Life across the divide: Comparative Studies of the Ecology and Physiology of Species across the Antarctic Intertidal Zone

Thesis

How to cite:

Waller, Catherine L (2007). Life across the divide: Comparative Studies of the Ecology and Physiology of Species across the Antarctic Intertidal Zone. PhD thesis The Open University.

Life across the divide: Comparative Studies of the Ecology and Physiology of Species across the Antarctic Intertidal Zone

A thesis submitted in accordance with the requirements of the Open University for the degree of

Doctor of Philosophy

By

Catherine L. Waller (B.A. hons, B.Sc. hons)

11 January 2007

Director of Studies:
Dr D.K.A. Barnes

Supervisor
Dr P. Convey

Sponsoring Establishment:
Natural Environment Research Council
British Antarctic Survey
High Cross
Madingley Road
Cambridge CB3 0ET
United Kingdom

DATE OF SUBMISSION: 12 JANUARY 2007
DATE OF AWARD: 14 JUNE 2007

The river is within us, the sea is all about us;

The sea is the land's edge also, the granite

Into which it reaches, the beaches where it tosses

Its hints of earlier and other creation:

The starfish, the horseshoe crab, the whale's backbone;

The pools where it offers to our curiosity

The more delicate algae and the sea anemone.

It tosses upour losses, the torn seine,

The shattered lobsterpot, the broken oar

And the gear of foreign dead men. The sea has many voices, many gods and many voices.

T.S.Eliot

Abstract

This thesis describes the first detailed comparative study of Antarctic communities across the gradient of environmental conditions from terrestrial to marine zones. Sampling was undertaken at both sub-Antarctic (Scotia Arc) and Peninsula sites. This study is also the most detailed and comprehensive investigation of intertidal assemblages south of 60°S undertaken to date.

Supralittoral, intertidal and, where possible, shallow sublittoral habitats were sampled along a latitudinal gradient from the Falkland Islands through the Scotia Arc (Bird Island, South Georgia and Signy Island (South Orkney Islands)) over one austral summer. Peninsula sites, in the vicinity of Rothera Research Station (Adelaide Island 67° 34.5'S), were studied in more detail over two austral summers, and one point sample was undertaken during the austral winter at Rothera Research Station.

Contrary to the findings of previous studies, the Antarctic intertidal was found to support an unexpectedly rich and diverse community, with a total of 61 species being found at sites around Rothera Research Station, Adelaide Island. This is more than double the previous maximum richness reported in an Antarctic study. Intertidal assemblages at more northern Scotia Arc sites were less diverse and numerically abundant, the most depauperate sites being on Bird Island and South Georgia.

Many of the taxa found are permanent residents in the intertidal near Rothera Research Station. Four-year-old colonies of the bryozoan *Inversiula nutrix* were found alive in summer samples, and a winter excavation of only 1 m^2 of the intertidal icefoot revealed 17 species of both mobile and sessile taxa alive and present under the outer layer of rocks. The taxa present were predominantly marine species with only one possibly obligate intertidal animal being found, the halacarid mite *Rhombognathus gressitti.*

The assemblages were virtually all located beneath the outer scoured surface of the intertidal rock matrix, in protected interstices. Both abundance and size of taxa increased with depth through the cobble boulder matrix suggesting that they are exploiting protected microhabitats in order to survive in this extreme environment.

Preliminary ecophysiological studies suggest that the limpet *Nacella concinna* is capable of freeze tolerance and is able to survive all of the osmotically active water freezing, whilst the nemertean *Antarctonemertes validum* shows evidence of the presence of thermal hysteresis proteins (THPs). As such this is the first Antarctic and only the second marine invertebrate likely to possess THPs.

Acknowledgements

I have always been fascinated by the sea. As a child it intrigued me that there is an area between "it" and terra firma; and that this half wet, half dry world is full of incredible animals. From my earliest memories of playing on the beach, I have been mesmerised, much to the exasperation I am sure, of my parents and long suffering sister. I would like to thank them all for allowing me to return home with numerous smelly treasures.

I could not have reached this place without the help and support of many people, my husband being foremost, so thank you Charles for putting up with rocks and obsessive behaviour. I have been more than fortunate in my wonderful supervisors Dave Barnes and Pete Convey. I cannot begin to tell you both how much you have helped me grow in confidence and stimulated me to think about things in the bigger picture (Dave you'll miss me when I'm gone – especially the coffee!!). THANK YOU BOTH!! My thanks go also to Simon Morley for valiantly fighting off the fur seals on a variety of beaches whilst I was investigating interesting rocks; and the Rothera wintering marine team, especially Dan Smale and Andy Miller, for digging holes through a metre of ice and looking what was on, or under more interesting (and cold) rocks. Thanks too to Christine Phillips, Pete Rothery, Jamie Oliver and the MAGIC team for all the help you have given me here in Cambridge.

My ex-tutors and good friends at Scarborough Centre for Coastal Studies have kept me sane (ish) over the last three years, offering me support in the lows and beer on most other occasions. Heartfelt thanks go out to Sue, Magnus, Brian and Shell.

I have also had a great support network here at B.A.S. Huw I love you!! I could never have stood up in front of 300 people without you. Katrin, I am so grateful for your care, concern and friendship. Elaine, Mags, Helen you have been great – thanks! Thanks also to all the residents past and present of office 341 for plenty of support and "displacement activities".

CONTENTS

List of figures

Chapter 1 – General introduction

Chapter 1 – General Introduction

INTRODUCTION

"If the Lord Almighty had consulted me before embarking on creation I should have recommended something simpler"

Alphonso X (Alphonso the Wise) 1221-1284

Ecology is defined as "the branch of biology that deals with organisms' relations to one another and to the physical environment in which they live" (Pearsall 1999). It is a relatively young science. Gilbert White's "A Natural History of Selborne" (White 1789) is arguably the first true ecological text. It reaches beyond the previous descriptive studies of natural history, and attempts to address analytical questions about underlying structuring factors that define communities, for example what governs the abundance of swifts and wasps in Selbourne (May 1999). It was not until the early 20th Century, however, that ecology became fully accepted as a scientific discipline. The British Ecological society (BES), founded in 1913 was the first of its kind (established much later than most scientific societies). As late as the mid part of the 20th Century the research articles published in its journal, and those of its American counterpart, were predominantly descriptive and classificatory with much of the emphasis on plant communities (May 1999). The complexity of ecosystem patterns, and the lack of a clear understanding of the underlying structuring mechanisms, have led to the position of ecologists being likened to that of the inorganic chemists before the development of the periodic table (Southwood 1977). However the third quarter of the century saw advances in empirical observations and, often explicitly mathematical, analytical approaches to answering these fundamental questions. Understanding of the mechanisms of spatial and temporal variability has advanced significantly over the last few decades, with the development of chaos and complexity theories to help describe the complicated spatiotemporal variability in ecological community structure. It is now becoming recognised that in order to even begin to understand the structuring mechanisms within communities, long-term and / or large-scale data sets are needed. However analyses of empirical studies within peer review journals have shown that only a small percentage of published research utilises datasets of over 5 years' length (1.7% of the 749 published in the journal Ecology between 1979 to 1989) (Tilman 1989). On a spatial scale, 44% of the manipulative field studies published between 1980 and 1986 in the same journal had a characteristic scale of less than 1 m with only 25% having a characteristic dimension over 10 m (Kareiva & Anderson 1989). Despite decades of work ecologists are still searching for general patterns in the way ecosystems are assembled and structured (Lawton 1999, Clarke 2003).

WHAT IS BIODIVERSITY?

"Biological diversity" is defined by the United Nations 1992 Convention on Biological Diversity (the "Rio Earth Summit") as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (UNEP1992). The term "biodiversity" (a simple concatenation of "biological diversity") was first coined by W.G. Rosen in 1985 (Harper & Hawksworth 1995). However, the concept of biological diversity in its modern meaning predates this by at least 10 years (Magurran 2004). At first sight the concept is simple, however the challenge to ecologists lies in measuring such a broad concept in ways that are meaningful. Any attempt to measure biological diversity quickly runs into the problem that it is a multidimensional abstraction (Purvis & Hector 2000), both spatially (from genetic to ecosystem or global scales) and temporally (from hours to epochs) (Huston 1996). More recent definitions have become more directed. For example, Hubbell (2001) defines biodiversity to be "synonymous with species richness and relative species abundance in space and time". The majority of studies have historically been conducted in terrestrial ecosystems and the level of knowledge of marine organisms and environments, although increasing, still in detail falls far short of that known on land. Even what many ecologists describe as the most fundamental pattern to be seen in global biodiversity, a cline of reduction from tropics to poles, is still not clearly described or understood, or even universally accepted or applicable. Data that suggest some regularity in diversity patterns (e.g. the paradigm of a cline in diversity from the tropics to the poles (e.g. Abbott 1968, Stehli 1968) are contradicted by data that show the opposite pattern (e.g. Paine 1966, Sanders 1968, Abele 1974). Even the underlying mechanisms suggested to explain the pattern e.g. Rapoport's Rule (Rapoport 1982, Stevens 1989), geographic area hypothesis (Rosenzweig 1995), energy productivity hypothesis (Wright 1983)) are disputed (e.g. Roy et al. 1998, Gaines 1999).

MEASURING DIVERSITY

No single process or theory can explain a phenomenon as complex as biodiversity, which is influenced by many different interacting factors and processes (e.g. ecological, evolutionary, geological and biogeochemical) (Huston 1996). However the importance of being able to quantify biodiversity is clear, as only then can fundamental questions such as how biodiversity is changing over time be addressed. The scale at which diversity is measured can result in a multiplicity of different definitions ranging from genetic through organismal to ecological diversity. In the context of the current study the term diversity is used in an ecological sense. However, defining the various aspects of ecological diversity can be problematic (Gaston & Spicer 1998). At its simplest, diversity may be represented by the number of species present ("species richness"). Despite having significant complications (particularly those associated with dependence on sample size) this has become one of the most commonly used surrogates for biodiversity. A wide range of methods for measuring diversity are suggested in ecological texts. Many of these measures partition biological diversity into two components, the number of taxa (richness, usually at species level) and evenness (the relative abundances of individuals between taxa). A community in which all species are approximately equally abundant would have a high level of evenness, whereas a community with a great variability in the number of individuals between species would have a low evenness value (Magurran 2004). Recent developments in multivariate statistical techniques, combined with increasingly powerful computational capacity have resulted in advances in the descriptions of community diversity patterns by means of sophisticated computer software packages (e.g. PRIMER software offering multivariate techniques for community analysis; EstimateS for species richness estimation and a range of α and β diversity measures; Ecosim which focuses on null models in ecology (Chao 1984, Clarke & Warwick 2001, Gotelli & Entsminger 2004)).

TRANS–ZONE APPROACH

Marine and terrestrial ecosystems vary in a number of key physical and chemical characteristics, which have influenced the evolution of their respective biota (Carr et al. 2003). However they are also strongly linked (e.g. Polis & Hurd 1995, Gende et al. 2002). Ecology, having its roots in "natural history", has resulted in the domination of general ecological texts and journals by terrestrial research. Stergiou & Brownman

(2005a), found in an analysis of editors and articles published in four general ecology journals (Ecology, Oecologia, Ecology Letters and Oikos), that 78% of editors were primarily involved in terrestrial ecology and 69.4% of articles related to the terrestrial zone. Only 9.9% focussed on marine issues. The lack of communication and collaboration between terrestrial and marine ecologists was highlighted in a recent thematic section in the journal Marine Ecology Progress Series (MEPS), in which a number of authors discuss the reasons behind this and the importance of collaborative projects (e.g. Stergiou & Brownman 2005 a,b). Ecological studies of marine and terrestrial systems are usually carried out in separate institutions (Steele 1995) and terrestrial and marine ecologists tend to favour particular hypotheses and observations, and discount those reported in other ecosystems (Chase 2000). However comparisons across these environments may identify widely applicable ecological processes and theories with which to address critical ecological issues such as climate change and sea level rise (Stergiou & Brownman 2005b).

The intertidal zone represents a bridge between these two ecosystems. When the tide is out the habitats are in many respects terrestrial, and the animals are exposed to many of the same environmental conditions as their terrestrial counterparts. During high tide the habitats become marine, and the animals and plants are subject to the conditions of the marine environment. In Antarctica, the contrast between terrestrial and marine environments are extreme, so much so that the consensus has been that little if anything can survive there. By considering communities from terrestrial across the barren intertidal and into the shallow sublittoral, the hypotheses (a) that few taxa are able to exist under intertidal conditions and (b) that those found present in the intertidal would be more stressed than individuals from their "normal" environment can be tested.

GENERAL INTRODUCTION TO THE INTERTIDAL ZONE

The extent of the intertidal zone worldwide is estimated at 1,634,701 km (Pruett & Cimino 2000), although this is necessarily a crude approximation as coastlines are fractal in nature, so any measurement is dependent upon the scale at which the data are collected. Globally, the intertidal is arguably one of the most studied environments, and has been subject to scrutiny since classical times. Aristotle, and later Pliny the Elder, both described their observations of the intertidal zone and the species found there. Over the last 300 years, intertidal research has developed from the systematic naming, description and cataloguing of specimens, commenced by Linnaeus, through descriptions of zonation patterns by early 19th century natural historians (e.g. Audouin & Milne–Edwards 1832, Verill 1882), to the burgeoning numbers of studies into large scale-effects in ecology over the past 20 years (Blackburn & Gaston 2003). The opening of marine biological research stations (the first in Naples in 1875 by Anton Dohrn) prompted the first serious studies of intertidal ecology (see Raffaelli & Hawkins 1997 p. vii). The intertidal zone has continued to be a cornerstone in the development and testing of marine ecological theories over the past 50 to 60 years. This has been the case in both broad-scale quantitative studies, such as the concept of zonation patterns (Stephenson & Stephenson 1949, Southward 1965, Lubchenco 1980), and experimental manipulations of the environment giving insights into the influences of intra and inter-specific competition, predation and disturbance (e.g. Connell 1961, 1972, Paine 1966, 1969, Dayton 1971, Menge 1976, Caswell 1978, Sousa 1979, Underwood 1980, 1986). The vast majority of these studies have been conducted on accessible temperate rocky shores and to a lesser extent saltmarsh (e.g. Luxton 1967, Long & Mason 1984), tropical mangrove (e.g. Acker 1972, Sheaves 1992, Lee 1999) and lagoon systems (e.g. Edwards 1978, Lae 1994).

