locations. Analogous trends are seen at some sub- and continental Antarctic sites (e.g. Smith & Steenkamp, 1990; Gordon & Timmis, 1992; Frenot *et al.*, 1997; Tweedie & Bergstrom, 2000; Smith, 2002). By contrast, one report of regional cooling in the Dry Valleys region of Victoria Land (Doran *et al.*, 2002; but see also Turner *et al.*, 2002) has linked local cooling with decreased primary productivity and invertebrate populations.

Climatic trends may not be constant throughout the year and this may have considerable biological significance. For example, the annual trend on the Antarctic Peninsula is driven by strong warming during winter, with much lower rates seen in summer (King & Harangozo, 1998). While this has little direct effect on summer conditions, the active season for terrestrial biota may be extended by shortening the winter period, through earlier spring thaws and later autumn freezing. By contrast, warming reported at Signy Island (South Orkney Islands, also in the maritime Antarctic) has occurred mostly in summer, with little change during winter (Smith, 1990; Block & Convey, 2001). On sub-Antarctic Macquarie Island, warming is most pronounced in late summer and early autumn, although the island cools during severe ENSO events (Adamson, Whetton & Selkirk, 1988).

In addition to increasing temperature, changes in other indices such as precipitation are documented. Precipitation patterns are likely to be linked with insolation, cloud cover and wind speed, and hence to temperature, especially at the microclimatic scale. Increases in precipitation have been predicted in the Antarctic coastal zone (Budd & Simmonds, 1991) and documented in the maritime Antarctic (Turner, Colwell & Harangozo, 1997). Again, these changes may be linked with ENSO. Decreased precipitation has been reported at sub-Antarctic Marion and Kerguelen Islands since the early 1950s (Smith & Steenkamp, 1990; Frenot *et al.*, 1997; Smith, 2002; Chapuis *et al.*, 2004) and, more recently, from maritime Antarctic Signy Island (Noon *et al.*, 2001). In the maritime Antarctic, there is also an increasing likelihood that summer precipitation will fall as rain rather than snow, and hence be immediately available to terrestrial ecosystems. On Macquarie Island, time series analysis of 50 years of meteorological data has shown increases in mean

monthly surface air temperature, wind speed, precipitation and evapotranspiration and decreases in air moisture content and sunshine hours (C. Tweedie, D. Doley & D. Bergstrom, unpublished data).

As well as direct precipitation, water availability in terrestrial habitats is governed by seasonal snow and glacial melt, and this is usually the only source of liquid water in continental Antarctica. Rapid rates of glacial retreat and loss of 'permanent' snow cover observed at a range of maritime and sub-Antarctic sites are particularly significant in this context (Smith, 1990; Gordon & Timmis, 1992; Fowbert & Smith, 1994; Frenot *et al.*, 1997; Pugh & Davenport, 1997; Fox & Cooper, 1998; Kiernan & McConnell, 2002). While increasing input of water to terrestrial ecosystems, earlier or increased melt may also exhaust reserves of ice or snow before the end of the summer, hence locally increasing water stress on terrestrial biota. If warming increases the frequency of winter thaws it may encourage formation of a sub-snow ice layer on the ground surface (described by Davey, Pickup & Block, 1992; Arnold *et al.*, 2003). In a recent Arctic study, this process was shown to have negative effects on some soil faunal communities (Coulson *et al.*, 2000).

The potential consequences of the annual formation of the Antarctic ozone hole, leading to greater penetration of UV-B radiation to the Earth's surface during the austral spring, have received much attention. This anthropogenic feature has existed only since the early 1980s (Farman, Gardiner & Shanklin, 1985) and, as yet, shows no sign of recovery. Though no link has yet been proposed with the biology of alien species, subtle biological consequences for indigenous biota are beginning to be reported, including dynamic changes in patterns of use of biochemical pathways associated with protective pigment production (Newsham *et al.*, 2002) and negative effects on population sizes of microarthropods (Convey *et al.*, 2002*b*).

(2) Implications for alien biota

The implications of climate change for existing Antarctica biota have been extensively discussed (e.g. Selkirk, 1992; Wynn-Williams, 1994, 1996*b*; Kennedy, 1995*a*; Convey, 1997, 2001*b*; Walton *et al.*, 1997), and investigated by using field manipulations and the naturally rapid rates of change in the Antarctic Peninsula region (e.g. Smith, 1990; Day *et al.*, 1999; Convey, 2001*b*). Climatic amelioration is also likely to enhance the ability of both natural long-distance colonists (especially those with long-surviving propagules; Smith, 1993) and human-assisted aliens to become established, particularly in the sub-Antarctic (Selkirk, 1992; Chown & Language, 1994; Kennedy, 1995*a*; Bergstrom & Chown, 1999). Several plants (notably the two angiosperms indigenous to the maritime Antarctic, *Colobanthus quitensis* and *Deschampsia antarctica*) have rapidly expanded their local ranges as climates have warmed. Terrestrial invertebrates are then able rapidly to colonize newly available habitats. However, to date, most ecological evidence, whilst extremely suggestive, remains circumstantial. There are few instances of long-distance colonization of new sites by species from elsewhere in the Antarctic [one example being

the moss *Polytrichum piliferum* on Signy Island (Convey & Smith, 1993)], and none for lower latitude species, that can even circumstantially be linked with climate amelioration. Although it is commonly assumed that climate amelioration will reduce environmental stresses, a recent study of the springtail, *Cryptopygus antarcticus*, highlights the danger of making this assumption (Block & Convey, 2001; see also Kennedy, 1995*a*). This study identified periods of increased desiccation stress during the austral summer, linking this with exhaustion of water supplies. Interactions between these processes may even result in local range limitation for this springtail species.

Field manipulation methods have been used to mimic predicted climatic changes (e.g. Wynn-Williams, 1992, 1996*b*; Day *et al.*, 1999; Convey *et al.*, 2002*b*; see Kennedy, 1995*c*, Table 1). These methods have several weaknesses (Kennedy, 1995*b,c*), and the more recent studies have developed means to minimize their effects, but they have been useful for assessing the likely responses of the indigenous biota to climate change. The use of screens has led to spectacular responses in the growth of microbial groups, bryophytes and higher plants (Smith, 1990, 1994; Wynn-Williams, 1993, 1996*b*; Kennedy, 1996). Fewer studies have been directed at faunal communities, but some arthropod populations have expanded rapidly (Kennedy, 1994), and trophic groups of soil nematodes have responded differently (Convey & Wynn-Williams, 2002; Convey, 2003). Faunal responses are likely to be mediated by those of the microbial groups on which many depend for food, as well as by the direct impact of environmental manipulation. The difficulties of predicting and interpreting consequences of multifactorial environmental change or manipulation are illustrated by a recently completed long-term manipulation study carried out near Palmer Station (Anvers Island, west Antarctic Peninsula) (Convey *et al.*, 2002*b*). Day (2001) and Searles *et al.* (2001) further highlighted that apparently small or insignificant changes at one level may combine to generate far more significant consequences at other levels in an ecosystem.

In the sub-Antarctic, climatic amelioration is likely to have two main effects. First, because alien species are already established on many islands, some may change from persistent to invasive status. Barendse & Chown (2000) argued that most alien insects on Marion Island have rapid life cycles that are likely to respond strongly to temperature, whilst indigenous species generally have a much slower life cycle and are less responsive or might succumb to higher temperatures. The change in status of several alien plants on Marion Island (Gremmen & Smith, 1999) might also be a consequence of climate change. Increases in vegetative or sexual reproduction may lead to natural colonization of nearby, currently pristine sites, as has happened at the infrequently visited Prince Edward Islands (Gremmen & Smith, 1999). Second, indigenous species may also respond rapidly. For instance, the diving beetle *Lancetes angusticollis*, present in lakes on South Georgia, may show a very rapid response to warming (Arnold & Convey, 1998), as an increase of only 1 °C in lake temperature would allow completion of an annual rather than the current biennial life cycle. As this beetle is the top predator in the lake ecosystem,

a significant but currently unknown impact on local trophic dynamics is to be expected.

Secondary or tertiary consequences linked with climatic change may also have large impacts. For instance, while the recent rapid recovery of Antarctic fur seal populations (Croxall, 1992; Guinet, Jouventin & Georges, 1994; Page *et al.*, 2003), previously hunted to the verge of extinction, is generally attributed to lack of feeding competition through anthropogenic reductions in great whale populations, recent seasonal changes in distribution of this species may also be linked with regional climate warming (Quayle *et al.*, 2003). The impact of these population changes on terrestrial and freshwater ecosystems has been drastic, with trampling and excessive nutrient input leading to the virtually complete destruction of large areas of terrestrial vegetation and the eutrophication of previously oligotrophic lake systems (Smith, 1988, 1997; Butler, 1999).

Table 5 presents some likely future responses of some alien species to environmental change and their impacts on indigenous biota. These predictions are based on the limited knowledge available, and it is likely that the impacts of alien species will be far more subtle and pervasive.

VI. CONCLUSIONS

(1) This study is the first major summary of knowledge of alien taxa for southern, high-latitude sub-Antarctic and Antarctic regions. The biota of most sub-Antarctic islands and some maritime and continental Antarctic ice-free areas include alien taxa. Opportunities for alien invasion have been restricted to the last two centuries, commencing with historical sealing and whaling industries and extending to the research, commercial and tourist activities of modern times.

(2) Risks of introduction of alien species to Antarctica and the sub-Antarctic, while lower than elsewhere, remain significant, as are the chances of existing persistent species becoming major invasives. Impacts of alien taxa on indigenous ecosystems range from negligible and transient, through persistence with very limited distribution, to major and complex ecosystem consequences of aggressive invasives.