Polar environments have received *pro rata* much less attention, due in part to a perception of their 'inhospitable' and barren appearance and in part the logistical practicalities of working in often extremely remote locations. Of the two polar regions, the Arctic has been more extensively studied than have southern polar shores (e.g. Gurjanov 1968, Green et al. 1983, Weslawski et al. 1993, Szymelfenig et al. 1995, Weslawski et al. 1997, 1999, McKindsey & Bourget 2001, Sokolova & Pörtner 2003, Barnes & Kuklinski 2004, Urban-Malinga et al. 2004, Kuklinski et al. 2006). This relates to the Arctic landmasses being political units divided between a number of sovereign nations, and the fact that many Arctic shores are close (relatively) to permanent human populations, a situation contrasting with the extreme isolation of an Antarctic continent administered through an international treaty in the absence of any indigenous human population. This inaccessibility and the consequential general lack of autecological study has resulted in a longstanding consensus that the Antarctic intertidal zone can support little more than transient summer populations of a small suite of macro-species. Of the handful of studies that have considered the Antarctic littoral zone south of the Polar Frontal Zone (PFZ), three are brief qualitative descriptions of the intertidal at Palmer Research Station on Anvers Island (Hedgpeth 1969a, Stout & Shabica 1970, Stockton 1973). The majority of the remaining studies have focussed on specific groups of taxa and have not addressed questions at the level of community (Smith & Simpson 1985, Gambi et al. 1994, Barnes et al. 1996, Davenport 1997, Davenport et al. 1997, Jazdzewski et al. 2001, Barnes & Brockington 2003). There are few studies considering biotic and abiotic factors structuring intertidal communities at these latitudes, the most comprehensive to date being those of Davenport & MacAllister (1996) and Pugh & Davenport (1997), addressing sites on South Georgia (Husvik and Cumberland West Bay).

THE CLIMATE IN POLAR REGIONS

Both polar regions are characterised by extreme seasonal photoperiod, low temperatures, and are heavily influenced by ice and snow. However, in almost all other respects, they differ markedly. The Arctic is an enclosed marine basin almost completely surrounded by continental landmasses with large freshwater and sedimentary inputs from the surrounding land. In contrast, Antarctica is a single continental landmass surrounded and isolated by deep and extensive cold ocean (Clarke & Crame 2003).

A fundamental distinction between polar terrestrial and marine environments is the variability in temperatures experienced by each zone. The marine environment is generally characterised by low but relatively or extremely constant temperatures, (Dayton, 1990, Clarke & Harris 2003) contrasting with terrestrial habitats which may experience 20°C or greater change in temperature in a day, and up to 80-100°C variation over the annual cycle, often including transgressions of the 0°C freezing boundary (Smith 1988a, Convey 1996a, Danks 1999, Peck et al. 2006, Convey in press).

ANTARCTIC MARINE ENVIRONMENTS

The Southern Ocean, defined as the area of the world's oceans south of the polar frontal zone (PFZ), constitutes around 8.8% of the world's oceans. The total area of this body of water has been estimated at 34.8 million km^2. Winter ice cover can be as much as 21 million km^2 while summer minimum cover is in the region of approximately 7 million km^2 (Fig. 1.1) (Gloersen et al. 1993).

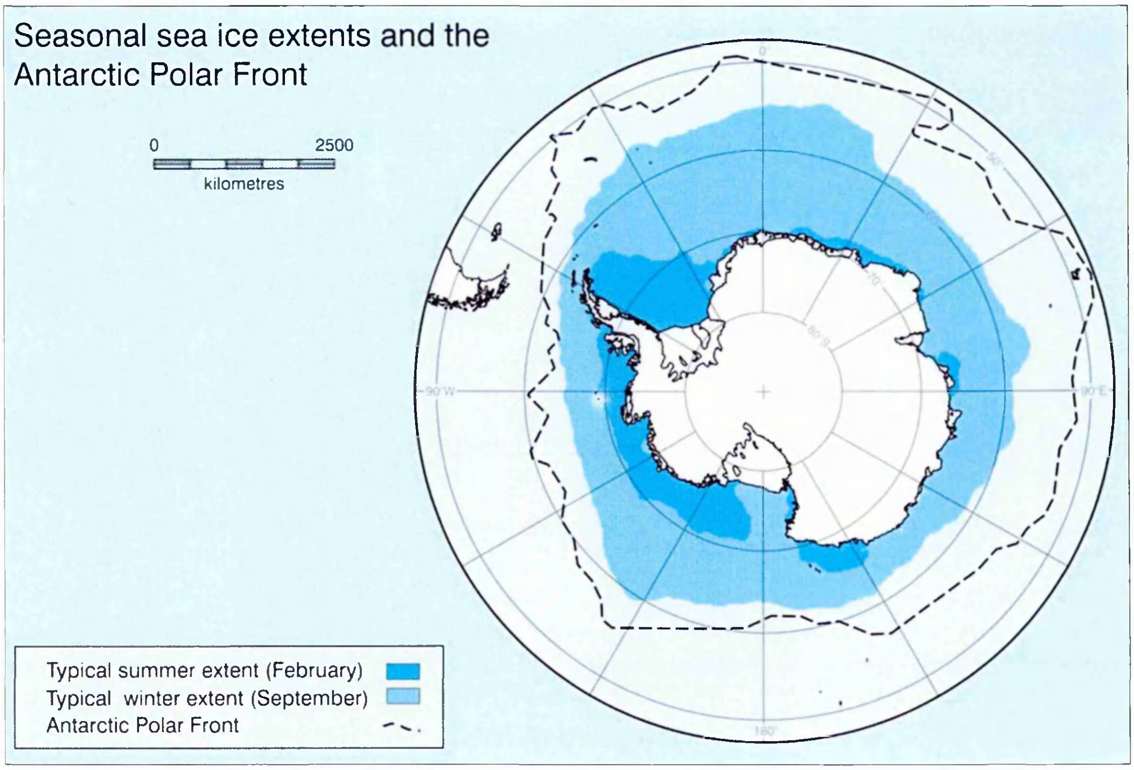


Fig. 1.1. Map of the Southern Ocean showing seasonal sea ice extents around the Antarctic continent and the approximate position of the polar frontal zone (PFZ).

Despite its large geographical extent the Southern Ocean is usually considered as a single marine biogeographical region (Longhurst 1998), extending to South Georgia and including the South Shetland, South Orkney and South Sandwich archipelagos. Heard, Macquarie and Kerguelen islands are considered on the basis of marine faunal evidence to be sub–Antarctic (Hedgpeth 1969b, Dell 1972). The present day oceanography of the region is structured by the deep-water separation of Antarctica from Australia and South America. This has resulted in a strong clockwise (westerly) circulation of surface water around the continent, driven by the prevailing winds (Clarke 2003). This Antarctic Circumpolar current (ACC) has long been considered as a barrier to the dispersal of marine species across the PFZ (Clarke & Harris 2003, Barnes 2005, Clarke et al. 2005, Barnes et al. 2006b, Peck et al. 2006). However, this view is being challenged, or at least the permeability of the barrier being questioned, with the discovery of sub-polar marine invertebrate larvae (Thatje & Fuentes 2003) and adult North Atlantic spider crabs *Hyas areneus* in the Antarctic Peninsula region (Tavares & De Melo 2004), and the findings of Antarctic krill in Chilean fjords (Antezana 1999) and Southern Ocean diatoms in western Tasmanian estuaries (Hodgson et al.1997).

Polar oceans are at the lower extreme of the temperature range available to marine organisms, but are characterised by relatively stable thermal characteristics with temperatures at one of the study sites forming the focus of this thesis (Ryder Bay, Adelaide Island) varying by around only 3°C over the annual cycle (Barnes et al. 2006a), and by as little as 0.2°C at McMurdo Sound in the Ross Sea region (Littlepage 1965). Disturbance due to the impact of ice is also an important structuring influence on the shallow marine benthos (Dayton et al. 1969, Gutt et al. 1996, Barnes 1999, Gutt 2001, Brown et al. 2004, Smale et al. in press) and is highly variable on both spatial and temporal scales, from summer ice scour (which can include iceberg impacts affecting even depths of several hundred metres) to winter fast ice formation.

ANTARCTIC TERRESTRIAL ENVIRONMENTS

The Antarctic continent covers an area of approximately 14 x 10^6 km^2, an area almost twice that of Australia. It is frequently described as the world's highest, windiest and coldest continent. Less than 1% of the landmass (estimated at 0.32% in 2004 (BAS 2004)) is free from permanent snow and ice. Paradoxically given the average > 2 km depth of ice across the continent, precipitation is generally very low, although the Antarctic Peninsula region receives greater levels than the remainder of the continent, which has been described as a cold desert (Longton 1988, Sømme 1995, Lyons et al. 1997). Terrestrial ecologists have classified areas of Antarctica into several biogeographic regions, based on climatic conditions and differing ecosystems and biological characteristics. Commonly these are recognised as the sub-, maritime- and continental Antarctic (e.g. Smith 1984, Longton 1988, Convey 2001a, Chown & Convey in press a).

The sub-Antarctic zone consists of a ring of isolated high latitude islands (differing in composition from the marine sub-Antarctic described above), which experience strongly oceanic climatic conditions. Year round monthly mean temperatures are low – on the coldest islands (South Georgia and Heard I.) in the range + 6° to –1°C (BAS unpublished, Walton 1984). At microhabitat scale, minimum temperatures are further buffered on these islands by winter snow cover (Convey 1996b, 2001b). On the more northern sub-Antarctic island groups (Marion / Prince Edward, Kerguelen, Crozet, Macquarie) mean monthly temperatures remain positive year-round, with prolonged freezing periods and snow cover unusual at least at low altitudes. The Maritime Antarctic region includes the West Antarctic Peninsula (WAP) as far south as Alexander Island (~72°), the South Shetland, South Orkney and South Sandwich archipelagos and the isolated Southern Ocean islands of Bouvetøya and Peter I Øya. The climate here is more strongly seasonal than that experienced by the sub-Antarctic islands, although the maritime influence again ameliorates extremes especially during the summer months (Convey 2001a). Mean air temperatures over the Maritime region are low but positive (< 2°C) for 1 to 4 months of the year (Smith 1984, Walton 1984). Rothera Point and neighbouring islands in Marguerite Bay lie in this region, and experience a typical macroclimate (Table 1.1).

Table 1.1. Mean monthly air temperatures recorded over the period December 1976 to October 2006 at Rothera Research Station Adelaide Island. (BAS meteorological data). http://www.antarctica.ac.uk/met/READER/surface/Rothera.All.temperature.html)

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1.4	0.7	-1.2	-3.0	-5.3	-8.8	-10.9	-10.6	-8.9	-5.9	-2.4	0.3

The continental region, including the Eastern side of the Antarctic Peninsula, comprises the largest and climatically most extreme area, with air temperatures rarely becoming positive even for short periods, snow and ice cover that may be recede seasonally from terrestrial habitats for periods of a only a few days to weeks and, south of the Antarctic Circle, a radiation climate ranging from permanent darkness in winter to permanent daylight in summer (Convey 2001b).

In the maritime zone most terrestrial habitats other than near-vertical cliffs are covered seasonally by snow and ice, the duration of which varies with location from weeks up to ~9-10 months. Because of this, as in the marine environment, there is a strong seasonality in biological processes. In contrast, many sub-Antarctic islands experience only small amounts of intermittent snow cover and have developed extensive peat deposits and richer soils than the other two zones (Smith 1984, Walton 1984, Convey 2001a). Recent climate change and the consequent shrinkage of snowfields and ice caps at some maritime locations (e.g. Smith 1990, Convey 2003) have resulted in new terrestrial habitats being exposed and available for colonisation. Studies of vascular plants in particular have shown them to be taking advantage of these more favourable conditions and opportunities (Fowbert & Smith 1994, Gerighausen et al. 2003).

ANTARCTIC INTERTIDAL ENVIRONMENTS

Little is known about the Antarctic intertidal zone. The few studies that have been conducted have taken place predominantly on the sub-Antarctic islands. The range of stresses and levels of disturbance experienced vary with latitude with progression through the Scotia Arc islands to the Antarctic Peninsula. South Georgian shores are rarely affected by sea ice, although ice scour may be significant occasionally or locally through either grounding of oceanic icebergs or calving of tidewater glaciers (Pugh & Davenport 1997). This has resulted in an intertidal environment that can support several species of macroalgae including the phaetophytes *Macrocystis pyrifer*, *Durvillaea antarctica* (giant kelp), the rhodophytes (*Bostrychia* sp., *Ceramium rubrum, Cladonata* sp., *Iridaea cordata*) and filamentous green algae. However large populations of marine mammals such as elephant seals (*Mirounga leonina*), fur seals (*Arctocephalus gazella*) and penguins can lead to considerable disturbance to both intertidal and terrestrial habitats through trampling and nutrient enrichment (Smith 1988b).

In contrast, the intertidal zone at sites on the Antarctic Peninsula experiences the dual effects of extensive summer ice scouring and winter encasement in an ice foot (Gutt et. al. 1996, Barnes 1999, Gutt 2001). This has led to a widely held perception of an apparently barren environment unable to support macroalgae or fauna other than a few transient opportunistic summer vagrants, such as the limpet *Nacella concinna*. More rarely, and then generally at more northern sites in the maritime Antarctic (e.g. South Orkney and South Sandwich archipelagos) a small number of rapidly maturing bryozoan species and occasional springtails, mites and enchytraeid worms are reported from the intertidal (Worland & Block 1986, Barnes et al. 1996, Convey et al. 2000, Barnes & Brockington 2003). It has been estimated that around 12-13.7 % of the peninsula coastline is bare rock i.e. not permanently encased in ice (approximately 5468 km) (BAS unpubl. data) and so potentially available for colonisation. This comprises many coast types common in non-polar regions, including boulder scree, bedrock and sedimentary shores of varying grain sizes, although intertidal sands, muds and lagoons are rare (Peck et al. 2006). The majority of the eastern coast of the Peninsula south of 65.6°S is comprised of floating ice shelf, whereas the western coast includes greater areas of exposed rock interspersed with smaller glaciers. The western Antarctic Peninsula (WAP, approximately 1339 km in length) includes the region of Antarctica that is currently warming most rapidly (Vaughan et al. 2003, Turner et al. 2005), and a recent study (Cook et al. 2005) has shown that of 244 Peninsula glaciers examined in an analysis of historical aerial photography, mapping and satellite data, 87% are retreating (Fig.1.2). This, as with ice retreat on land, potentially increases the area of intertidal zone available for colonisation, either by local terrestrial and marine species or by a southwards shift of more northern species ranges.