(3) To date, research has focused on higher and more visible taxa such as vascular plants, macro-invertebrates and, particularly, mammals. The majority of these are representatives of widespread families and/or are European in origin, reflecting either direct European sources or victualling supplies often being obtained through southern ports already awash with European invasives.

(4) Major correlates of invasion are island size (reflecting habitat heterogeneity and human visitors) and temperature. Warmer locations have greater numbers of aliens. On the Antarctic continent, no species of vascular plant or macro-invertebrates have yet established despite their release into these environments, while only a very small number of aliens have persisted in the maritime Antarctic. The sub-Antarctic Kerguelen and Crozet Islands, with a relatively mild climate and long history of human occupancy and industry (whaling and farming), currently host the greatest

Table 5. Summary of climatic trends (arrows indicate direction of trend) on sub-Antarctic island groups and maritime and continental Antarctic regions, with some likely/possible future responses of significant alien species and their impacts on indigenous ecosystems (*denotes probable transition from persistent to invasive alien status)

Location	Climate trends	Predicted changes in invasive species	Species/habitats affected
Marion Island	↑ temperature ↓ precipitation	↑ <i>Agrostis stolonifera</i> ↑ <i>Sagina procumbens</i> ↑ mice populations ↑ <i>Pogonognathellus flavescens</i>	Loss of extent of native communities – decrease in <i>Acaena magellanica</i> cover
Prince Edward Island	↑ temperature ↓ precipitation	↑ <i>Sagina procumbens</i> * ↑ <i>Poa annua</i> ↑ <i>Cerastium fontanum</i>	Loss of extent of native communities
Kerguelen Islands	↑ temperature ↓ precipitation	↑ <i>Taraxacum officinalis</i> ↑ <i>Poa annua</i> ↑ <i>Poa pratensis</i> ↑ <i>P. trivialis</i> ↑ <i>Ooptyerus soledadinus</i> ↑ <i>Myzus ascalonicus</i> ↑ mice populations	Loss of extent of native communities, decrease in <i>Acaena magellanica</i> cover; decreased abundance of invertebrates in presence of <i>O. soledadinus</i>
Heard Island	↑ temperature ↓ glacial extent	↑ <i>Poa annua</i> *	Major change in all indigenous plant communities with expansion of <i>Poa annua</i> and arrival of additional alien species
Crozet Islands	stable	↑ <i>Taraxacum officinalis</i> ↑ <i>Sagina procumbens</i> ↑ <i>Stellaria uliginosa</i>	Loss of extent of native plant communities
Macquarie Island	↑ temperature ↑ wind speed ↑ precipitation ↑ evapotranspiration ↓ humidity ↓ sunshine hours	↑ rat and mice numbers ↑ rabbit numbers	Increased mortality of burrowing petrels; increased impacts on native plant communities; increase in numbers of disturbance-tolerant alien plant taxa
South Georgia	↑ temperature ↓ glacial extent	↑ <i>Trechisibus antarcticus</i> ↑ <i>Ooptyerus soledadinus</i> ↑ <i>Hypogastrura</i> spp. ↑ Reindeer and rat numbers and distribution ↑ <i>Poa annua</i> and other alien plants	Life-history changes in native invertebrates; loss of extent of native plant communities; increase of disturbance-tolerant alien taxa such as <i>P. annua</i> ; arrival of additional alien species
Maritime Antarctic (analogous effects also apply to continental coastline)	↑ temperature ↑ precipitation locally (but also local decreases) ↑ UV-B receipt during periods of ozone depletion	↑ extent of existing populations of persistent aliens	Impacts likely to continue to be minor, but poorly understood; further alien colonization (including microbial groups) expected; water supply exhaustion may lead to local extinctions
Victoria Land Dry Valleys (continental Antarctic)	Short term cooling reported but disputed ↑ UV-B receipt during periods of ozone depletion	None established Likely increase in arrivals and establishment of alien micro-organisms	Decrease in production and soil invertebrate populations; increase in alien arrival and establishment (especially microbial groups)

numbers of alien plants and vertebrates, while Macquarie Island hosts the largest documented number of alien invertebrates (noting that the level of study varies widely between locations, while little or no data exist for smaller meiofaunal or microbial groups at any location).

(5) Unless stringent measures are taken to reduce the propagule load on humans, their food, cargo, and transport vessels it is reasonable to predict that, as the number of human vectors visiting sub-Antarctic and Antarctic ice-free areas increases, so will the introduction and establishment of new invasive taxa and, therefore, subsequent modification of ecosystem functioning. The greatest care must be taken to prevent the import of vertebrates, particularly rodents and cats. Moreover, in the case of intra-regional transfers, the interpretation of biological data on the evolution of Antarctic biota will be significantly compromised.

(6) Current climatic trends will further enhance alien invasion. Under most threat are relatively milder areas with increased human visitation and the most dramatic changes in environmental conditions. South Georgia, with climate warming, glacial retreat and a large and increasing number of visitors, undoubtedly stands out as the most threatened area.

(7) There is a clear and urgent need for the establishment of long-term monitoring programmes. Without such data, prerequisite for establishing appropriate risk management protocols, it will be difficult or impossible to identify and assess future invasions, monitor the status of species already established or assess the effectiveness of any mitigation measures adopted. The Committee on Environmental Protection (<http://www.cep.aq>), established under the Madrid Protocol, has an important role to play in such a process, and should establish the means to do so.

(8) A range of further mitigation measures should be considered in concert with monitoring. Practicable approaches include (and are variously incorporated into existing management plans for some locations): cessation of imports of foreign biological material and soil, and on-station cultivation of biological material; stringent measures to ensure rodent-free status of ships and aircraft; logistical planning to minimise the risk of intra-regional and local transfer of propagules to pristine locations; control of visitor numbers and access to more sensitive or pristine sites; cleaning/sterilization of high risk transport locations for aliens, such as cargo surfaces, foodstuffs and clothing (important in both inter- and intra-regional contexts); and targeted and carefully planned eradication, where practicable and desirable.

(9) Alien species may themselves be a research resource in the context of understanding why some species are more successful at invading than others and how this success might be altered as both local and regional environments change.

Note added in proof: Tavares & De Melo (2004) reported the discovery of the majid spider crab *Hyas araneus* in the Antarctic Peninsula marine waters. This North Atlantic species is the only record of a non-indigenous marine species in Antarctic seas. It may have arrived in Antarctica via ships' sea-chests or ballast water.

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VIII. REFERENCES

- ADAMSON, D. A., WHETTON, P. & SELKIRK, P. M. (1988). An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and southern hemisphere circulation patterns. *Papers and Proceedings of the Royal Society of Tasmania* **122**, 107–112.
- ANDRÁSSY, I. (1998). Nematodes in the sixth continent. *Journal of Nematode Morphology and Systematics* **1**, 107–186.
- ANON. (1994). *Heard Island Wilderness Reserve. Management Plan*. Australian Antarctic Division, Hobart.
- ANON. (1996). *Prince Edward Islands Management Plan*. Department of Environmental Affairs and Tourism, Pretoria.
- ANON. (2002). *Casey Fly Report*. Casey Environment Committee, Australian Antarctic Division internal report. 12 August 2002, 7pp.
- ARNOLD, R. J. & CONVEY, P. (1998). The life history of the world's most southerly diving beetle, *Lancetes angusticollis* (Curtis) (Coleoptera: Dytiscidae), on subantarctic South Georgia. *Polar Biology* **20**, 153–160.
- ARNOLD, R. J., CONVEY, P., HUGHES, K. A. & WYNN-WILLIAMS, D. D. (2003). Seasonal periodicity of physical and edaphic factors, and microalgae in Antarctic fellfields. *Polar Biology* **26**, 396–403.
- AZMI, O. R. & SEPPELT, R. D. (1998). The broad-scale distribution of microfungi in the Windmill Islands region, Antarctica. *Polar Biology* **19**, 92–100.
- BARENDSE, J. & CHOWN, S. L. (2000). The biology of *Bothrometopus elongatus* (Coleoptera, Curculionidae) in a mid-altitude fellfield on sub-Antarctic Marion Island. *Polar Biology* **23**, 346–351.
- BARNES, D. K. A. (2002). Invasions by marine life on plastic debris. *Nature* **416**, 808–809.
- BARNES, D. K. A. & FRASER, K. P. P. (2003). Rafting by five phyla on man-made flotsam in the Southern Ocean. *Marine Ecology Progress Series* **262**, 289–291.
- BEDNAREK-OCHYRA, H., VÁNA, J., OCHYRA, R. & SMITH, R. I. L. (2000). *The Liverwort Flora of Antarctica*. Polish Academy of Sciences, Institute of Botany, Cracow.
- BERGSTROM, D. M. & CHOWN, S. L. (1999). Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology and Evolution* **14**, 472–477.
- BERGSTROM, D. M. & SELKIRK, P. M. (1997). The distribution of bryophytes on subantarctic Heard Island. *The Bryologist* **100**, 349–355.

- BERRUTI, A. & SCHRAMM, M. (1981). More non-marine vagrant birds at the Prince Edward Islands. *Cormorant* **9**, 133–135.
- BESTER, M. N., BLOOMER, J. P., VAN AARDE, R. J., ERASMUS, B. H., VAN RENSBURG, P. J. J., SKINNER, J. D., HOWELL, P. G. & NAUDE, T. W. (2002). A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65–73.
- BLACKBURN, T. M. & DUNCAN, R. P. (2001). Determinants of establishment success in introduced birds. *Nature* **414**, 195–197.
- BLOCK, W., BURN, A. J. & RICHARD, K. J. (1984). An insect introduction to the maritime Antarctic. *Biological Journal of the Linnean Society* **23**, 33–39.
- BLOCK, W. & CONVEY, P. (2001). Seasonal and long-term variation in body water content of an Antarctic springtail – a response to climate change? *Polar Biology* **24**, 764–770.
- BONNER, W. N. (1984). Introduced mammals. In *Antarctic Ecology*, Vol. 1 (ed. R. M. Laws), pp. 237–278. Academic Press, London.
- BOUCHÉ, M. B. (1982). Les Lombriciens (Oligochaeta) des Terres Australes Françaises. *Comité National Français des Recherches Antarctiques* **51**, 175–180.
- BOWEN, L. & VANVUREN, D. (1997). Insular endemic plants lack defenses against herbivores. *Conservation Biology* **11**, 1249–1254.
- BROADY, P. A. (1996). Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation* **5**, 1307–1335.
- BROADY, P. A. & SMITH, R. A. (1994). A preliminary investigation of the diversity, survivability and dispersal of algae introduced into Antarctica by human activity. *Proceedings of the NIPR Symposium on Polar Biology* **7**, 185–197.
- BROTHERS, N. P. (1984). Breeding distribution and status of burrow-nesting petrels on Macquarie Island. *Australian Wildlife Research* **11**, 113–131.
- BROTHERS, N. P., EBERHARD, I. E., COPSON, G. R. & SKIRA, I. J. (1982). Control of Rabbits *Oryctolagus cuniculus* on Macquarie Island by myxomatosis. *Australian Wildlife Research* **9**, 477–485.
- BROTHERS, N. P. & SKIRA, I. J. (1984). The Weka on Macquarie Island. *Notornis* **31**, 145–154.
- BUDD, W. F. & SIMMONDS, L. (1991). The impact of global warming on the Antarctic mass balance and global sea level. In *Proceedings of the International Conference on the Role of Polar Regions in Global Change* (eds. G. Weller, C. L. Wilson and B. A. B. Severin), pp. 489–494. Geophysics Institute, University of Alaska, Fairbanks.
- BURGER, A. E., WILLIAMS, A. J. & SINCLAIR, J. C. (1980). Vagrants and the paucity of land bird species at the Prince Edward Islands. *Journal of Biogeography* **7**, 305–310.
- BUTLER, H. G. (1999). Seasonal dynamics of the planktonic microbial community in a maritime Antarctic lake undergoing eutrophication. *Journal Plankton Research* **21**, 2393–2419.
- CASE, T. J. (1996). Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* **78**, 69–96.
- CHAPUIS, J. L., BOUSSÈS, P. & BARNAUD, G. (1994a). Alien mammals, impact and management in the French subantarctic islands. *Biological Conservation* **67**, 97–104.
- CHAPUIS, J.-L., CHANTAL, J. & BIJLENGA, G. (1994b). La myxomatose dans les îles subantarctiques de Kerguelen, en l'absence de vecteurs, trente années après son introduction. *Compte-Rendus de l'Académie des Sciences, Paris, Sciences de la Vie* **317**, 174–182.
- CHAPUIS, J. L., FRENOT, Y. & LÉBOUVIER, M. (2004). Recovery of native plant communities after eradication of rabbits from the subantarctic Iles Kerguelen, and influence of climate change. *Biological Conservation* **117**, 167–179.
- CHAPUIS, J.-L., LE ROUX, V., ASSELINE, J., LEFEVRE, L. & KERLEAU, F. (2001). Eradication of the rabbit (*Oryctolagus cuniculus*) by poisoning, on three islands of the subantarctic Archipelago of Kerguelen. *Wildlife Research* **28**, 323–331.
- CHEKCHAK, T., CHAPUIS, J.-L., PISANU, B. & BOUSSÈS, P. (2000). Introduction of the rabbit flea, *Spilopsyllus cuniculi* (Dale), to a subantarctic island (Kerguelen Archipelago) and its assessments as a vector of myxomatosis. *Wildlife Research* **27**, 91–101.
- CHEVRIER, M., VERNON, P. & FRENOT, Y. (1997). Potential effects of two alien insects on a subantarctic wingless fly in the Kerguelen Islands. In *Antarctic Communities: Species, Structure and Survival* (eds. B. Battaglia, J. Valencia and D. W. H. Walton), pp. 424–431. Cambridge University Press, Cambridge, UK.
- CHOWN, S. L. (1990). Possible effects of Quaternary climatic change on the composition of insect communities of the South Indian Ocean Province Islands. *South African Journal of Science* **86**, 386–391.
- CHOWN, S. L. & AVENANT, N. (1992). Status of *Plutella xylostella* at Marion Island six years after its colonisation. *South African Journal of Antarctic Research* **22**, 37–40.
- CHOWN, S. L. & BLOCK, W. (1997). Comparative nutritional ecology of grass-feeding in a subantarctic beetle: the impact of introduced species on *Hydromedion sparsutum* from South Georgia. *Oecologia* **111**, 216–224.
- CHOWN, S. L. & GASTON, K. J. (2000). Island-hopping invaders hitch a ride with tourists in the Southern Ocean. *Nature* **408**, 637.
- CHOWN, S. L., GASTON, K. J. & GREMMEN, N. J. M. (2000). Including the Antarctic: insights for ecologists everywhere. In *Antarctic Ecosystems: Models for Wider Ecological Understanding* (eds. W. Davison, C. Howard-Williams and P. A. Broady), pp. 1–15. New Zealand Natural Sciences, Christchurch.
- CHOWN, S. L., GASTON, K. J. & WILLIAMS, P. H. (1998a). Global patterns in species richness of pelagic seabirds: the Procellariiformes. *Ecography* **21**, 342–350.
- CHOWN, S. L., GREMMEN, N. J. M. & GASTON, K. J. (1998b). Ecological biogeography of Southern islands: species-area relationships, human impacts and conservation. *American Naturalist* **152**, 562–575.
- CHOWN, S. L. & LANGUAGE, K. (1994). Recently established Diptera and Lepidoptera on sub-Antarctic Marion Island. *African Entomology* **2**, 57–60.
- CHOWN, S. L., RODRIGUES, A. S., GREMMEN, N. J. M. & GASTON, K. J. (2001). World Heritage status and the conservation of Southern Ocean islands. *Conservation Biology* **15**, 550–557.
- CHOWN, S. L. & SMITH, V. R. (1993). Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508–516.
- CLARKE, C. (2003). AIRLINK Newsletter, Australian Antarctic Division, [http://www.aad.gov.au/MediaLibrary/asset/MediaItems/ml_377276109490741_Air%20Trans%20News%20\(low%20res\).pdf](http://www.aad.gov.au/MediaLibrary/asset/MediaItems/ml_377276109490741_Air%20Trans%20News%20(low%20res).pdf)
- CLARKE, J. R. & KERRY, K. R. (1993). Diseases and parasites of penguins. *Korean Journal of Polar Research* **4**, 79–86.
- CLAYTON, M. N., WIENCKE, C. & KLÖSER, H. (1997). New records and sub-Antarctic marine benthic macroalgae from Antarctica. *Polar Biology* **17**, 141–149.
- COLLESS, D. H. (1962). Insects of Macquarie Island. Diptera: Sciaridae. *Pacific Insects* **4**, 955–957.
- COLLESS, D. H. (1970). A new species of Macrocera from the Crozet Islands (Diptera: Mycetophilidae). *Proceedings of the Royal Entomological Society of London (B)* **39**, 27–28.