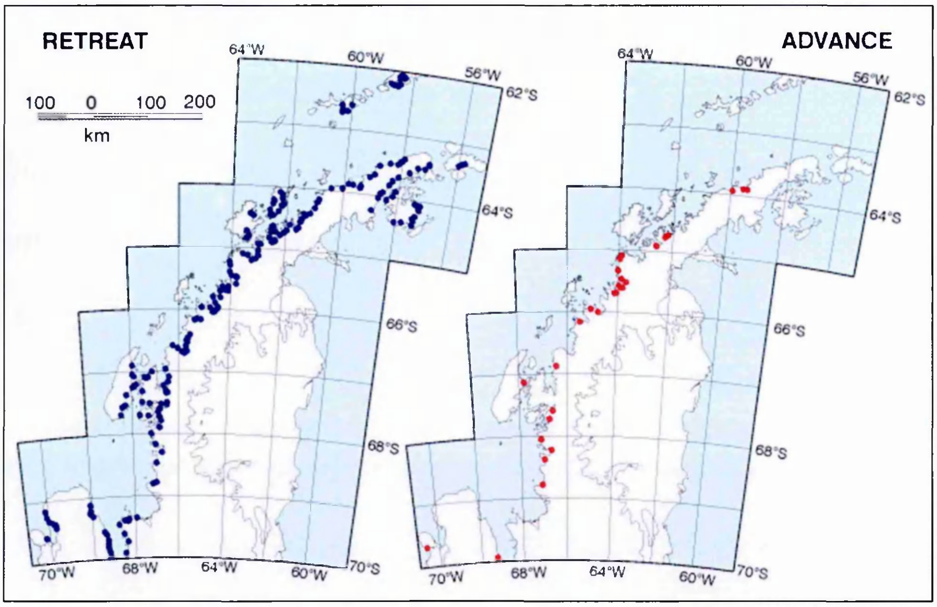


Fig.1.2. Map of the Antarctic Peninsula showing overall changes observed in glacier fronts since earliest records (average 1953). (Reproduced with permission from Cook et al. 2005)

INTRODUCTION TO TAXA

Antarctic marine organisms experience a relatively narrow range of temperatures over seasonal and ecological timescales, and many have been shown to be highly stenothermal (Peck 2002, Peck et al. 2004). In contrast, Antarctic terrestrial organisms are faced with highly variable thermal conditions over both daily and seasonal timescales. Consequentially they must be eurythermal and more plastic in their response (Clarke 1991). Terrestrial diversity also provides a sharp contrast to that of the surrounding seas. While the latter are rich and diverse (Arntz et al. 1997, Clarke & Johnston 2003), the land has the lowest diversity known on Earth, with a general overall pattern of decreasing diversity with increasing latitude, at least in large-scale comparisons between the sub-, maritime and continental Antarctic (Convey 2001a, Clarke 2003). In comparison with the maritime and continental regions the sub–Antarctic island terrestrial faunas are species rich and relatively well known (Chown & Convey in press b). There are no true terrestrial vertebrate animals in Antarctica (other than two ducks and a single passerine bird in parts of the sub-Antarctic, and two species of sheathbill largely associated with marine vertebrate colonies), and the dominant macrofaunal group are arthropods (Block 1984).

The arthropod fauna of the Antarctic continent is dominated by representatives of only two phyla (Chelicerata and Uniramia). These include four groups of Acari (mites) (meso-, pro-, a-, cryptostigmatids) and Collembola (springtails), while Diptera also have a minority presence in the maritime Antarctic, represented by two species of chironomid midge. Although these taxa are composed of small animals (e.g. ranging from a mean live mass of 3.57μg in the smallest species such as *Nanorchestes antarcticus* to 196.21μg in the large cryptostigmatid *Alaskozetes antarcticus* (Block 1984)) they can occur in large numbers in suitable habitats (e.g. a density of c.1.5 x10^6 *Cryptopygus antarcticus* m^{-2} has been reported by Convey and Smith 1997). Larger invertebrates such as annelids (earthworms and enchytraeids), land molluscs, the higher insects (Diptera, Hymenoptera and Coleoptera) and spiders are in most cases limited to warmer and less extreme areas in the sub-Antarctic (Block 1984, Convey in press) (Table 1.2). Microscopic taxa such as tardigrades, nematodes and rotifers can also be abundant in snow free terrestrial substrata across all three biogeographical regions (Block 1984, Convey 2001b).

Table 1.2 Number of known representatives (species) in of the major native terrestrial invertebrate phyla from the three Antarctic biogeographical zones (reproduced from Convey in press).

Group	**Sub-Antarctic**	**Maritime Antarctic**	**Continental Antarctic**
Protozoa *	83		33
Rotifera *	>59	>50	13
Tardigrada *	>34	26	19
Nematoda *	>22	28	14
Platyhelminthes	4	2	0
Gastrotricha	5	2	0
Annelida (Oligochaeta)	23	3	0
Mollusca	3 / 4	0	0
Crustacea (terrestrial)	4	0	0
Crustacea (nonmarine)	44	10	14
Insecta (total)	210	35	49
Mallophaga	61	25	34
Diptera	44	2	0
Coleoptera	40	0	0
Collembola	>30	10	10
Arachnida (total)	167	36	29
Araneida	20	0	0
Acarina *	140	36	29
Myriapoda	3	0	0

* Future research will result in large changes due to current lack of sampling coverage and taxonomic uncertainty

Antarctic marine systems have been shown to be rich and diverse, with high levels of endemism in some taxa (e.g. pycnogonids, isopods, bryozoans), although other groups are absent or poorly represented (e.g. reptant decapod crustaceans and balanomorph barnacles) (Dayton 1990, Arntz et al. 1994, Boschi 2000, Clarke & Johnston 2003). The total species list for the Southern Ocean benthos currently numbers over 4100 (see Table 1.3 for major groups of taxa). Most existing studies focus on deep-water habitats, largely of the continental shelf and slope (White 1984, Arntz et al. 1994), and especially in the Weddell Sea (e.g. Voβ 1988, Galeron et al. 1992). Suspension feeders, notably bryozoans, sponges, hydrozoans, ascidians and anthozoans, are strongly represented, as are polychaetes (Clarke & Johnson 2003).

Table 1.3 Species richness and taxonomic diversity of some of the better represented groups of Antarctic benthic taxa (data modified from Clarke & Johnson 2003).

Phylum	Subphylum or class	Order	Estimated species richness	
			Arntz	Clarke & Johnson
Porifera			~300	250
Cnidaria	Medusozoa		~200	186
	Anthozoa		85	86
Priapula			3	3
Arthropoda	Crustacea	Amphipoda	520	496
	Malacrostraca	Isopoda	346	257
		Tanaidacea	50	80
		Decapoda	(19)	13
	Cirripedia		37	50
Chelicerata	Archnida	Acarina		45
	Pycnogonida		>150	175
Nemertea				31
Mollusca	Polyplacophora			<10
	Gastropoda			530
	Bivalvia			110
	Scaphopoda			6
	Cephalopoda			~34
Sipuncula			~15	15
Annelida	Polychaeta		>650	645
Brachyopoda			16	19
Bryozoa			310	322
Echinodermata	Crinoidea		22	28
	Asteroidea			108
	Ophiuroidea			119
	Echinodea		44	49
	Holothuroidea		88	106
Chordata	Urochordata		>130	118
	Vertebrata	Agnatha		2
		Chondrichthyes		8
		Osteichthyes		198

Shallow benthic communities have been less well studied (Arntz et al. 1994). However echinoderms, bryozoans, sponges, cnidarians, malacostracan crustaceans (especially amphipods) and molluscs are well represented (e.g. Jazdzewski et al. 1986, Kirkwood & Burton 1988, Clarke 1992, Gambi et al. 1994, Barnes & De Grave 2001, Jazdzewski et al. 2001, Barnes & Brockington 2003). Echinoderms, in particular *Sterechinus neumayeri* and *Odontaster validus*, are abundant and visually obvious taxa in many very shallow benthic (< 40 m depth) communities (e.g. Beckley & Branch 1992, Gambi et al. 1994, Barnes & Brockington 2003, Bowden 2006, pers. obs.) as are gastropod molluscs (especially *Nacella* spp.) (Shabica 1972, Picken 1985, Beckley & Branch 1992, Davenport & McAllister 1996, Smith & Simpson 2002, Barnes & Brockington 2003). Cryptofauna such as Bryozoa and spirorbid polychaetes also strongly influence community structure at these depths (Barnes & Arnold 2001, Barnes & De Grave 2001, Barnes & Brockington 2003). A brief synopsis of the major shallow water phyla of Southern Ocean benthos is given below.

Phylum Echinodermata

Echinoderms have been collected by almost every biological expedition to the Southern Ocean and are typically large and conspicuous. The shallow benthic echinoderm taxa are predominantly comprised of the asteroids *Odontaster validus,* (Gruzov 1977, Beckley & Branch 1992, Gambi et al. 1994, Barnes & Brockington 2003) and *Anasterias directa* and *A. mawsoni* at Macquarie I. (Smith & Simpson 2002), the echinoid *Sterechinus neumayeri* (Barnes & Brockington 2003) and the holothurians

Cucumaria antarctica and *Psolus antarctica.* (Gambi et al. 1994, Barnes & Brockington 2003, Barnes et al. 2006c).

Phyum Bryozoa

Bryozoans are a relatively well-known group in the Southern Ocean. The fauna is dominated by cheilostomes (Clarke & Johnston 2003). Representatives of this phylum are amongst the few taxa that have been shown previously to survive in the intertidal and very shallow (~3m) sublittoral zones (Barnes & Arnold 2001, Barnes & De Grave 2000, 2001, Barnes & Brockington 2003).

Phylum Annelida

Spirorbid and serpulid polychaetes are highly abundant in the very shallow sublittoral benthos with *Serpula narconensis* colonies of up to 2 m diameter being reported at depths of 8-30 m in Ellis fjord (Vestfold Hills) close to Davis Research Station (Kirkwood & Burton 1988). Twelve species of errant polychaetes have been reported from Terra Nova Bay on the Victoria Land coast at depths of 0.5 – 16 m (Gambi et al. 1994) and seven species from Adelaide Island (Barnes & Brockington 2003).

Phylum Mollusca

Gastropods, especially *Nacella concinna* (Hedgpeth 1969a, Blankley & Grindley 1985, Kirkwood & Burton, 1988, Barnes & Brockington 2003) and *Laevilittorina caliginosa* (Gambi et al. 1994, Jazdzewski et al. 2001, Smith & Simpson 2002), are amongst the most common taxa found in very shallow sub littoral and intertidal assemblages. Bivalves, notably of the genera *Kidderia* and *Lasaea* can also occur in high densities at shallow sub littoral and intertidal sites (Stout & Shabica 1970, Gambi et al. 1994), with densities of ~2000 individuals m^{-2} being reported from intertidal sites at Marion Island (Blankley & Grindley 1985).

Phylum Crustacea

Certain crustacean groups are well represented in shallow benthic communities, notably Amphipoda and Isopoda, (Gruzov 1977, Gambi et al. 1994, Jazdzewski et al. 2001), where they can occur at densities in the order of 10^3 m^{-2} in the immediate sub-littoral zone (Gambi et al. 1994, Jazdzewski et al. 2001).

Phylum Porifera

Of the Antarctic representatives of Porifera, the class Demospongiae is the most speciose (190 species), whereas only 14 species of Calcarea have been recorded from the Antarctic. Glass sponges (Hexactinellida) are also a very important ecological group represented by 29 species in the Southern Ocean (Clarke & Johnston 2003). Barnes et al. (2006c) reported very large specimens (~60 cm tall) of the hexactinellid sponge *Rosella nuda* at very shallow depths in Moraine Fjord, South Georgia. 10 species (of 6 orders) of the class Demospongiae have been reported from the shallow benthos at Adelaide Island (Barnes & Brockington 2003) and 34 species at Ellis Fjord (Kirkwood & Burton 1988).

AIMS OF THE PRESENT STUDY

In the context of the extremely limited knowledge of the intertidal zone at any locality within the sub- or maritime Antarctic regions the broad objective of this study was to undertake a thorough, quantitative analysis and description of the environment and its faunal assemblages at sites across a latitudinal gradient into the Antarctic, using consistent sampling techniques and comparable measures. In order to characterise the Antarctic intertidal environment there was a need to compare communities and environmental conditions experienced across the adjacent terrestrial, intertidal and sublittoral zones, and to commence preliminary investigations of ecophysiological characteristics and life history strategies across a range of taxa. This foundation was based on the prevalent view of the intertidal as, at best, a transient and more stressful habitat available to some members of both the adjacent terrestrial and marine ecosystems.

The four main questions addressed in this thesis are:

1. Is there such a thing as a true Antarctic intertidal community?
2. How does life in the Antarctic intertidal compare with that in the adjacent supralittoral and sublittoral zones?
3. What strategies do taxa utilise to survive in this environment in summer and can macro-biota survive winter conditions in situ?
4. Are any intertidal communities found to exist analogous to those present at lower latitudes?