- COMNAP (2003). Council of Managers of National Antarctic Programs <http://www.comnap.aq>
- CONVEY, P. (1996). The influence of environmental characteristics on the life history attributes of Antarctic terrestrial biota. *Biological Reviews* **71**, 191–225.
- CONVEY, P. (1997). Environmental change: possible consequences for life histories of Antarctic terrestrial biota. *Korean Journal of Polar Research* **8**, 127–144.
- CONVEY, P. (2001a). Antarctic Ecosystems. In *Encyclopedia of Biodiversity*, Vol. 1 (ed. S. A. Levin), pp. 171–184. Academic Press, San Diego.
- CONVEY, P. (2001b). Terrestrial ecosystem response to climate changes in the Antarctic. In “*Fingerprints*” of Climate Change – *Adapted Behaviour and Shifting Species Ranges* (eds. G.-R. Walther, C. A. Burga and P. J. Edwards), pp. 17–42. Kluwer, New York.
- CONVEY, P. (2003). Soil faunal community response to environmental manipulation on Alexander Island, southern maritime Antarctic. In *VIII SCAR International Biology Symposium: Antarctic Biology in a Global Context* (eds. A. H. L. Huiskes, W. W. C. Gieskes, J. Rozema, R. M. L. Schorno, S. van der Vies and W. J. Wolff), pp. 74–78. Backhuys, Leiden.
- CONVEY, P., BARNES, D. K. A. & MORTON, A. (2002a). Artefact accumulation on Antarctic oceanic island shores. *Polar Biology* **25**, 612–617.
- CONVEY, P. & BLOCK, W. (1996). Antarctic dipterans: ecology, physiology and distribution. *European Journal of Entomology* **93**, 1–13.
- CONVEY, P., GREENSLADE, P. & PUGH, P. J. A. (2000a). Terrestrial fauna of the South Sandwich Islands. *Journal of Natural History* **34**, 597–609.
- CONVEY, P., GREENSLADE, P., ARNOLD, R. J. & BLOCK, W. (1999). Collembola of sub-Antarctic South Georgia. *Polar Biology* **22**, 1–6.
- CONVEY, P., PUGH, P. J. A., JACKSON, C., MURRAY, A. W., RUHLAND, C. T., XIONG, F. S. & DAY, T. A. (2002b). Response of Antarctic terrestrial arthropods to multifactorial climate manipulation over a four year period. *Ecology* **83**, 3130–3140.
- CONVEY, P. & SMITH, R. I. L. (1993). Investment in sexual reproduction by Antarctic mosses. *Oikos* **68**, 293–302.
- CONVEY, P., SMITH, R. I. L., HODGSON, D. A. & PEAT, H. J. (2000b). The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating. *Journal of Biogeography* **27**, 1279–1295.
- CONVEY, P., SMITH, R. I. L., PEAT, H. J. & PUGH, P. J. A. (2000c). The terrestrial biota of Charcot Island, eastern Bellingshausen Sea, Antarctica an example of extreme isolation. *Antarctic Science* **12**, 406–413.
- CONVEY, P. & WYNN-WILLIAMS, D. D. (2002). Antarctic soil nematode response to artificial environmental manipulation. *European Journal of Soil Biology* **38**, 255–259.
- COOPER, J., CRAFFORD, J. E. & HECHT, T. (1992). Introduction and extinction of brown trout (*Salmo trutta* L.) in an impoverished sub-Antarctic stream. *Antarctic Science* **4**, 9–14.
- COPSON, G. R. (1986). The diet of the introduced rodents *Mus musculus* L. and *Rattus rattus* L. on Subantarctic Macquarie Island. *Australian Journal of Wildlife Research* **13**, 441–445.
- COPSON, G. R., BROTHERS, N. P. & SKIRA, I. J. (1981). Distribution and abundance of the rabbit *Oryctolagus cuniculus* (L.) at subantarctic Macquarie Island. *Australian Wildlife Research* **8**, 597–611.
- COPSON, G. R. & WHINAM, J. (1998). Response of vegetation on Subantarctic Macquarie Island to reduced rabbit grazing. *Australian Journal of Botany* **46**, 15–24.
- COPSON, G. & WHINAM, J. (2001). Review of ecological restoration programme on subantarctic Macquarie Island: pest management progress and future directions. *Ecological Management and Restoration* **2**, 129–138.
- COULSON, S. J., LEINAAS, H. P. IMS, R. A. & ØVIK, G. (2000). Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography* **23**, 299–306.
- COURCHAMP, F., CHAPUIS, J.-L. & PASCAL, M. (2003). Mammal invaders on islands: impact, control and control impact. *Biological Reviews* **78**, 347–383.
- COURCHAMP, F., LANGLAIS, M. & SUGIHARA, G. (1999). Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* **68**, 282–292.
- CRAFFORD, J. E. (1986). A case study of an alien invertebrate (*Limnophyes pusillus*, Diptera, Chironomidae) introduced on Marion Island: selective advantages. *South African Journal of Antarctic Research* **16**, 115–117.
- CRAFFORD, J. E. & CHOWN, S. L. (1990). The introduction and establishment of the diamondback moth (*Plutella xylostella* L., Plutellidae) on Marion Island. In *Antarctic Ecosystems Ecological Change and Conservation* (eds. K. R. Kerry and G. Hempel), pp. 354–358. Springer, Berlin.
- CRAFFORD, J. E. & SCHOLTZ, C. H. (1987). Quantitative differences between the insect faunas of Subantarctic Marion and Prince Edward Islands: a result of human intervention? *Biological Conservation* **40**, 255–262.
- CRAFFORD, J. E., SCHOLTZ, C. H. & CHOWN, S. L. (1986). The insects of subantarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen biogeographical province. *South African Journal of Antarctic Research* **16**, 41–84.
- CROOKS, K. R. & SOULÉ, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**, 563–565.
- CROXALL, J. P. (1992). Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society, London B* **338**, 319–328.
- CUMPSTON, J. S. (1968). *Macquarie Island*. Antarctic Division, Department of External Affairs, Melbourne Australia, 380pp.
- DAHL, C. (1970a). Diptera: Trichoceridae of Kerguelen Island. *Pacific Insects Monographs* **23**, 274–275.
- DAHL, C. (1970b). Diptera: Trichoceridae of South Georgia. *Pacific Insects Monographs* **23**, 271–273.
- DAEHLER, C. C. (2001). Two ways to be an invader, but one is more suitable to ecology. *Bulletin of the Ecological Society of America* **82**, 101–102.
- D’ANTONIO, C. M. & DUDLEY, T. L. (1995). Biological invasions as agents of change on islands versus mainlands. In *Islands. Biological Diversity and Ecosystem Function* (eds. P. M. Vitousek, L. L. Loope and H. Adersen), pp. 103–121. Springer, Berlin.
- DARLINGTON, P. J. (1970). Coleoptera: Carabidae of South Georgia. *Pacific Insects Monographs* **23**, 234.
- DAVAINE, P. & BEALL, E. (1997). Salmonid introductions into virgin ecosystems (Kerguelen Islands, Subantarctic): Stakes, results, prospects. *Bulletin Francais de la Pêche et de la Pisciculture* **344–345**, 93–110.
- DAVEY, M. C., PICKUP, J. & BLOCK, W. (1992). Temperature variation and its biological significance in fellfield habitats on a maritime Antarctic island. *Antarctic Science* **4**, 383–388.
- DAVIES, L. (1973). Observations on the distribution of surface-living land arthropods on the subantarctic Ile de la Possession, Iles Crozet. *Journal of Natural History* **7**, 241–253.

- DAVIS, M. A. & THOMPSON, K. (2000). Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* **81**, 226–230.
- DAY, T. A. (2001). Multiple trophic levels in UV-B assessments – completing the ecosystem. *New Phytologist* **152**, 183–186.
- DAY, T. A., RUHLAND, C. T., GROBE, C. W. & XIONG, F. (1999). Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia* **119**, 24–35.
- DEHARVENG, L. (1981). Collemboles de les Iles Subantarctiques de l'Océan Indien mission J. Travé 1972–1973. *CNFRA* **28**, 33–108.
- DEHARVENG, L. & TRAVÉ, J. (1981). Ecologie des Oribates (Acaréens) et des Collemboles (Insectes) de Kerguelen. *Comité National Français des Recherches Antarctiques* **48**, 109–140.
- DI CASTRI, F. (1989). History of biological invasions with special emphasis on the Old World. In *Biological Invasions: A Global Perspective* (eds J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson), pp. 1–29. John Wiley, Chichester, UK.
- DINGWALL, P. R. (1995). *Progress in conservation of the subantarctic islands*. IUCN, Gland.
- DORAN, P. T., PRISCU, J. C., BERRY LYONS, W., WALSH, J. E., FOUNTAIN, A. G., MCKNIGHT, D. M., MOORHEAD, D. L., VIRGINIA, R. A., WALL, D. H., CLOW, G. D., FRITSEN, C. H., MCKAY, C. P. & PARSONS, A. N. (2002). Antarctic climate cooling and terrestrial ecosystem response. *Nature* **415**, 517–520.
- DÓZSA-FARKAS, K. & CONVEY, P. (1997). *Christensenia*, a new enchytraeid genus from Antarctica. *Polar Biology* **17**, 482–486. [nb this paper subsequently modified – see Erratum, *Polar Biology* **20**, 292 (1998)]
- DREUX, P. (1965). Faune entomologique de l'île aux Cochons (Archipel Crozet). *Terres Australes Antarctiques Françaises* **31**, 57–69.
- DREUX, P. (1972). Premières données sur la faune entomologique de l'île de L'est (Archipel Crozet). *Terres Australes Antarctiques Françaises* **55–56**, 45–54.
- DREUX, P., FRENOT, Y., JOUVENTIN, P., MASS, L. & VERDIER, O. (1988). First scientific expedition to Ile des Pingouins, Archipel Crozet. *Polar Record* **24**, 235–238.
- DUCKHOUSE, D. A. (1970). Psychodidae of South Georgia. *Pacific Insects Monographs* **23**, 283.
- DUKES, J. S. & MOONEY, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* **14**, 35–139.
- EDWARDS, D. D., MCFETERS, G. A. & VENKATESAN, M. I. (1998). Distribution of *Clostridium perfringens* and fecal sterols in a benthic coastal marine environment influenced by the sewage outfall from McMurdo Station, Antarctica. *Applied and Environmental Microbiology* **64**, 2596–2600.
- EDWARDS, J. A. (1980). An experimental introduction of vascular plants from South Georgia to the maritime Antarctic. *British Antarctic Survey Bulletin* **49**, 73–80.
- EDWARDS, J. A. & GREENE, D. M. (1973). The survival of Falklands Islands transplants at South Georgia and Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* **33 & 34**, 33–45.
- ERNSTING, G. (1993). Observations on life cycle and feeding ecology of two recently-introduced predatory beetle species at South Georgia, subantarctic. *Polar Biology* **13**, 423–428.
- ERNSTING, G., BLOCK, W., MACALISTER, H. & TODD, C. (1995). The invasion of the carnivorous carabid beetle *Trechisibus antarcticus* on South Georgia (subantarctic) and its effect on the endemic herbivorous beetle *Hydromedion spassatum*. *Oecologia* **103**, 34–42.
- ERNSTING, G., BRANDJES, G. J., BLOCK, W. & ISAACS, J. A. (1999). Life-history consequences of predation for a subantarctic beetle: evaluating the contribution of direct and indirect effects. *Journal of Animal Ecology* **68**, 741–752.
- FALLA, R. A., SIBSON, R. B. & TURBOTT, E. G. (1978). *Collins Guide to the Birds of New Zealand and Outlying Islands*. HarperCollins, Auckland.
- FARMAN, J. C., GARDINER, B. G. & SHANKLIN, J. D. (1985). Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* **315**, 207–210.
- FOWBERT, J. A. & SMITH, R. I. L. (1994). Rapid population increase in native vascular plants in the Argentine Islands, Antarctic Peninsula. *Arctic and Alpine Research* **26**, 290–296.
- FOX, A. J. & COOPER, A. P. R. (1998). Climate-change indicators from archival aerial photography of the Antarctic Peninsula. *Annals of Glaciology* **27**, 636–642.
- FRANZMANN, P. D. (1996). Examination of Antarctic prokaryotic diversity through molecular comparisons. *Biodiversity and Conservation* **5**, 1295–1305.
- FRENOT, Y. (1985). Etude de l'introduction accidentelle de *Dendrobaena rubida tenuis* (Oligochaeta, Lumbricidae) à l'île de la Possession. *Bulletin d'Ecologie* **16**, 47–53.
- FRENOT, Y. (1992). Introduced populations of *Dendrodrilus rubidus* spp. (Oligochaeta, Lumbricidae) at Crozet, Kerguelen and Amsterdam Islands: effects of temperature on growth patterns during the juvenile stages. *Soil Biology and Biochemistry* **24**, 1433–1439.
- FRENOT, Y., GLOAGUEN, J. C., MASSÉ, L. & LEBOUVIER, M. (2001). Human activities, ecosystem disturbances and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological Conservation* **101**, 33–50.
- FRENOT, Y., GLOAGUEN, J. C. & TRÉHEN, P. (1997). Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. In *Antarctic Communities: Species, Structure and Survival* (eds B. Battaglia, J. Valencia and D. W.H. Walton), pp. 358–366. Cambridge University Press, Cambridge, UK.
- GABRIEL, A. G. A., CHOWN, S. L., BARENDSE, J., MARSHALL, D. J., MERCER, R. D., PUGH, P. J. A. & SMITH, V. R. (2001). Biological invasions on Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421–430.
- GARTSHORE, N. (1987). Rare bird sightings on the Prince Edward Islands, December 1983–May 1987. *Cormorant* **15**, 48–58.
- GASTON, K. J., JONES, A. G., HÄNEL, C. & CHOWN, S. L. (2003). Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London B* **270**(1519), 1091–1098.
- GAUTHIER-CLERC, M., JAULHAC, B., FRENOT, Y., BACHELARD, C., MONTEIL, H., LE MAHO, Y. & HANDRICH, Y. (1999). Prevalence of *Borrelia burgdorferi* (the Lyme disease agent) antibodies in King penguin *Aptenodytes patagonicus* in Crozet Archipelago. *Polar Biology* **22**, 141–143.
- GAUTHIER-CLERC, M., JIGUET, F. & LAMBERT, N. (2002). Vagrant birds at Possession Island, Crozet Islands and Kerguelen Island from December 1995 to December 1997. *Marine Ornithology* **30**, 38–39.
- GAVAGHAN, H. (2002). Life in the deep freeze. *Nature* **415**, 828–830.
- GLEESON, J. P. & VAN RENSBURG, P. J. J. (1982). Feeding ecology of the house mouse, *Mus musculus* on Marion Island. *South African Journal of Antarctic Research* **12**, 34–39.

- GORDON, J. E. & TIMMIS, R. J. (1992). Glacier fluctuations on South Georgia during the 1970s and 1980s. *Antarctic Science* **4**, 215–226.
- GREENE, S. W. (1964). The vascular flora of South Georgia. *British Antarctic Survey Scientific Reports* No. 45, 58pp.
- GREENE, S. W. & WALTON, D. W. H. (1975). An annotated check list of the subantarctic and Antarctic vascular flora. *Polar Record* **17**, 473–484.
- GREENSLADE, P. (1986). Additions to the Collembolan fauna of Heard Island. *Records of the South Australian Museum* **19**, 91–96.
- GREENSLADE, P. (1987). Invertebrate conservation in the Antarctic and subantarctic. In *The role of invertebrates in conservation and biological survey* (ed. J. D. Majer), pp. 119–121. Western Australian Department of Conservation & Land Management.
- GREENSLADE, P. (1990). Notes on the biogeography of the free-living terrestrial invertebrate fauna of Macquarie Island with an annotated checklist. *Papers and Proceedings of the Royal Society of Tasmania* **124**, 35–50.
- GREENSLADE, P. (1995). Collembola from the Scotia Arc and Antarctic Peninsula including descriptions of two new species and notes on biogeography. *Polskie Pismo Entomologiczne* **64**, 305–319.
- GREENSLADE, P. (2002). Assessing the risk of exotic Collembola invading subantarctic islands: prioritizing quarantine management. *Pedobiologia* **46**, 338–344.
- GREENSLADE, P. & WISE, K. A. J. (1984). Additions to the collembolan fauna of the Antarctic. *Transactions of the Royal Society of South Australia* **108**(4), 203–205.
- GREGORY, M. R. & RYAN, P. G. (1997). Pelagic plastics and other seaborne persistent synthetic debris: a review of Southern Hemisphere perspectives. In *Marine Debris: Sources, Impacts and Solutions* (eds. J. M. Coe and D. B. Rogers), pp. 49–66. Springer-Verlag, New York.
- GREMME, N. M. J., CHOWN, S. L. & MARSHALL, D. J. (1998). Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, subantarctic. *Biological Conservation* **85**, 223–231.
- GREMME, N. J. M. & SMITH, V. R. (1999). New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* **21**, 401–409.
- GRESSITT, J. L. (1961). Problems in the zoogeography of Pacific and Antarctic Insects. *Pacific Insects Monograph* **2**, 1–94.
- GRESSITT, J. L. (ed.) (1970). Subantarctic entomology, particularly of South Georgia and Heard Island. *Pacific Insects Monograph* **23**, 1–374.
- GRESSITT, J. L. (1971). Antarctic entomology with emphasis on biogeographical aspects. *Pacific Insects Monograph* **25**, 167–178.
- GUINET, C., JOUVENTIN, P. & GEORGES, J.-Y. (1994). Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St Paul and Amsterdam) islands and their possible relationships to El Niño southern oscillation. *Antarctic Science* **6**, 473–478.
- HÄNEL, C. & CHOWN, S. L. (1998). The impact of a small, alien macro-invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* Meigen (Diptera, Chironomidae) at Marion Island. *Polar Biology* **20**, 99–106.
- HARDY, D. E. (1962). Insects of Macquarie Island. Diptera: Coelopidae. *Pacific Insects* **4**, 963–971.
- HEADLAND, R. K. (1989). *Chronological list of Antarctic expeditions and related historical events*. Cambridge University Press, Cambridge, 730pp.
- Heritage Expeditions (2002). <http://www.heritage-expeditions.com>
- HEYWOOD, V. H. (1989). Patterns, extents and modes of invasions by terrestrial plants. In *Biological Invasions: A Global Perspective* (eds. J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson), pp. 31–60. John Wiley, Chichester, UK.
- HOLDGATE, M. W., LEMAITRE, R. W., SWALES, M. K. & WACE, N. M. (1956). The Gough Island scientific survey, 1955–1956. *Nature* **178**, 234–236.
- HOLDHAUS, K. (1931). Über die Insektenfauna der Insel Süd-Georgien. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* **63**, 163–182.
- HUGHES, K. A. (2003a). Aerial dispersal and survival of sewage-derived faecal coliforms in Antarctica. *Atmospheric Environment* **37**, 3147–3155.
- HUGHES, K. A. (2003b). The influence of seasonal environmental variables on the distribution of presumptive fecal coliforms around an Antarctic research station. *Applied and Environmental Microbiology* **5**, 555–565.
- HUGHES, K. A. & BLENKHARN, N. (2003). A simple method to reduce discharge of sewage microorganisms from an Antarctic research station. *Marine Pollution Bulletin* **46**, 353–357.
- HUGHES, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* **15**(2), 56–61.
- HULLÉ, M., PANNETIER, D., MAURICE, D., COURMONT, L., CHAILLON, C., CHAILLON, P.-E., SACCONI, P., HÉBERT, C., GRACIA, M., BUFFIN, J., SIMON, J.-C. & FRENOT, Y. (2003). Aphids from Kerguelen and Crozet Islands, Subantarctic. In *VIII SCAR International Biology Symposium: Antarctic Biology in a Global Context* (eds. A. H. L. Huiskes, W. W. C. Gieskes, J. Rozema, R. M. L. Schorno, S. van der Vies and W. J. Wolff), pp. 308–312. Backhuys, Leiden.
- HUYSER, O., RYAN, P. G. & COOPER, J. (2000). Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* **92**, 299–310.
- IAATO (2002). International Association of Antarctic Tour Operators <http://www.IAATO.org>
- JEANNEL, R. (1940). Croisière du Bougainville aux Iles Australes Françaises. *Mémoires du Muséum National d'Histoire Naturelle, series A* **14**, 1–268.
- JENKIN, J. F. (1997). Vegetation of the McDonald Islands, subantarctic. *Polar Biology* **18**, 260–272.
- JONES, A. G., CHOWN, S. L. & GASTON, K. J. (2003). The free living pterygote insects of Gough Island. *Systematics and Biodiversity* **1**, 213–273.
- JOUVENTIN, P., STAHL, J. C., WEIMERSKIRCH, H. & MOUGIN, J. L. (1984). The seabirds of the French subantarctic islands and Adélie land, their status and conservation. In *Status and Conservation of the World's Seabirds* (eds. J. P. Croxall, P. G. H. Evans and R. W. Schreiber), pp. 609–625. International Council for Bird Preservation, Cambridge, Technical Publication No. 2.
- KASHYAP, A. K. & SHUKLA, S. P. (2001). Algal species diversity of Schirmacher Oasis, Antarctica: a survey. *Antarctic Biology in a Global Context, Abstracts of VIII SCAR International Biology Symposium*, Amsterdam. Abstract **S5P62**.
- KENNEDY, A. D. (1994). Simulated climate change: a field manipulation study of polar microarthropod community response to global warming. *Ecography* **17**, 131–140.
- KENNEDY, A. D. (1995a). Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics* **26**, 683–704.