Chapter 2 – The study area

Chapter 2 – The study area

GENERAL CHARACTERISTICS

The majority of the research presented in this thesis was conducted at the British Antarctic Survey research station at Rothera Point, Adelaide Island, western Antarctic Peninsula (67°34'.5 S, 68°07.0' W Fig. 2.1a) over the austral summers of 2003-2004 and 2004-2005. The environmental data and site descriptions in this chapter appertain to that portion of the research. Site descriptions and environmental characteristics of Falkland Island and Scotia Arc sites are summarised in chapter six. Six sites around Rothera Research station were sampled, two on Rothera point and four on Lagoon Island, located approximately five kilometres west-southwest of the research station (Fig.2.1 b).

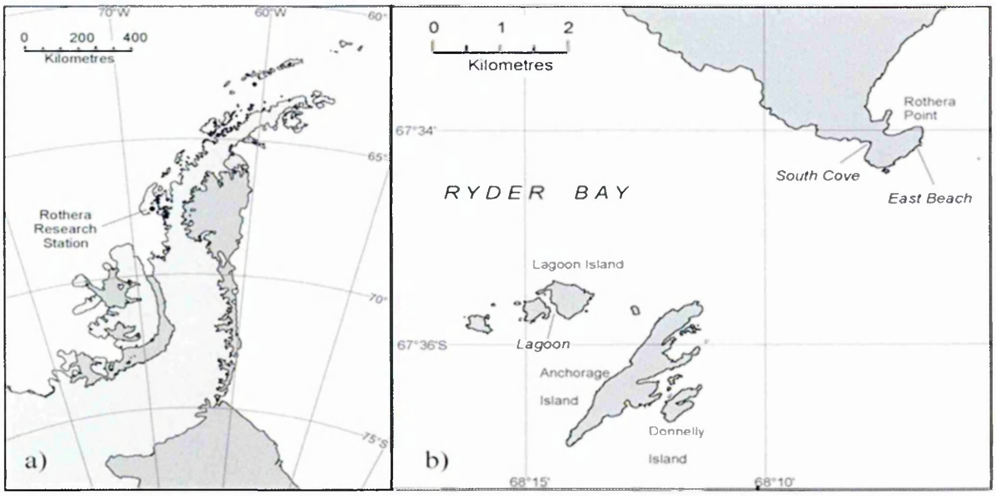


Fig. 2.1. a) Location of Rothera research station on Adelaide Island and b) general location of study sites.

Routine meteorological data including temperature, wind speed and direction have been collected at Rothera since 1976. Long-term monitoring of seawater temperature, salinity and chlorophyll concentrations has been made in Ryder Bay since 1997 under the Rothera Oceanographic Time Series (RaTS) programme. Prior to this study intertidal temperature data have not been published for any Antarctic locality. Intertidal temperatures were measured using Thermochron DS1921G-F5 I-button data loggers (Maxim/Dallas Semiconductors, Sunnyvale, California). Each button logger was sealed inside an empty limpet shell with marine silicone. This in turn was securely fitted inside a drill hole inside a small boulder. The boulders were painted with orange gloss paint to aid recognition when retrieving them (Plate 2.1a). The boulders were returned to the intertidal at low water spring tide on 9th April 2004 (Low water = 0.14m above chart datum). The loggers were programmed to record temperature every 210 minutes, giving a memory capacity of 298 days for data collection. Three boulders were positioned at the extreme low tide, three in the mid tide zone and another three were positioned in the high tide zone. The loggers were retrieved once the ice foot uncovered them in the following summer (Plate 2.1b). The low loggers were recovered on 14th December 2004, mid and high intertidal on 30th December 2004. One boulder from the high intertidal subset was not relocated. The data were downloaded and the loggers redeployed. Due to the combined effects of bad weather and poor tidal conditions this was not possible until 1st February 2005. Loggers were left *in situ* for the following month and were programmed to record temperature every 20 minutes for the duration.

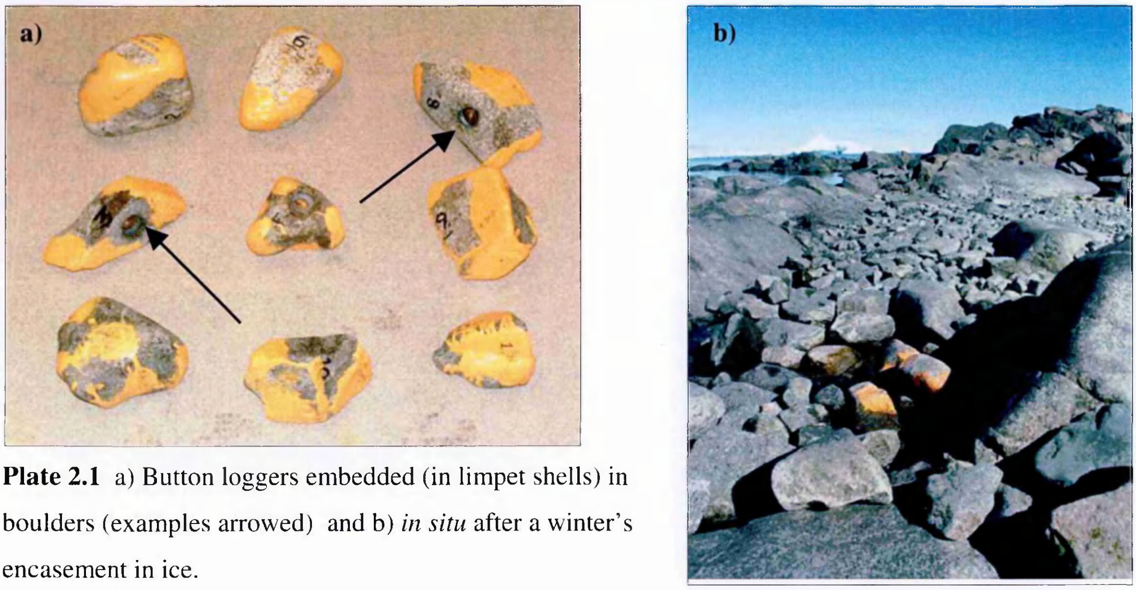


Plate 2.1 a) Button loggers embedded (in limpet shells) in boulders (examples arrowed) and b) *in situ* after a winter's encasement in ice.

ENVIRONMENTAL CONDITIONS

Within the environs of the study sites, and over the study period, mean daily air temperature ranged from –27°C to +5°C whilst annual sublittoral temperatures varied seasonally from around –1.8°C to +1.8°C. Temperatures in the intertidal zone were intermediate between these two extremes with mean daily temperatures in the low intertidal zone remaining relatively constant at around –5°C throughout the winter period (June to October) rising to around +3°C in the summer period (nominally designated as November to March). The high intertidal zone was more variable with mean daily winter temperatures reaching a low of –15°C and summer high of +5°C (Fig. 2.3). Variability over a daily cycle in the high intertidal in the summer (February) of 2005 ranged from ~-1°C to +17°C. This was the maximum variability in temperature recorded over a 24-hour period (see Chapter 3).

The prevailing wind direction was from the north (Fig. 2.4) with wind speeds rarely exceeding 35 knots. The maximum daily wind speed recorded over the study period was 38.25 knots (Beaufort force eight) in July 2004. Both terrestrial and intertidal environments are subject to increased UV-A and UV-B irradiation in the summer months due to the effects of stratospheric ozone depletion (Fig. 2.5).

The tidal regime around Rothera Point is characteristic of a Pacific tidal cycle with a mixed diurnal – semidiurnal duration of between one and four tides over a 24-hour period. Tidal amplitudes range from ~0.25m neap tides to ~2m spring tides (Fig. 2.6) with a maximum duration of exposure to air of around 8 hours. Salinities recorded in the intertidal environment in the summer of 2003 /4 varied from 17 to 40 PSU due to the dual influences of melting ice and concentration due to evaporation. Fast ice encases the intertidal zone for a period of approximately 7-8 months each year and in the ice free summer period ice scouring is frequent. On occasions during the summer fieldwork seasons the intertidal zone at all sites was observed to be impacted by brash ice semi-continuously for periods of between 24 and 48 hours.

In temperate latitudes wave exposure greatly influences the structure of both shallow benthic and intertidal communities and also the morphological characteristics of individual species (e.g. the shape of limpet shells (Branch & Branch 1981) isopods (Hull et al. 2001) or morphometrics of algae (Denny 1988, Norton, 1991, Ruuskanen et al. 1999, Scott et al. 2001)). Whilst wave exposure is an important factor on southern polar shores, the impact of floating ice scouring the environment is probably of greater significance (Barnes 1999). Quantifying the degree of exposure of Antarctic shores is problematic. The metrics used to define the level of exposure in temperate environments are often unsuitable as they are based on the presence of characteristic suites of biological taxa at varying levels of wave exposure (e.g. Ballantine 1961, Southward 1958). These measures are not appropriate for quantifying Antarctic intertidal sites at Adelaide Island, as the environment at this locality is superficially denuded of life. An alternative cartographic method is to use either the Baardseth index (see Ruuskanen et al. 1999) or an effective fetch value (e.g. Håkanson 1981). The Baardseth index generates an exposure value based on the physical characteristics of the shoreline, considering the protection afforded by surrounding landmasses. The index is calculated by placing the centre of a transparent disc of 7.5km diameter over the study site location on the chart (1:50 000 scale). The disc is divided into 40 sectors (each spanning 9^{o} of arc). Sectors containing islands, skerries, portions of mainland or ice piedmont are ignored. The Baardseth index (Baardseth 1970) is the sum of the free sectors, with a value of zero indicating extreme shelter, and 40 ultimate exposure, as this index does not consider the influence of prevailing winds. An alternative method is to use an effective fetch value. The value is based on 15 distance measurements from the study site to the opposite shore. The central radius is put in the prevailing wind direction. The distance ($\chi_i$in km) from the sample site to a shore or an island is measured for every deviation angle γ_i where γ_i equals $\pm 6^{\circ}$, $\pm 12^{\circ}$, $\pm 18^{\circ}$, $\pm 24^{\circ}$, $\pm 30^{\circ}$, $\pm 36^{\circ}$, $\pm 42^{\circ}$. The effective fetch (L_f) may be calculated from the formula $L_f = (\Sigma\chi_i \cos\gamma_i)/(\Sigma\cos\gamma_i)$ (Håkanson 1981). At the study sites around Rothera the prevailing northerly winds determine the areas impacted most severely by floating ice. Therefore this method of quantifying the degree of exposure was used. Rugosity of the substrata was defined using the Wentworth classification scale (Wentworth 1922) (Table 2.1).

Table 2.1 GPS co-ordinates, exposure rating and Wentworth classification for study sites.

	GPS		**Exposure**	**Wentworth**
Study site	**Latitude**	**Longitude**	**index**	**index**
South Cove	67° 34’ 11’’S	68° 08’ 89’’S	0	Boulder/cobble
East Beach	67° 34’ 14’’S	68° 06’ 80’’S	0.004	Boulder/cobble
Lagoon 1	67° 35’ 72’’S	68°14’ 29’’W	0.17	Cobble
Lagoon 2	67° 35’ 69’’S	68°14’ 48’’W	0.08	Boulder/cobble
Lagoon 3	67° 35’ 74’’S	68°15’ 01’’W	1.06	Cobble/pebble
Lagoon 4	67° 35’ 70’’S	68° 15’ 03’’S	0.35	Cobble/pebble

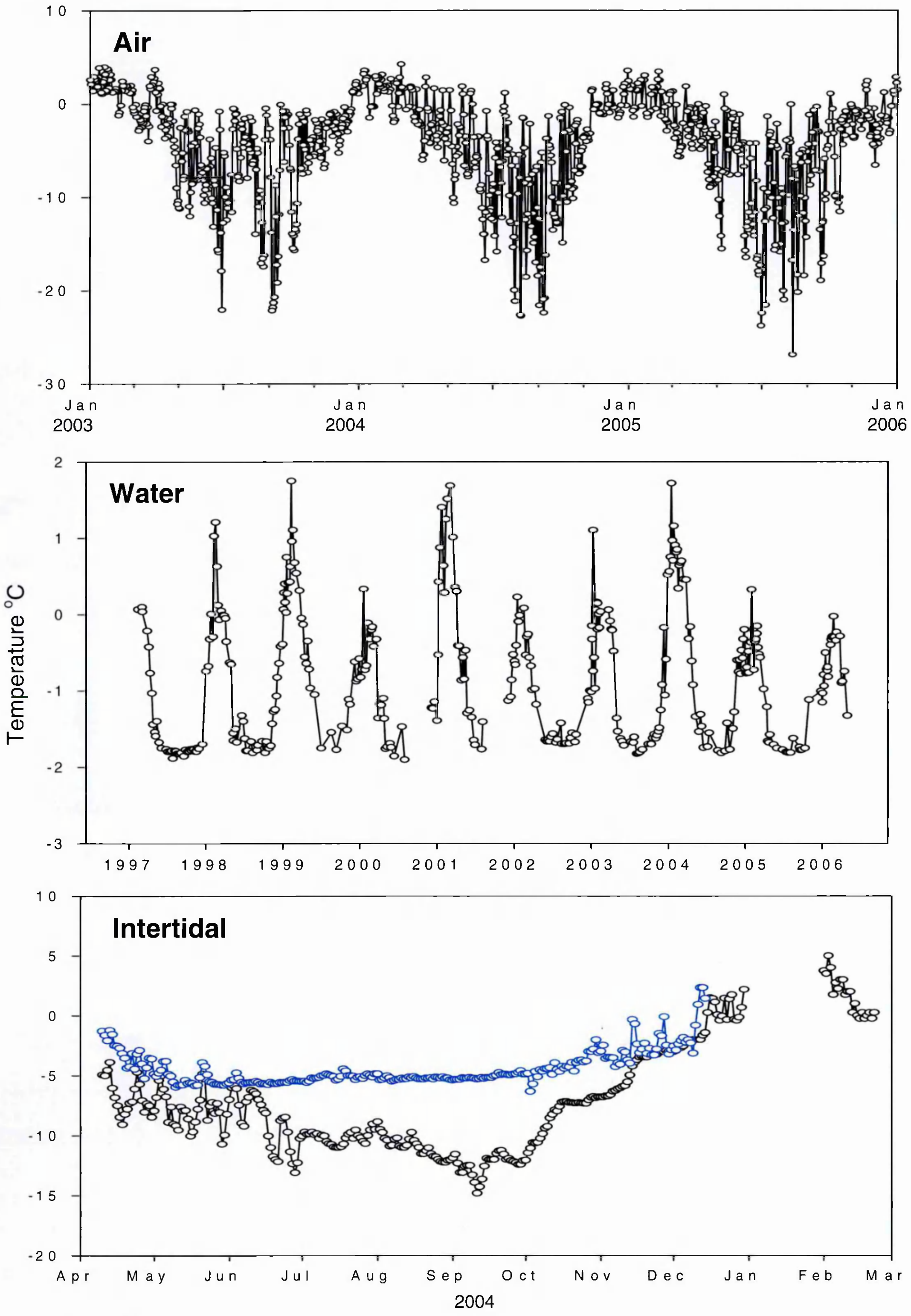


Fig. 2.3. From top: Mean air, seawater and intertidal temperatures (high intertidal open circles, black line; low intertidal blue) recorded at Rothera Research Station. Air temperature data provided by the British Antarctic Survey meteorological department, seawater temperatures (at 15m depth) taken from Rothera oceanographic time series (RaTS) database and intertidal data collected as described above.