- KENNEDY, A. D. (1995*b*). Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology* **1**, 29–42.
- KENNEDY, A. D. (1995*c*). Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. *Functional Ecology* **9**, 340–350.
- KENNEDY, A. D. (1996). Antarctic fellfield response to climate change: a tripartite synthesis of experimental data. *Oecologia* **107**, 141–150.
- KERRY, E. (1990). Microorganisms colonising plants and soil subjected to different degrees of human activity, including petroleum contamination, in the Vestfold Hills and Mac.Robertson land. *Polar Biology* **10**, 423–430.
- KERRY, K., RIDDLE, M. & CLARKE, J. (1999). *Diseases of Antarctic Wildlife*. A Report for The Scientific Committee on Antarctic Research (SCAR) and The Council of Managers of National Antarctic Programs (COMNAP), 104pp.
- KIERNAN, K. & MCCONNELL, A. (2002). Glacier retreat and melt-lake expansion at Stephenson Glacier, Heard Island World Heritage Area. *Polar Record* **38**(207), 297–308.
- KING, J. C. & HARANGOZO, S. A. (1998). Climate change in the western Antarctic Peninsula since 1945: observations and possible causes. *Annals of Glaciology* **27**, 571–575.
- KLOPPERS, F. J. & SMITH, V. R. (1998). First report of *Botryotinia fuckeliana* on Kerguelen Cabbage on the Sub-Antarctic Marion Island. *Plant Disease* **82**, 710.
- KOOYMAN, G. L. (2002). Evolutionary and ecological aspects of some Antarctic and sub-Antarctic penguin distributions. *Oecologia* **130**, 485–495.
- LEADER-WILLIAMS, N. (1988). *Reindeer on South Georgia: The Ecology of an Introduced Population*. Cambridge University Press, Cambridge, 319pp.
- LEADER-WILLIAMS, N., SMITH, R. I. L. & ROTHERY, P. (1987). Influence of introduced reindeer on the vegetation of South Georgia: results from a long-term exclusion experiment. *Journal of Applied Ecology* **24**, 801–822.
- LEADER-WILLIAMS, N., WALTON, D. W. H. & PRINCE, P. A. (1989). Introduced Reindeer on South Georgia. A management dilemma. *Biological Conservation* **47**, 1–11.
- LEDoux, J. C. (1991). Araignées des îles subantarctiques françaises (Crozet et Kerguelen). *Revue arachnologie* **9**, 119–164.
- LEE, C. E. (2002). Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* **17**, 386–391.
- LEE, K. E. (1968). Oligochaeta from subantarctic islands. *British Australian and New Zealand Research Expedition Report 1929–1931, Report B* **8**, 149–165.
- LE ROUX, V., CHAPUIS, J. L., FRENOT, Y. & VERNON, P. (2002). Diet of the house mouse (*Mus musculus domesticus*) at Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biology* **25**, 49–57.
- LESEL, R. (1967). Contribution à l'étude écologique de quelques mammifères importés aux îles Kerguelen. *Terres Australes et Antarctiques Françaises* **38**, 3–40.
- LEWIS, P. N., HEWITT, C. L., RIDDLE, M. & McMINN, A. (2003). Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. *Marine Pollution Bulletin* **46**, 213–223.
- LOCKWOOD, J. L. (1999). Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conservation Biology* **13**, 560–567.
- LODGE, D. M. (1993). Species invasions and deletions: community effects and responses to climate and habitat change. In *Biotic Interactions and Climate Change* (eds. P. M. Kareiva, J. G. Kingsolver and R. B. Huey), pp. 367–387. Sinauer Associates, Sunderland.
- LONGTON, R. E. (1988). *Biology of Polar Bryophytes and Lichens*. Cambridge University Press, Cambridge.
- LONSDALE, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536.
- MACK, R. N. (1996). Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation* **78**, 107–121.
- MACK, R. N., SIMBERLOFF, D., LONSDALE, W. M., EVANS, H., CLOUT, M. & BAZZAZ, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**(3), 689–710.
- MARSHALL, D. J. & CHOWN, S. L. (2002). The acarine fauna of Heard Island. *Polar Biology* **25**, 688–695.
- MARSHALL, D. J., GREMMEN, N. J. M., COETZEE, L., O'CONNOR, B. M., PUGH, P. J. A., THERON, P. D. & UEKERMANN, E. A. (1999). New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* **21**, 84–89.
- MARSHALL, W. A. (1996). Biological particles over Antarctica. *Nature* **383**, 680.
- MCINTOSH, E. & WALTON, D. W. H. (2000). *Environmental Management Plan for South Georgia*. Government of South Georgia and South Sandwich Islands, 105pp.
- MCKINNEY, M. L. (2001). Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation* **100**, 243–252.
- MCKINNEY, M. L. & LOCKWOOD, J. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**, 450–453.
- MCQUILLAN, P. B. & MARKER, P. (1984). The kelpflies (Diptera: Coelopidae) of Macquarie Island. *Tasmanian Naturalist* **79**, 17–20.
- MICOL, T. & JOUVENTIN, P. (1995). Restoration of Amsterdam Island, South Indian Ocean, following control of feral cattle. *Biological Conservation* **73**, 199–206.
- MINASAKI, R., FARRELL, R. L., DUNCAN, S., HELD, B. W. & BLANCHETTE, R. A. (2001). Mycological biodiversity associated with historic huts and artefacts of the heroic period in the Ross Sea region. *Antarctic Biology in a Global Context*, Abstracts of VIII SCAR International Biology Symposium, Amsterdam. Abstract **S5P28**.
- MOORE, D. M. (1968). The vascular flora of the Falkland Islands. *British Antarctic Survey Scientific Report* **60**, 1–190.
- MORGAN, I. R., CAPLE, I. W., WESTBURY, H. A. & CAMPBELL, J. (1978). *Disease investigations of penguins and elephant seals on Macquarie Island*. Internal report Westmeadows, Victoria. Attwood Veterinary Research Laboratory.
- MORGAN, I. R. & WESTBURY, H. A. (1981). Virological Studies of Adeline Penguins (*Pygoscelis adeliae*) in Antarctica. *Avian Diseases* **25**, 1019–1026.
- MOSER, D. & BETTS, M. (2002). *Capacity of Tourist Ships Making Peninsula Landings Continues to Grow*. Antarctic Non-government Activity News (ANAN) No. 88. Australian Antarctic Division <http://www-old.antdiv.gov.au/goingsouth/tourism/News/2002/18dec.asp>
- MOSER, D. & BETTS, M. (2003). South Georgia tourism record set: possible visit limits at vulnerable sites? Antarctic Non-government Activity News (ANAN) No. 99. Australian Antarctic Division <http://www.aad.gov.au/default.asp?casid=10291>
- MYERS, J. H., SIMBERLOFF, D., KURIS, A. M. & CAREY, J. R. (2000). Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* **15**, 216–320.

- NAVAREEN, R., FORREST, S. C., DAGIT, R. G., BLIGHT, L. K., TRIVELPIECE, W. Z. & TRIVELPIECE, S. G. (2001). Zodiac landings by tourist ships in the Antarctic Peninsula region, 189–99. *Polar Record* **37**, 121–132.
- NEWSHAM, K. K., HODGSON, D. A., MURRAY, A. W. A., PEAT, H. J. & SMITH, R. I. L. (2002). Response of two Antarctic bryophytes to stratospheric ozone depletion. *Global Change Biology* **8**, 972–983.
- NOON, P. E., BIRKS, H. J. B., JONES, V. J. & ELLIS-EVANS, J. C. (2001). Quantitative models for reconstructing catchment ice-vent using physical-chemical characteristics of lake sediments. *Journal of Palaeolimnology* **25**, 375–392.
- OELKE, H. & STEINIGER, F. (1973). *Salmonella* in Adélie Penguins (*Pygoscelis adeliae*) and South Polar Skuas (*Catharacta maccormicki*) on Ross Island, Antarctica. *Avian Diseases* **17**, 568–573.
- OLSEN, B., BERGSTRÖM, S., MCCAFFERTY, D. J., SELLIN, M. & WISTRÖM, J. (1996). *Salmonella enteritidis* in Antarctica: zoonosis in man or humanosis in penguins? *The Lancet* **348**, 1319–1320.
- ØVSTEDAL, D. O. & SMITH, R. I. L. (2001). *Lichens of Antarctica and South Georgia. A Guide to their Identification and Ecology*. Cambridge University Press, Cambridge, 411pp.
- PAGE, B., WELLING, A., CHAMBELLANT, M., GOLDSWORTHY, S., DORR, T. & VAN VEEN, R. (2003). Population status and breeding season chronology of Heard Island fur seals. *Polar Biology* **26**, 219–224.
- PASCAL, M. (1980). Structure et dynamique de la population de chats haret de l'archipel des Kerguelen. *Mammalia* **44**, 171–182.
- PASCAL, M. (1982). Les espèces mammaliennes introduites dans l'archipel de Kerguelen (Territoire des TAAF). Bilan des recherches entreprises sur ces espèces. In *Colloque sur les écosystèmes subantarctiques, Paimpont 1–4 juillet 1981* (eds. P. Jouventin, J. C. Massé and P. Tréhen), pp. 333–343. Comité National Français des Recherches Antarctiques.
- PIMENTEL, D., LACH, L., ZUNIGA, R. & MORRISON, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**, 53–65.
- PRINZIG, A., DURKA, W., KLOTZ, S. & BRANDL, R. (2002). Which species become aliens? *Evolutionary Ecology Research* **4**, 385–405.
- PUGH, P. J. A. (1993). A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* **27**, 323–421.
- PUGH, P. J. A. (1994). Non-indigenous acari of Antarctica and the sub-Antarctic islands. *Zoological Journal of the Linnean Society* **110**, 207–217.
- PUGH, P. J. A. (2004). Biogeography of spiders (Araneae: Arachnida) on the islands of the Southern Ocean. *Journal of Natural History* **38**, 1461–1487.
- PUGH, P. J. A., DARTNALL, H. J. G. & MCINNES, S. J. (2002). The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* **36**, 1047–1103.
- PUGH, P. J. A. & DAVENPORT, J. (1997). Colonisation vs. disturbance: the effects of sustained ice-scouring on intertidal communities. *Journal of Experimental Marine Ecology* **210**, 1–21.
- PYE, T. & BONNER, W. N. (1980). Feral brown rats, *Rattus norvegicus*, South Georgia (South Atlantic Ocean). *Journal of Zoology* **192**, 237–255.
- PYE, T., SWAIN, R. & SEPPELT, R. D. (1999). Distribution and habitat use of the feral black rat (*Rattus rattus*) on subantarctic Macquarie Island. *Journal of Zoology* **247**, 429–438.
- PYŠEK, P. (1998). Is there a taxonomic pattern to plant invasions? *Oikos* **82**, 282–294.
- QUATE, L. W. (1962). Insects of Macquarie Island. Diptera: Psychodidae. *Pacific Insects* **4**, 958.
- QUAYLE, W. C., CONVEY, P., PECK, L. S., ELLIS-EVANS, J. C., BUTLER, H. G. & PEAT, H. J. (2003). Ecological responses of maritime Antarctic lakes to regional climate change. In *Antarctic Peninsula Climate Variability: Historical and Palaeoenvironmental Perspectives* (eds. E. Domack, A. Burnett, A. Leventer, P. Convey, M. Kirby and R. Bindshadler), pp. 159–170. *Antarctic Research Series*, American Geophysical Union.
- QUAYLE, W. C., PECK, L. S., PEAT, H., ELLIS-EVANS, J. C. & HARRIGAN, P. R. (2002). Extreme responses to climate change in Antarctic lakes. *Science* **295**, 645.
- RÉALE, D. (1996). Effet des contraintes environnementales sur la reproduction des femelles de deux espèces d'ovins, le mouton (*Ovis aries*) et le mouflon (*Ovis montanus*), introduits dans l'archipel de Kerguelen. Thèse de Doctorat, Université de Rennes 1.
- RICHARDSON, D. M., PYŠEK, P., REJMÁNEK, M., BARBOUR, M. G., PANETTA, F. D. & WEST, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**, 93–107.
- RYAN, P. G. (1987). Origin and fate of artefacts stranded on islands in the African Sector of the southern ocean. *Environmental Conservation* **14**, 341–346.
- SALA, O. E., CHAPIN, F. S., ARMESTO, J. J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L. F., JACKSON, R. B., KINZIG, A., LEEMANS, R., LODGE, D. M., MOONEY, H. A., OESTERHELD, M., POFF, N. L., SYKES, M. T., WALKER, B. H., WALKER, M. & WALL, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774.
- SAX, D. F., GAINES, S. D. & BROWN, J. H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *American Naturalist* **160**, 776–785.
- SAY, L., GAILLARD, J. M. & PONTIER, D. (2002). Spatio-temporal variation in cat population density in a subantarctic environment. *Polar Biology* **25**, 90–95.
- SCOTT, J. (1996). *A Feral Cat threat abatement plan for Macquarie Island*. Tasmanian Parks and Wildlife Service, Department of Environment and Land Management.
- SCOTT, J. J. (1989). New records of vascular plants from Heard Island. *Polar Record* **25**, 37–42.
- SEARLES, P. S., KROPP, B. R., FLINT, S. D. & CALDWELL, M. M. (2001). Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. *New Phytologist* **152**, 213–221.
- SÉGUY, E. (1940). Croisière du Bougainville aux Iles Australes Françaises. IV. Diptères. *Mémoires du Muséum National d'Histoire Naturelle, series A* **14**, 203–268.
- SÉGUY, E. (1971). Diptera. In *Marion and Prince Edward Islands, Report of the South African Biological and Geological Expedition 1965–1966* (eds. E. M. Van Zinderen Bakker, J. M. Winterbottom and R. A. Dyer), pp. 344–348. A.A. Balkema, CapeTown.
- SELKIRK, P. M. (1992). Climate change and the subantarctic. In *Impact of Climate Change, Antarctica, Australia* (ed. P. G. J. Quilty), pp. 43–51. Australian Government Publishing Service, Canberra.
- SELKIRK, P. M., SEPPELT, R. D. & SELKIRK, D. R. (1990). *Subantarctic Macquarie Island: Environment and Biology*. Cambridge University Press, Cambridge, UK, 285pp.
- SELMI, S. & BOULINIER, T. (2001). Ecological biogeography of Southern Ocean Islands: the importance of considering spatial issues. *American Naturalist* **158**, 426–437.

- SHAW, J. D., BERGSTROM, D. M. & HOVENDEN, M. (in press). The impact of feral rats (*Rattus rattus*) on population recruitment of a subantarctic megaherb (*Pleurophyllum hookeri*). *Austral Ecology*.
- SKOTNICKI, M. L., SELKIRK, P. M., BROADY, P., ADAM, K. D. & NINHAM, J. A. (2001). Dispersal of the moss *Campylopus pyriformis* on geothermal ground near the summits of Mount Erebus and Mount Melbourne, Victoria Land, Antarctica. *Antarctic Science* **13**, 280–285.
- SKOTNICKI, M. L., SELKIRK, P. M., KITAJIMA, E., MCBRIDE, T. P., SHAW, J. & MACKENZIE, A. (2003). The first subantarctic plant virus report: Stilbocarpa bacilliform badnavirus (SMBV) from Macquarie Island. *Polar Biology* **26**, 1–7.
- SKVARCA, P., RACK, W., ROTT, H. & IBARZÁBAL Y DONÁNVELO, T. (1998). Evidence of recent climatic warming on the eastern Antarctic Peninsula. *Annals of Glaciology* **27**, 628–632.
- SLABBER, S. & CHOWN, S. L. (2002). The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biology* **25**, 855–858.
- SMITH, J. J., HOWINGTON, J. P. & MCFETERS, G. A. (1994). Survival, physiological response, and recovery of enteric bacteria exposed to a polar marine environment. *Applied and Environmental Microbiology* **60**, 2977–2984.
- SMITH, J. J. & MCFETERS, G. A. (1999). Microbial issues of sewage disposal from Antarctic bases: dispersion, persistence, pathogens and “genetic pollution”. In *Disease of Antarctic Wildlife. A report for the Scientific Committee on Antarctic Research (SCAR) and the Council of Managers of National Antarctic Programs (CONMAP)* (eds. K. M. Kerry, M. Riddle and J. Clarke), pp. 56–57. Australian Antarctic Division, Kingston.
- SMITH, J. M. B. (1986). *Specks in the Southern Ocean*. University of New England, Armidale, 108pp.
- SMITH, R. I. L. (1984). Terrestrial Plant Biology of the Sub-Antarctic and Antarctic. In *Antarctic Ecology* (ed. R. M. Laws). Academic Press, London.
- SMITH, R. I. L. (1988). Destruction of Antarctic terrestrial ecosystems by a rapidly increasing fur seal population. *Biological Conservation* **45**, 55–72.
- SMITH, R. I. L. (1990). Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In *Antarctic Ecosystems Ecological Change and Conservation* (eds. K. R. Kerry and G. Hempel), pp. 32–50. Springer-Verlag, Berlin.
- SMITH, R. I. L. (1993). The role of bryophyte propagule banks in primary succession: case study of an Antarctic fellfield soil. In *Primary Succession on Land* (eds. J. Miles and D. W. H. Walton), pp. 55–78. Blackwell, Oxford.
- SMITH, R. I. L. (1994). Vascular plants as indicators of regional warming in Antarctica. *Oecologia* **99**, 322–328.
- SMITH, R. I. L. (1996). Introduced plants in Antarctica: potential impacts and conservation issues. *Biological Conservation* **76**, 135–146.
- SMITH, R. I. L. (1997). Impact of an increasing fur seal population on Antarctic plant communities: resilience and recovery. In *Antarctic Communities: Species, Structure and Survival* (eds. B. Battaglia, J. Valencia and D. W. H. Walton), pp. 432–436. Cambridge University Press, Cambridge, UK.
- SMITH, S. D., HUXMAN, T. E., ZITZER, S. F., CHARLET, T. N., HOUSMAN, D. C., COLEMAN, J. S., FENSTERMAKER, L. K., SEEMANN, J. R. & NOWAK, R. S. (2000). Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* **408**, 79–82.
- SMITH, V. R. (2002). Climate change in the sub-Antarctic: an illustration from Marion Island. *Climate Change* **52**, 345–357.
- SMITH, V. R., AVENANT, N. L. & CHOWN, S. L. (2002). The diet of house mice on a sub-Antarctic island. *Polar Biology* **25**, 703–715.
- SMITH, V. R. & STEENKAMP, M. (1990). Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**, 14–24.
- SMITH, V. R. & STEENKAMP, M. (1992a). Macroinvertebrates and litter nutrient release on a sub-Antarctic island. *South African Journal of Botany* **58**, 105–116.
- SMITH, V. R. & STEENKAMP, M. (1992b). Soil macrofauna and nitrogen on a sub-Antarctic island. *Oecologia* **92**, 201–206.
- STONEHOUSE, B. (1994). Tourism and protected areas. In *Developing the Antarctic Protected Area System* (eds. R. I. L. Smith, D. W. H. Walton and P. R. Dingwall), pp. 79–84. IUCN, Gland.
- TAVARES, M. & DE MELO, G. A. S. (2004). Discovery of the first known benthic invasive species in the Southern Ocean: the North America spider *Hyas araneus* found in the Antarctic Peninsula. *Antarctic Science* **16**, 129–131.
- TILMAN, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474.
- TRAVÉ, J. (1987). Contribution à la connaissance des acariens littoraux de l'archipel de Kerguelen: quelques aspects des stratégies adaptatives. *Comité National Français des Recherches Antarctiques* **58**, 111–127.
- TRÉHEN, P. & VOISIN, J. F. (1984). Sur la présence de *Merizodus soledadinus* Guérin à Kerguelen (Coléoptère, Trechidae). *L'Entomologiste* **40**, 53–54.
- TURBOTT, E. G. (1990). *The Checklist of the Birds of New Zealand and the Ross Dependency, Antarctica*. New Zealand Ordnance Survey, Wellington.
- TURNER, J., COLWELL, S. R. & HARANGOZO, S. (1997). Variability of precipitation over the coastal western Antarctic Peninsula from synoptic observations. *Journal of Geophysical Research* **102**, 13999–14007.
- TURNER, J., KING, J. C., LACHLAN-COPE, T. A. & JONES, P. D. (2002). Recent temperature trends in the Antarctic. *Nature* **418**, 291–292.
- TWEDDIE, C. E. & BERGSTROM, D. M. (2000). A climate change scenario for surface air temperature at subantarctic Macquarie Island. In *Antarctic Ecosystems: Models for Wider Ecological Understanding* (eds. W. Davison, C. Howard-Williams and P. A. Broady), pp. 272–281. New Zealand Natural Sciences, Christchurch.
- USHER, M. B. (1984). Spiders in the Falkland Islands. Newsletter from the Falkland Islands Foundation **2**, 4–6.
- VAN AARDE, R. J. (1980). The diet and feeding behaviour of feral cats *Felis catus* on Marion Island. *South African Journal of Wildlife Research* **10**, 123–128.
- VERMEIJ, G. J. (1996). An agenda for invasion biology. *Biological Conservation* **78**, 3–9.
- VERNON, P., VANNIER, G. & TRÉHEN, P. (1998). A comparative approach to the entomological diversity of polar regions. *Acta Oecologica* **19**, 303–308.
- VERNON, P. & VOISIN, J. (1990). Faune entomologique de la Grande Ile des Apôtres (Archipel Crozet, Océan Indien Austral). *Bulletin Société entomologique Française* **95**, 263–268.
- VITOUSEK, P. M., D'ANTONIO, C. M., LOOPE, L. L. & WESTBROOKS, R. (1996). Biological invasions as global environmental change. *American Scientist* **84**, 468–478.
- VOGEL, M. (1985). The distribution and ecology of epigeic invertebrates on the sub-Antarctic Island of South Georgia. *Spixiana* **8**, 153–163.