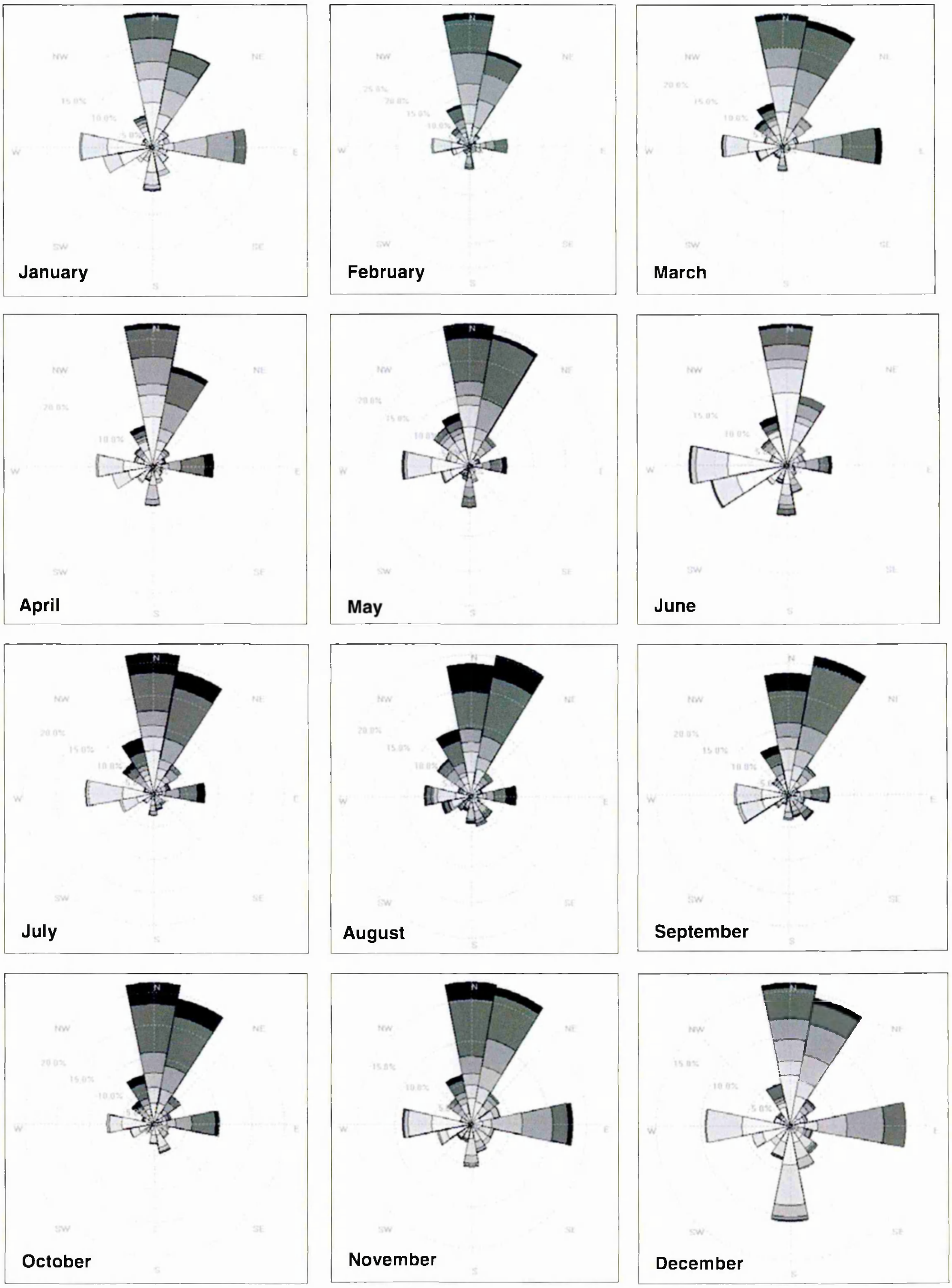


Fig. 2.4. Monthly wind rose plots showing mean monthly wind speeds (in knots) and directions over the study period January 2003- December 2005. Rothera meteorological data. (http://www.antarctica.ac.uk/cgi-bin/metdb-form-2.pl?tabletouse=U_MET.ROTHERA_SYNOP&complex=1&idmask=.....&acct=cmet)

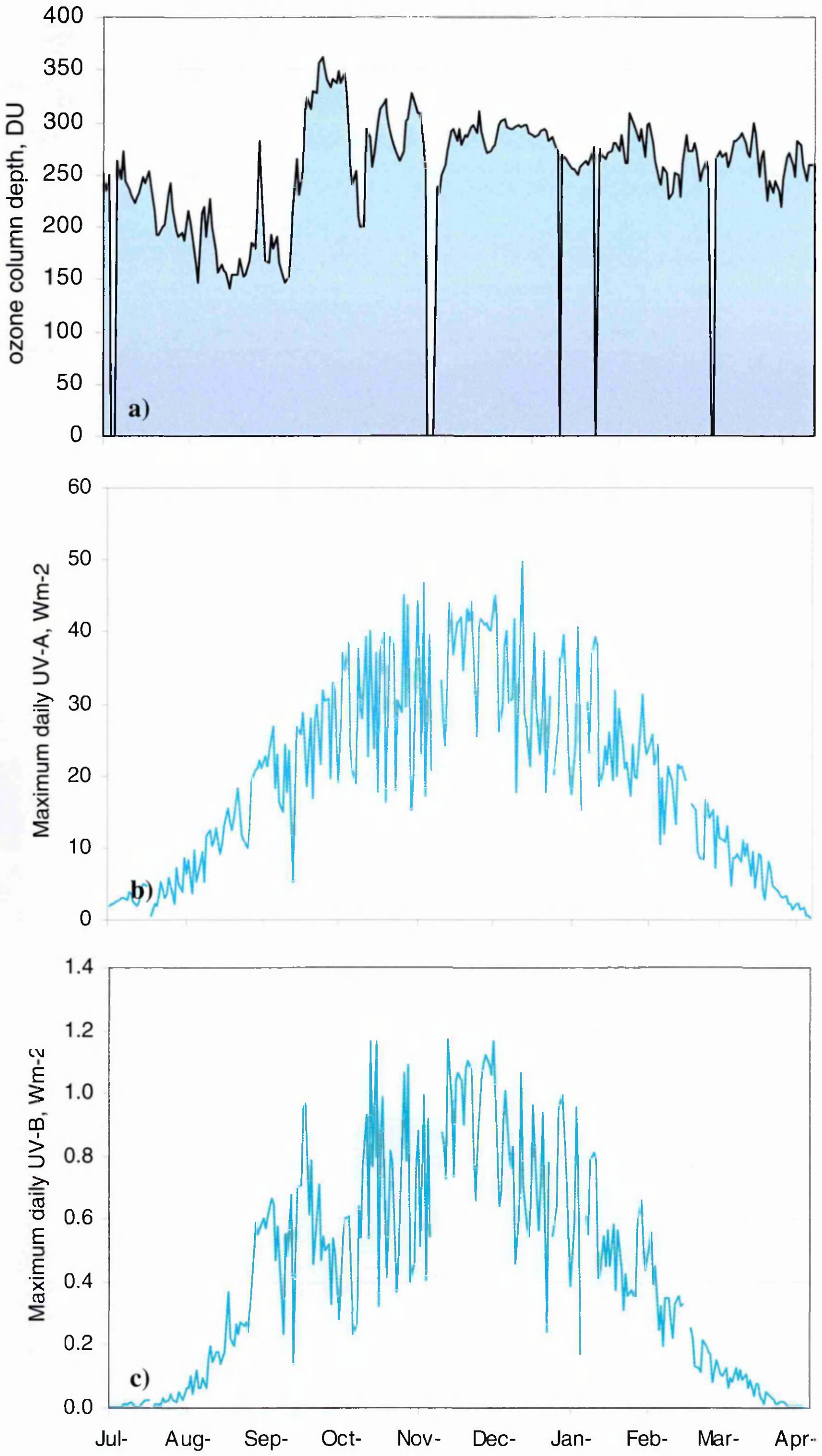


Fig. 2.5. a,b,c. Mean monthly ozone column depth a) and levels of UV-A b) and UV –B c). The data are daily minima (ozone) or maxima (UV intensity). Data courtesy of P.Geissler, B.A.S. unpublished data.

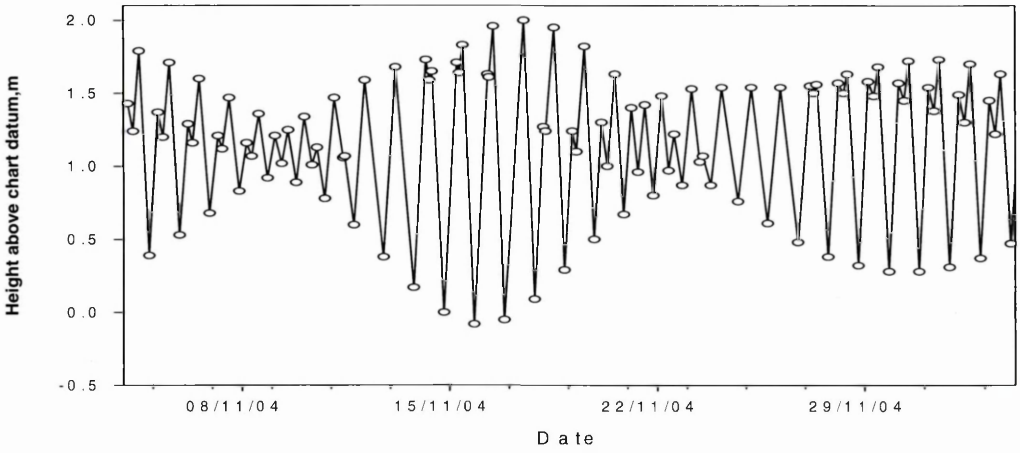


Fig. 2.6. Graphical representation of monthly tidal cycle at Rothera Point; amplitude (spring and neap tides) and mixed diurnal – semidiurnal regime (data generated from POLTIPS software programme, Proudman Oceanographic Laboratory, Prenton, U.K.)

SAMPLING PROTOCOL

Due to the nature of the intertidal environment encountered at sites investigated in this research, a sampling protocol encompassing not only the immediate intertidal surface environment but also the deeper layers within the matrix was adopted. Both the surface and lower layers of rocks and the interstices between them were examined. In the intertidal, rocks within each quadrat were checked for fauna until either no more animals were found, bedrock was encountered or the rocks were submerged and so at a level equivalent to the immediate subtidal (Fig. 2.7).

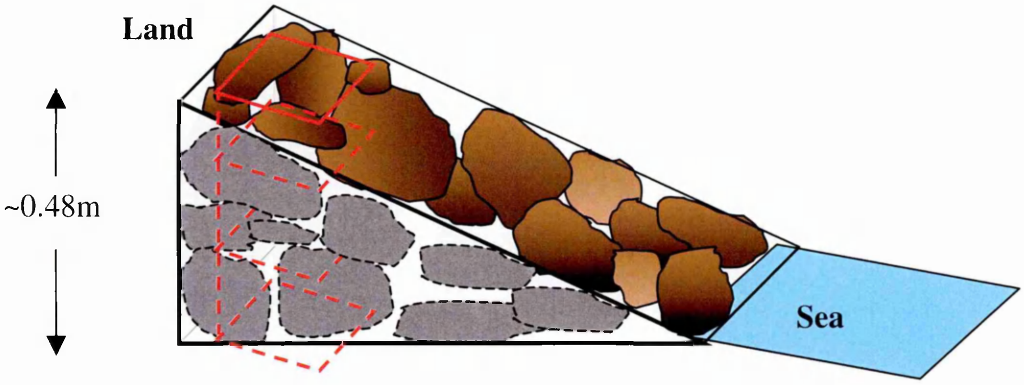


Fig. 2.7. Schematic diagram of sampling protocol with depth through the cobble matrix.

SITE DESCRIPTIONS

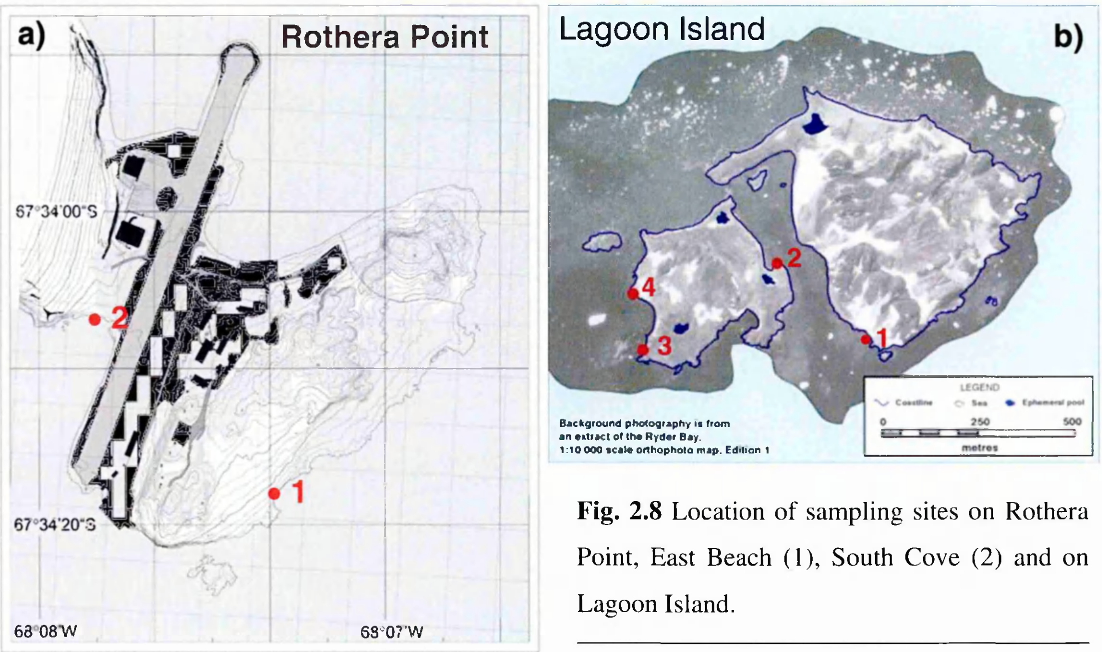
The sites described in this chapter are those investigated in the three environmental studies detailed in Chapters 3, 4 and parts of 6. Taxa for the cold tolerance study (Chapter 5) were collected on an *ad hoc* basis from locations around Rothera Point, the majority from South Cove. The locations were selected balancing the need for a range of sites at differing localities, over as wide an area as possible and practical constraints of accessibility and environmental conditions (primarily the presence of the icefoot) at the start of the study period. The intertidal environment in this area has few visually obvious clues as to the presence or absence of fauna so no conscious bias influenced the choice of sampling point within each site. Generally specific points were chosen for pragmatic reasons such as the presence / absence of elephant seals or brash ice. The timing and amplitude of spring tides meant that only three quadrats could be thoroughly sampled before re-immersion.

Sites were located East Beach (Fig. 2.8 a, site 1) and at the windsock end of South Cove (Fig. 2.8a, site 2) as these were accessible in all but the most severe conditions. Four sites on Lagoon Island were also chosen as they were free of ice at the start of the study (Fig. 2.8b, Plate 2.2 c to e). GPS co-ordinates and physical characteristics are given in Table 2.1.

South Cove

The substratum of the study site at South Cove comprised mainly unconsolidated cobbles (64 to 256mm) with some boulders (>256mm) and areas of bedrock (Plate 2.2a). The orientation of South Cove protects this site from the prevailing winds with an exposure index of 0. However brash ice cover of 95 to 100%

for a duration of 24 to 48 hours was observed on several occasions over the study period (Plate 2.2g) due to strong southerly winds.



Background photography is from an extract of the Ryder Bay. 1:10 000 scale orthophoto map. Edition 1

Fig. 2.8 Location of sampling sites on Rothera Point, East Beach (1), South Cove (2) and on Lagoon Island.

East Beach

The sample points at East Beach were characterised by more compacted cobble pavements and areas of unconsolidated cobbles interspersed with boulders on bedrock (Plate 2.2b). The exposure index here for the prevailing northerly wind conditions was slightly higher than at South Cove (0.004). However the exposure index when the wind direction is north- easterly is 10.4. Approximately north- easterly winds are also frequent (see Fig. 2.4). This resulted in brash ice and small bergs impacting the intertidal zone at this site more frequently and persisting for longer durations than at South Cove.

Lagoon Island

Sites on Lagoon Island varied from very compacted cobble "pavements" with almost no biogenic sediments within the matrix (Site 1, Plate 2.2c) to predominantly pebble environments with intermediate levels of organic matter present (Site 4, Plate 2.2f). These sites were all more exposed than those on Rothera Point however brash ice was observed less frequently, although this may be due to the fact that observations could not be made as frequently as at the other two sites.

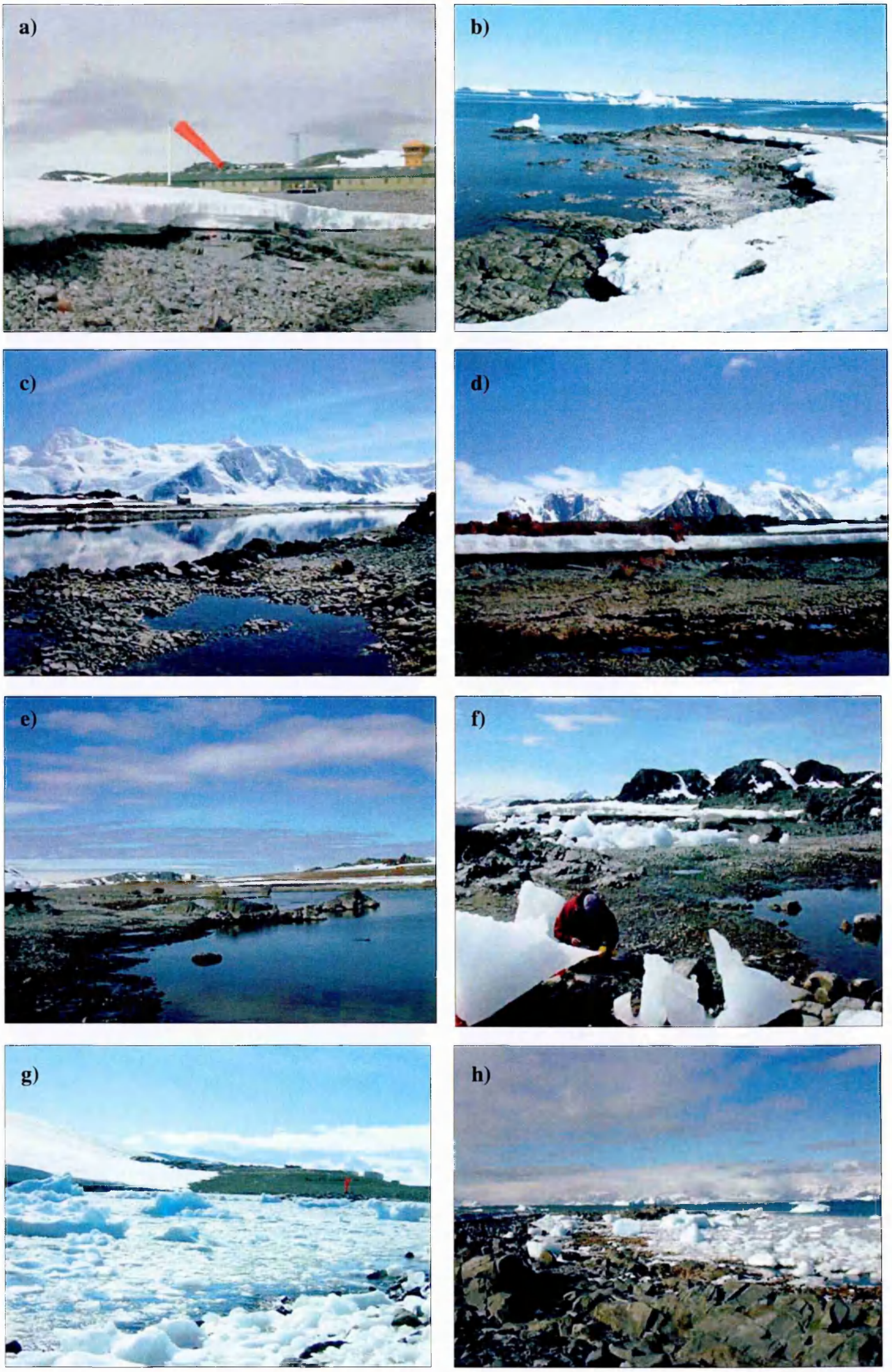


Plate 2.2 Sampling sites at South cove a), East Beach b), Lagoon Island sites 1 c), 2 d), 3 e) and 4 f). Images g) and h) show typical levels of brash ice and small bergs in the intertidal environment at South Cove g) and East Beach h).

Chapter 3 – Communities across the land - sea interface

[The data in this chapter are also presented in: Waller C.L., Barnes D.K.A., Convey P. (2006) Ecological contrasts across an Antarctic land-sea interface. Austral Ecology **31**: 656-666]

Chapter 3 – Communities across the land – sea interface

INTRODUCTION

Adjacent terrestrial and marine ecosystems contrast sharply throughout the global coastline, but at polar latitudes both similarities and differences are particularly striking. Organisms on land and in the sea both experience extreme and chronic low temperatures, varying periods of ice and /or snow cover and, on an annual timescale, the maximum possible variation in light climate. While the final of these points applies equally to both polar regions, at comparable latitudes the first two reach greater and more prolonged extremes in the Antarctic than the Arctic (Dayton 1990, Convey 1996a, Danks 1999) such that virtually all of the terrestrial environments of the Antarctic continent, and much of the surrounding ocean, have no close comparisons in the Arctic.

Antarctic marine life is rich and diverse, at species through to phylum levels, (see Arntz et al. 1994, Brey et al. 1994, Clarke & Johnston 2003) with high levels of endemism (Arntz et al. 1997), in contrast with the small pockets of seasonally ice- or snow-free land, which are populated by depauperate communities including only a few higher taxa, such as mites, collembolans, nematodes and tardigrades (Bergstrom & Chown 1999, Convey 2001a, Convey & McInnes 2005). Marine species experience only tiny fluctuations in temperature and other factors such as salinity (see Clarke et al. 1988), are typically highly stenothermal (Pörtner et al. 2001, Peck 2002) and generally face relatively small seasonal changes in energetic demand (Lehtonen 1996, Fraser et al. 2002). Virtually the reverse is true for terrestrial habitats, which may experience 20^0C or greater change in temperature in a day, and up to 80-100°C variation over the annual cycle, often including transgressions of the 0°C freezing boundary (Smith 1988a, Convey 1996b, Peck et al. 2006). Species here are faced with rapid and often unpredictable alternation between periods of torpor and activity (Burn 1984, Worland & Convey 2001).

In comparison with the lower latitude environments that are inevitably most familiar, Antarctic marine and terrestrial habitats appear to illustrate one end point of the extremes available on the planet. However, to date most polar ecologists have paid little attention to the boundary or interface between the two. Superficial consideration quickly suggests that the intertidal zone has the potential to suffer from the worst of the conditions already described above. Furthermore, organisms living in the intertidal may experience salinity as low as 12 PSU (‰) due to freshwater runoff, possibly even lower if submerged in a melt stream, air temperatures which may vary by 20°C during exposure in the tidal cycle, and the devastating disturbance caused by ice scour in summer and ice encasement in winter (Barnes 1999, Gutt 2001, Brown et al. 2004).

Both Antarctic marine and terrestrial ecosystems have received considerable but separate study, at least in the vicinity of major (mostly coastal) research stations. A further contrast that is apparent between polar and non-polar environments lies in the level of study and knowledge of the nature (physical and biological characteristics) of the intertidal zone. Considering its extent (estimated at approximately 356,000km worldwide (CIA world factbook)) the intertidal zone has been intensively studied on a global scale. However, it remains virtually unknown south of ~60°S. To date, no Antarctic studies have taken advantage of the potential of applying a simultaneous comparative approach even across the better-known marine and terrestrial environments. Indeed, Peck et al. (2006), in a review of the influence of differing patterns and intensities of environmental variables, are the first to have attempted a trans-environmental synthesis of existing Antarctic data across the full gradient through terrestrial, intertidal and marine environments.

The composition, structure, life history, ecophysiological strategies and dynamics of terrestrial plant and animal communities have been studied in some detail across the sub- and maritime Antarctic region between 50° and 72°S (e.g. Gressitt 1970, Block 1984, Burn 1984, Smith 1984, Cannon & Block 1988, Convey 1996b, Chown et al. 1998, Bergstrom & Chown 1999, Worland & Convey 2001). Furthermore, understanding of terrestrial biological responses to contemporary climate change processes in these communities is advancing rapidly (Fowbert & Smith 1994, Day et al. 1999, Convey et al. 2002, Convey 2003, Convey et al. 2003, Chown & Convey in press b). Marine studies have concentrated more on peninsular and continental Antarctica (see Arntz et al. 1994 for review), with less attention paid to the sub-Antarctic. However, even in these regions, the little that is known of intertidal communities has predominantly been gained from brief summer observations on the sub- and maritime Antarctic islands (de Villiers 1976, Blankley & Grindley 1985, Barnes et al. 1996, Chown 1996, Pugh & Davenport, 1997). Even these qualitative observations of species present have been completed for probably only <0.1% of Antarctica's continental intertidal zone south of ~60°S, with most information available from a single site, namely the vicinity of Palmer Research Station, Anvers Island (Hedgpeth 1969a, Stockton 1973, Stout & Shabica 1970).

A single quantitative comparative study of intertidal and shallow sublittoral patterns has been undertaken to date, at Rothera Research Station, Adelaide Island (Barnes &

Brockington 2003). Other than this study, and although based on few data, the prevalent view is that, south of the sub-Antarctic islands and shores, the intertidal is denuded of life due to the general severity of the environment, and that such macrobiota as are found at the interface between the land and sea are characterised by small transient or opportunistic marine species, such as the limpet *Nacella concinna* (Shabica 1971, 1972) and more rarely by a small number of rapidly maturing bryozoans (Barnes et al. 1996), and occasional suporalittoral or intertidal springtails and enchytraeid worms (Convey et al. 2000b).

This chapter describes and compares fundamental features of faunal communities present in the immediate subtidal, intertidal and terrestrial environments at sites in the vicinity of Rothera Research Station, Adelaide Island, Antarctica (67°34'20"S, 68°07'50"W, Fig. 3.1). The primary hypotheses being tested are that the marine environment will have considerably higher species richness, biomass and abundance than the terrestrial, and that both will be greater than that found in the intertidal. A comparative study of ages and sizes of individuals in the intertidal and subtidal zones was conducted, to test the hypothesis that animals in a more stressed environment (intertidal) would be smaller and shorter lived.

MATERIALS AND METHODS

Study Sites.