- VOGEL, M. & NICOLAI, V. (1983). Invertebrates collected at the old whaling station, Grytviken, South Georgia. *Polar Record* **135**, 607–609.
- VOGEL, M. & PLASSMANN, E. (1985). Mycetophilids on islands in the Southern Ocean, with description of a new species from the Falkland Islands. *Spixiana* **8**, 281–284.
- WALTHER, G.-R., POST, E., CONVEY, P., MENEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J.-M., HOEGH-GULDBERG, O. & BAIRLEIN, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395.
- WALTON, D. W. H. & SMITH, R. I. L. (1973). Status of the alien vascular flora of South Georgia. *British Antarctic Survey Bulletin* **36**, 79–97.
- WALTON, D. W. H., VINCENT, W. F., TIMPERLEY, M. H., HAWES, I. & HOWARD-WILLIAMS, C. (1997). Synthesis: polar deserts as indicators of change. In *Ecosystem Processes in Ice-Free Landscapes* (eds. W. B. Lyons, C. Howard-Williams and I. Hawes), pp. 275–279. Balkema, Rotterdam.
- WATSON, K. C. (1967). The terrestrial arthropoda of Macquarie Island. *Australian National Antarctic Research Expedition Reports, Series B, Zoology* **99**, 1–90.
- WILLIAMSON, M. (1996). *Biological invasions*. Chapman & Hall, London, UK.
- WILLIAMSON, M. & FITTER, A. (1996). The varying success of invaders. *Ecology* **77**, 1661–1666.
- WISE, K. A. J. (1971). The Collembola of Antarctica. *Pacific Insects Monograph* **25**, 57–74.
- WOEHLER, E. J., COOPER, J., CROXALL, J. P., FRASER, W. R., KOOYMAN, G. L., MILLER, G. D., NEL, D. C., PATTERSON, D. L., PETER, H.-U., RIBIC, C. A., SALWICKA, K., TRIVELPIECE, W. Z. & WEIMERSKIRCH, H. (2001). A statistical assessment of the status and trends of Antarctic and subantarctic seabirds *Report on SCAR BBS Workshop on Southern Ocean seabird populations* 1–43.
- WOMERSLEY, H. (1937). Collembola (Springtails). *British Australian and New Zealand Research Expedition Report 1929–1931, Report B* **4**, 1–7.
- WYNN-WILLIAMS, D. D. (1992). Plastic cloches for manipulating natural terrestrial environments. In *BIOTAS Manual of Methods for Antarctic Terrestrial and Freshwater Research* (ed. D. D. Wynn-Williams). Scientific Committee on Antarctic Research, Cambridge.
- WYNN-WILLIAMS, D. D. (1993). Microbial processes and the initial stabilisation of fellfield soil. In *Primary Succession on Land* (eds. J. Miles and D. W. H. Walton), pp. 17–32. Blackwell, Oxford.
- WYNN-WILLIAMS, D. D. (1994). Potential effects of ultraviolet radiation on Antarctic primary terrestrial colonizers: cyanobacteria, algae, and cryptogams. *Antarctic Research Series* **62**, 243–257.
- WYNN-WILLIAMS, D. D. (1996a). Antarctic microbial diversity: the basis of polar ecosystem processes. *Biodiversity and Conservation* **5**, 1271–1293.
- WYNN-WILLIAMS, D. D. (1996b). Response of pioneer soil microalgal colonists to environmental change in Antarctica. *Microbial Ecology* **31**, 177–188.
- ZAVALETA, E. S., HOBBS, R. J. & MOONEY, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* **16**, 454–459.

APPENDIX 1. Location of sites mentioned in the text.

Latitudes and longitudes are expressed in decimal degrees

Islands or continental regions	Latitude	Longitude
Cold temperate		
Tristan da Cunha	37.10 S	12.25 W
Inaccessible	37.25 S	12.75 W
Nightingale	37.42 S	12.50 W
Amsterdam	37.83 S	77.52 E
Saint Paul	38.72 S	77.53 E
Gough	40.33 S	9.54 W
Snares	48.12 S	166.00 E
Antipodes	49.68 S	178.77 E
Auckland	50.83 S	166.60 E
West Falklands	51.50 S	60.50 W
East Falklands	51.50 S	58.50 W
Campbell	52.50 S	169.17 E
Subantarctic		
Apôtres (Crozet)	45.97 S	50.43 E
Cochons (Crozet)	46.10 S	50.23 E
Possession (Crozet)	46.42 S	51.50 E
Est (Crozet)	46.43 S	52.20 E
Pingouins (Crozet)	46.50 S	50.40 E
Prince Edward	46.63 S	37.95 E
Marion	46.90 S	36.75 E
Bounty	47.72 S	179.00 E
Kerguelen	49.37 S	69.50 E
McDonald	53.03 S	72.60 E
Heard	53.10 S	73.50 E
Bird	54.00 S	38.05 W
South Georgia	54.25 S	37.00 W
Macquarie	54.62 S	158.90 E
Maritime		
South Sandwich	56.30–59.47 S	26.23–28.18 W
Half Moon	59.95 S	62.61 W
Signy	60.54 S	45.56 W
King George (South Shetland)	62.22 S	59.00 W
Deception Island	62.57 S	60.38 W
Cierva Point	64.02 S	61.02 W
Anvers Island	64.50 S	64.00 W
Léonie Island	67.58 S	68.33 W
Continental		
Windmill Island (Casey station)	66.28 S	110.53 E
MacRobertson Land	67.43 S	60.83 E
Adelaide Island	67.57 S	68.13 W
Vestfold Hills (Davis station)	68.58 S	77.97 E
Schirmacher Oasis	70°45' S	11.77 E
Victoria Land	72.00–86.00 S	150.00–170.00 W
Dronning Maud Land	75.00 S	65.00 E
Ross Island	77.50 S	168.00 E
Mc Murdo	77.51 S	166.37 E
Mt Howe	87.37 S	149.50 W