Three study sites were selected at East Beach, South Cove and Lagoon Island (Lagoon site 3) in the vicinity of Rothera Research Station, Rothera Point (Fig. 3.1) and are described in detail in the preceding chapter. Sampling was undertaken in the intertidal and shallow subtidal (6m) over several three-day periods in the austral summers (December - January) of 2000-01 and 2003-04. Samples were collected at the mid-tide level and 6m depth in 2001 and the low water spring tide level (LWS) and 6m depth in 2004. Terrestrial sites were sampled as near as practicable above and adjacent to each intertidal site. Further nearshore terrestrial sites were also sampled in order to reflect the variety of different habitats typically found in this area.

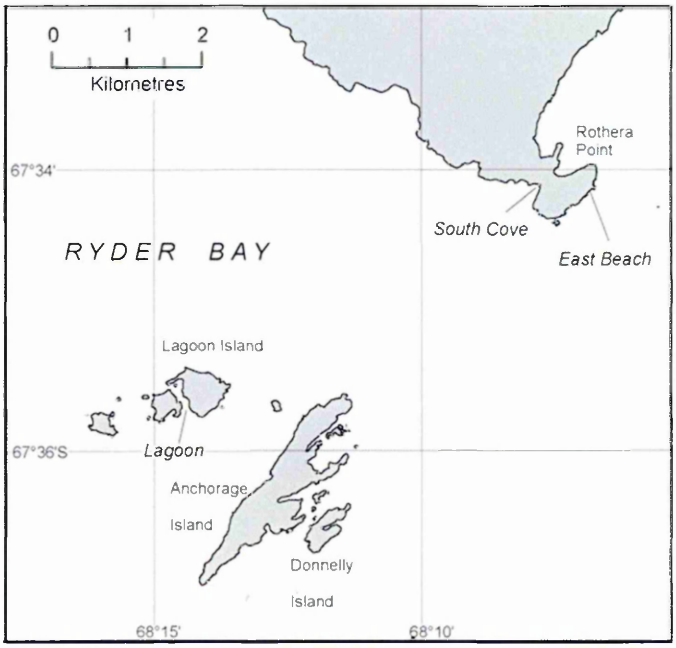


Fig 3.1. Locations of sampling sites at South Cove, East Beach and Lagoon Island (in italics) in the vicinity of Rothera Research station.

The marine environment was similar across sites. Each location experienced very little variation in salinity, a seasonal range in sea temperature from ~-1.9°C to +1.9°C, and sea surface freezing to form winter fast ice for a period of several months. The formation of anchor ice was rare. Ice scour was common at 6m (see Brown et al. 2004) and hyposaline lens formation in shallow water has occasionally been observed in previous studies (Barnes & Brockington 2003). The substratum in the subtidal was characterised by boulders, cobbles and pebbles interspersed with fine silt at all sites. The intertidal environment, which is typical for this location, comprised compacted cobble "pavements", interspersed with boulders and pebbles. The intertidal experiences a tidal range of ~0.25 to ~2.0m (neap/spring tides) and a mixed diurnal/semidiurnal Pacific tidal cycle as described in chapter 2. Where winter fast ice connects to the shore an ice foot builds up and can encase the intertidal zone for ~6 months of the year. The substratum of the terrestrial zone was essentially similar to that in the marine, being boulders and cobbles on bedrock and sediment. In many coastal locations in Marguerite Bay these terrestrial habitats lie on "raised beaches", indicative of previous sea levels, and support a variety of biological habitats, including patches of moss, algae or lichen and frost-sorted soil polygons (Convey & Smith 1997). Like the sea in this region, terrestrial habitats are overlain by snow and ice for ~ 8 months or more per annum.

Sampling protocol.

Three replicate 0.25m^2 quadrats were randomly placed at each of the three subtidal and intertidal sites. The size of quadrat and replication were selected both on the pragmatic basis of giving the ability to complete both subtidal (SCUBA) and intertidal surveys within practical time constraints, and providing an acceptable estimate of overall species richness. Both the surface and lower layers of rocks and the interstices between them were examined. In the intertidal, rocks within each quadrat were checked for fauna until either no more animals were found, bedrock was encountered or the rocks were submerged and so at a level equivalent to the immediate subtidal. Subtidal rocks were examined until bedrock was reached or no further animals were found. All macrofauna (> 1 mm in size) were collected and identified to the lowest possible taxonomic levels. Non-encrusting animals were collected, counted and dried (60°C for 24 hours), and dry-mass (DM) values measured. Encrusting fauna were similarly collected (after removal of rocks to the laboratory), and abundance and dry-mass values were estimated by scaling up (to m^2) measurements of those animals present on 5 randomly selected rocks from each quadrat. Terrestrial samples consisted of very high numbers of small organisms, so samples from each quadrat were also sub-sampled and the data scaled up to represent unit area. As these samples (consisting of moss, *Prasiola* (alga), lichen and/or soil) of ~ 50 cm^2 were collected, the percentage cover of each habitat in each $0.25m^2$ area was estimated. Animals were then extracted using a Tullgren extraction (cf. Convey & Smith 1997) and assigned to the lowest taxonomic level possible. Sizes of individuals of 6 species present in two contiguous zones (sub- and intertidal) were measured to the nearest 0.1mm for a minimum of 30 randomly selected individuals per zone. Ages of cheilostome bryozoans were estimated by counting growth rings present and counting the number of colonies in each age group on 45 randomly selected rocks from each zone (15 from each site).

Data analyses.

Data were tested to check compliance with assumptions for ANOVA and transformed ($\log_{10}$) when appropriate. Within and between zone variability in species richness, individual abundance and biomass were then compared using GLM ANOVA. Where significant differences were present *post hoc* Tukey tests were performed to ascertain which variables caused these differences. Intertidal and subtidal communities similarities were compared using nMDS ordination on Bray Curtis similarity matrices of square root transformed data (Clarke & Warwick 2001). Mean within-species size comparisons across zones were made using Student's T tests. Intertidal and subtidal data obtained in this study were also compared with results obtained from the same study area in 1999 (Barnes & Brockington 2003).

RESULTS

Environmental variability.

In the intertidal zone, water salinity varied markedly, from 17-40 PSU, indicating the twin influences of dilution from freshwater runoff and concentration through evaporation. In the adjacent subtidal zone salinity varied little from ~34 PSU. Both the subtidal and intertidal study sites were covered by fast ice (of highly variable thickness) for much of the winter (approximately 8 months), and both were impacted by floating ice during the summer (as described in chapter 2). On at least four occasions in early 2004 small pieces of (brash) ice covered the intertidal study sites for between 12 and 24hrs. Some scouring of the intertidal zone was observed on a weekly basis and on two occasions small icebergs were observed to impact both intertidal and subtidal study areas for > 48 hours. During the 2003-4 study period air temperatures at the intertidal and terrestrial study sites on Adelaide Island ranged between 2 and 12°C over a 12 hour period. On the same timescale water temperatures in the intertidal ranged from 1.9 to 3.3°C (Fig. 3.2a). Data recorded by *in situ* temperature loggers during February 2005 showed even greater variability with an intertidal range of 18 degrees (-1°C to 17°C) over a 6 hour period (Fig. 3.2b). In the immediately adjacent subtidal zone the sea temperature was more constant, varying only between -1.3 and +0.3°C over 10 days.

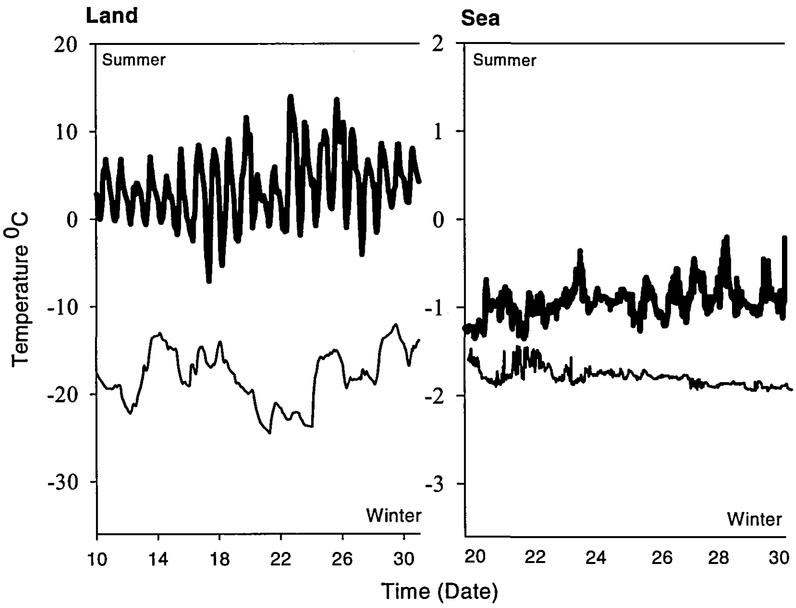


Fig. 3.2a. Maritime Antarctic variation in terrestrial and marine temperature regimes during summer (December) and winter (July). Data show comparisons of temperature variation in summer (thick upper line) and winter (thin lower line) over several days in soil and marine environments (sea at 20m). (Data from Peck et al. 2006, with permission)

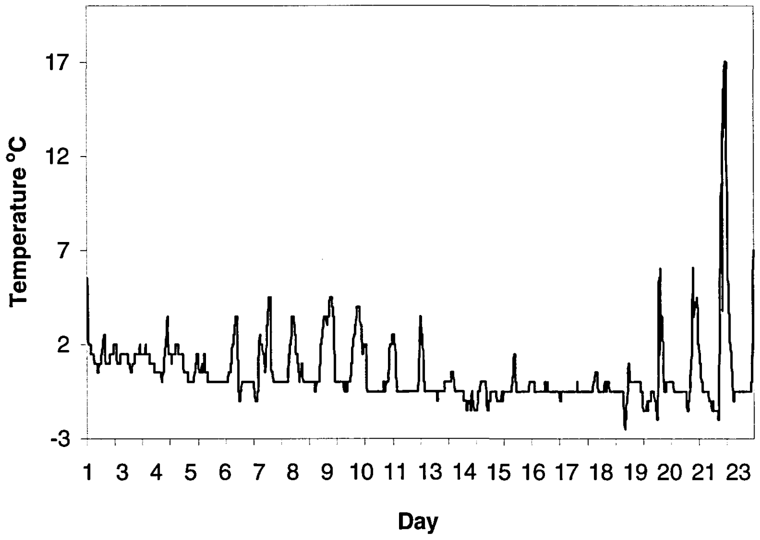


Fig. 3.2b. Maximum variation in summer intertidal temperatures recorded during Feb 2005 at mid tidal level. The maxima are mainly associated with low waters, i.e. when exposed to air temperatures.

Richness patterns.

Species richness differences at the land-sea interface obtained in the current study are summarised in Figure 3.3 showing the extent of temporal and spatial variability. The relative similarities between intertidal and sublittoral sites are also highlighted in the nMDS ordination (Fig. 3.4). While caution must be taken in considering richness measures from relatively small sample sizes, species accumulation curves for sub tidal and intertidal replicates suggest that that the majority of species detectable were sampled (Fig. 3.5). Taxa found in each zone are listed in Table 3.1.

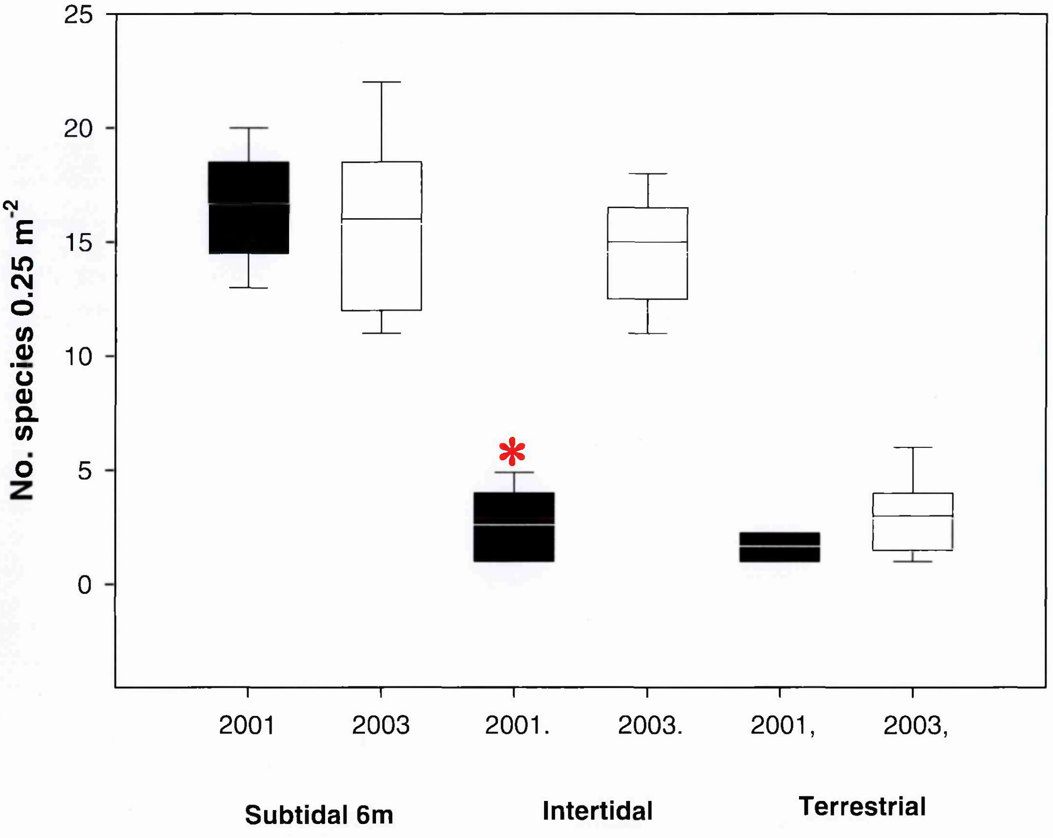


Fig. 3.3. Box and whisker plot displaying mean, 25th and 75th percentiles and maximum and minimum number of species found in the subtidal, intertidal and terrestrial zones in 2001 (black) and 2003 (white) summers. Note that 2001 intertidal samples (highlighted by the red asterisk) were collected at mid tide height ~ 0.8m above chart datum whereas 2003 samples were collected from low water spring tide level, ~0.3m above chart datum.

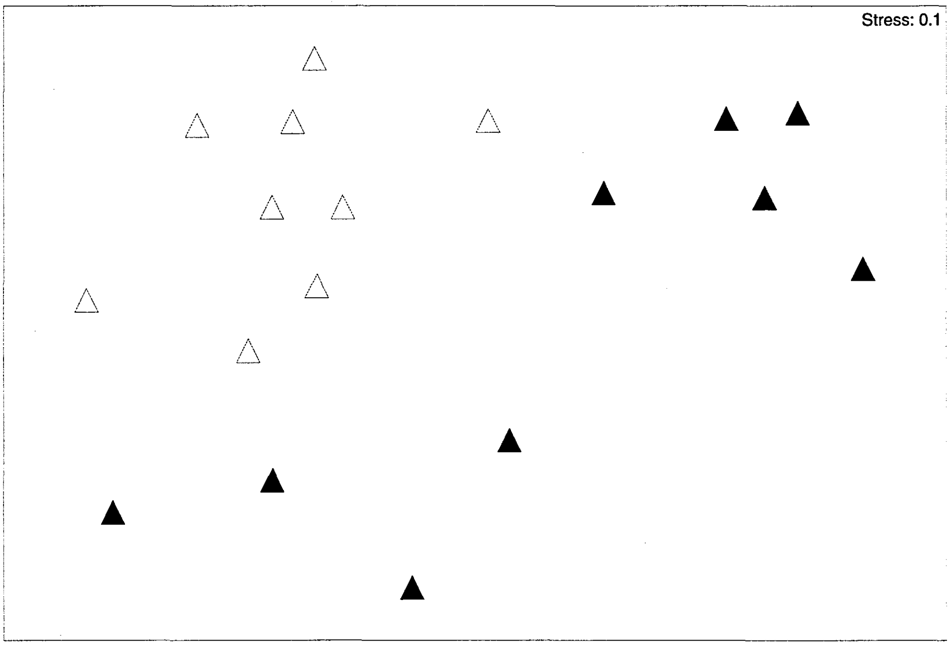


Fig. 3.4. nMDS ordination of community composition in summer 2003-4 in the intertidal and subtidal zones. Bray Curtis similarities are calculated on square root transformed data of abundances of species. △ denote intertidal samples and ▲ sublittoral (6m) sampling points.

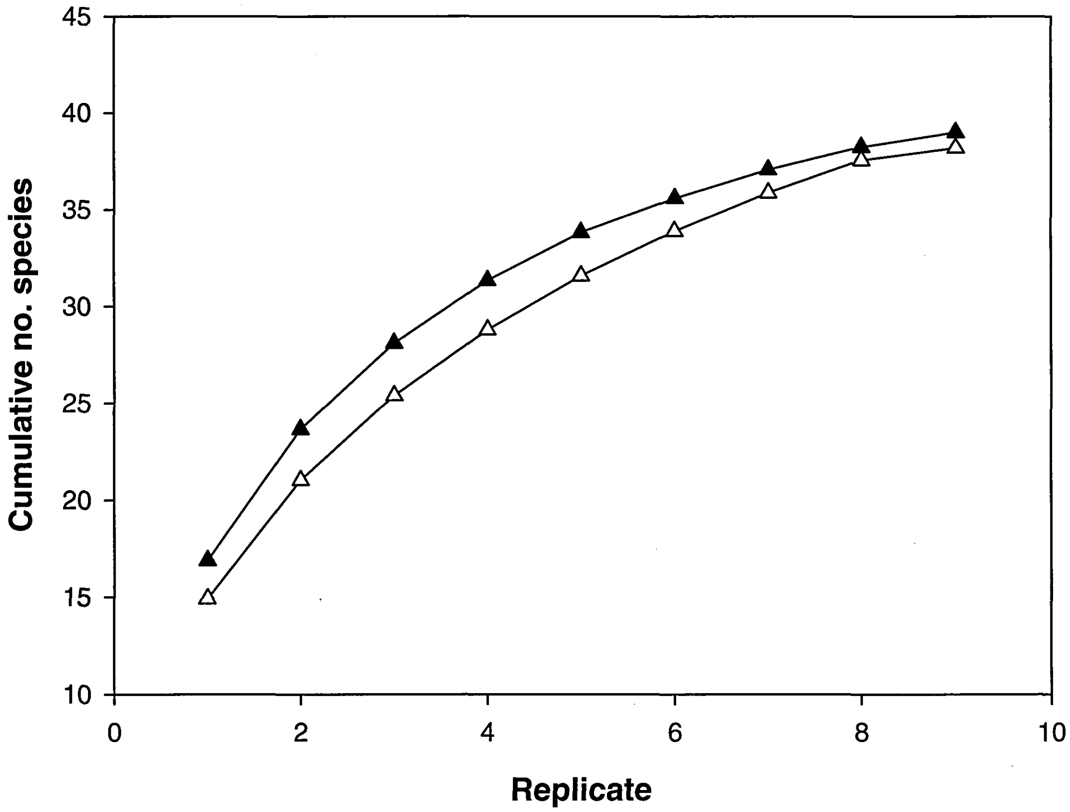


Fig. 3.5. Species accumulation curves for subtidal (▲) and intertidal (△) samples, 2003-4.

Table 3.1. Full taxon list for 2003-2004 samples with indication (•) of zone(s) in which each was recorded.

Class	Family/Genus- species	Subtidal	Intertidal	Terrestrial
Gastropoda	*Nacella concinna*	•	•	
	Margarella antarctica	•	•	
	Laevilittorina caliginosa	•	•	
	Onoba luvqueti	•	•	
	? Guyvalvoria sp.		•	
	Eubranchus sp.	•	•	
Bivalvia	*Cyamiomactra laminifera*		•	
	Mysella charcoti	•		
	Adacnarca nitens	•		
	Yoldia eightsi	•		
Echinoidea	*Sterechinus neumayeri*	•	•	
Asteroidea	*Odontaster validus*	•		
Anthozoa	Burrowing anemone		•	
Polyplacophora	chiton	•		
Malacostraca	*Prostebbingia gracilis*		•	
	Stenothoidae sp.	•	•	
	Prostebbingia brevicornis	•		
	Cheirimendon femoratus	•	•	
	Paramoera walkeri	•		
	Hippomedon kergueleni	•		
	Gondogeneia antarctica	•	•	
	Paraceradocus gibber	•		
	Cymodocella sp.	•	•	
	Notasellus sarsi		•	
	Munna antarctica	•	•	
Copepoda	*Tigriopus angulatus*		•	
Pisces	*Harpagifer antarcticus*	•		
	Artedidraconidae sp. (juvenile)		•	
Polychaeta	*Barrukia cristata*	•	•	
	Terrebellidae	•	•	
	Capitella sp.	•		
	Aglaophamus trissophyllus	•		
	Protolaeospira stalagmia	•		
	Protolaeospira levinsi	•	•	
	Protolaeospira pedalis	•	•	
	Serpulidae	•		
Pycnogona	*Achelia communis*	•	•	
Anopla	*Antarctonemertes validum*	•	•	
	Parbolasia sp.	•	•	
	Parborlasia corrugata	•		
Hydrozoa	*Gonionemus* sp.	•	•	
	Tubularia sp	•	•	
Gymnolaemata	*Celleporella antarctica*	•	•	
	Celleporella bougainvillei	•	•	
	Hippadanella inerma	•	•	
	Aimulosia antarctica	•	•	
	Arachnopusia inchoata	•	•	
	Micropora brevissima	•		
	Fenestrulina rugula	•	•	
	Ellisina antarctica	•	•	
	Beania erecta	•		
	Inversiula nutrix	•	•	
Stenolaemata	*Tubulipora* sp.	•	•	
	Idmidronea sp.		•	
	Discoporalla sp.	•	•	
Arachnida	*Rhombognathus gressitti*		•	
	Alaskozetes antarcticus			•
	Halozetes belgicae			•
	Gamasellus racovitzai		•	•
	Stereotydeus villosus			•
	Rhagidia gerlachei			•
	Nanorchestes sp.			•
	Eupodes sp.			•
Entognathous Hexapoda	*Cryptopygus antarcticus*		•	•
	Friesea grisea			•

The shallow subtidal study areas were taxonomically rich at both species and class level. Spatial patchiness at quadrat or site level did not contribute significantly to overall variability at either species or class level - in ANOVAs performed on data at species and class level, zone was the only significant variable (Tables 3.2a and 3.2b). Thus zonal differences in richness could not be attributed simply to local spatial variability. The zonal differences were driven by large differences in species richness between the terrestrial and both the subtidal and intertidal zones (Tukey P<0.001 in both cases).

Table 3. 2 a. Results of 2 way ANOVA for variability in species richness by site and zone in 2003-4 samples.

Source	**DF**	**Adj MS**	**F**	**P**
Zone	2	165.139	3.54	<0.001
Site	2	8.302	0.32	0.729
Zone*site	4	0.2897	2.01	0.136
Error	18	0.1439		

Table 3.2b. Results of 2 way ANOVA for variability in richness at class level by site and zone in 2003-4 samples.

Source	**DF**	**Adj MS**	**F**	**P**
Zone	2	1.229	204.07	<0.001
Site	8	0.0021	0.89	0.712
Zone*site	4	0.0393	6.53	0.002
Error	14	0.0060		

A maximum of twenty-two species in 11 classes were recorded in 0.25m^2 in the subtidal zone and 18 species in 8 classes in the intertidal during the 2003-4 summer.

Post hoc Tukey tests showed that species richness in the subtidal zone at both these taxonomic levels was not significantly different to that found in the intertidal zone (P=0.869 & P=0.836, respectively). Trend visualization (nMDS, Fig 3.4) showed the assemblages of the intertidal study sites to be more similar to each other than to those in the subtidal. The nMDS also revealed assemblages of the subtidal sites to have considerably more variability than those in the intertidal. The biota of the terrestrial zone sharply contrasted with those of the intertidal and subtidal, comprising a maximum of 6 species from 2 classes. Whilst there was considerable overlap between the classes and species found in the intertidal and subtidal zones, there were no taxa in common between either of these zones and the terrestrial zone. In contrast, previous sampling three years earlier, in 2001, found individuals of two species (the mite *Gamasellus racovitzai* and the springtail *Cryptopygus antarcticus*) at both mid tide level and in the terrestrial zone, while other terrestrial species (particularly oribatid mites) have previously been noted to be able to survive submersion and exposure to marine conditions (Schenker 1986, Convey et al. 2000). In the 2001/2 samples, intertidal and terrestrial species richness levels were more comparable (means of 2.6 and 1.6 species $0.25m^{-2}$ respectively).

Biomass.

Total biomass did not significantly differ between sites (Table 3.3) but there was a significant difference between subtidal and terrestrial zones (Tukey P=0.042). Thus, as with variability in richness, the lack of site differences suggests that between zone variability was not influenced along purely spatial grounds.

Data obtained in 2003/4 indicated comprised a mean faunal biomass of 4.1 g m^{-2} in the terrestrial zone, which was an order of magnitude lower than that found in the intertidal (39.1 g m^{-2}) or in the subtidal (63.5 g m^{-2}). Subtidal biomass values obtained in 2001/2 were considerably higher than those of 2003/4 (295 g m^{-2} vs 63 g m^{-2} respectively) (Fig. 3.6). Although the biomass per unit area of terrestrial communities was an order of magnitude lower than that of the intertidal or subtidal, the mass range of individual organisms was more extreme. The mean dry mass of individual terrestrial animals was ~0.012 mg, compared with 49.2 mg for intertidal animals and 407 mg for those in the subtidal, a range of 4 orders of magnitude.

Table 3.3 Results of 2 way ANOVA for variability in overall faunal biomass by site and zone for 2003-4 data.

Source	DF	Adj MS	F	P
Zone	2	8.984	7.41	0.004
Site	2	1.335	1.10	0.354
Zone*site	4	2.732	2.25	0.104
Error	18	1.213		

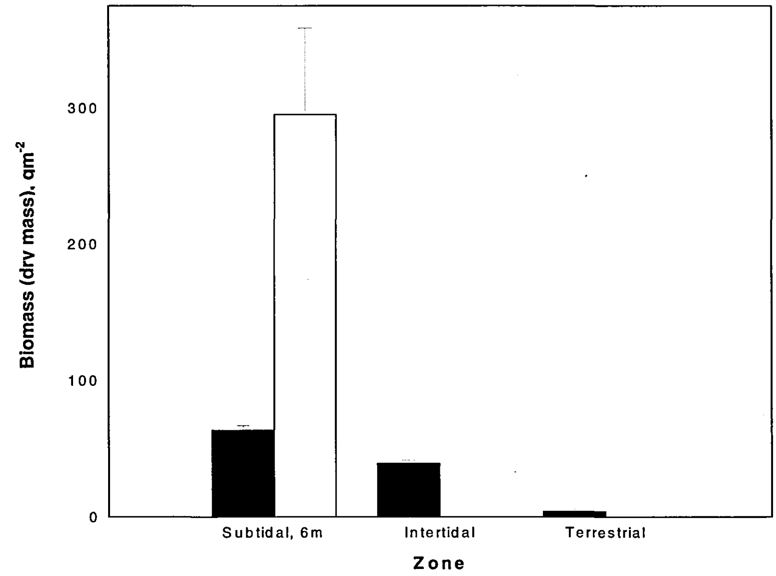


Fig 3.6. Mean faunal biomass (+SE) of both encrusting and non encrusting species from subtidal, intertidal and terrestrial zones in 2003 (black) and subtidal zone in 2001 (white).

Abundance.

Although in the terrestrial environment individuals and communities comprised little biomass, population densities were very high, with a mean of 328,978 individuals m^{-2} obtained in 2003/4. Subtidal abundance was also high (11,403 individuals m^{-2}), an order of magnitude less than in the terrestrial zone but considerably greater than in the intertidal zone (2,021 individuals m^{-2}) (Fig.3.7). Despite such considerable zonal differences, there were also large and significant inter-site differences (Table 3.4). The intertidal also showed temporal variability, with two orders of magnitude difference in densities found over the three sampled years.

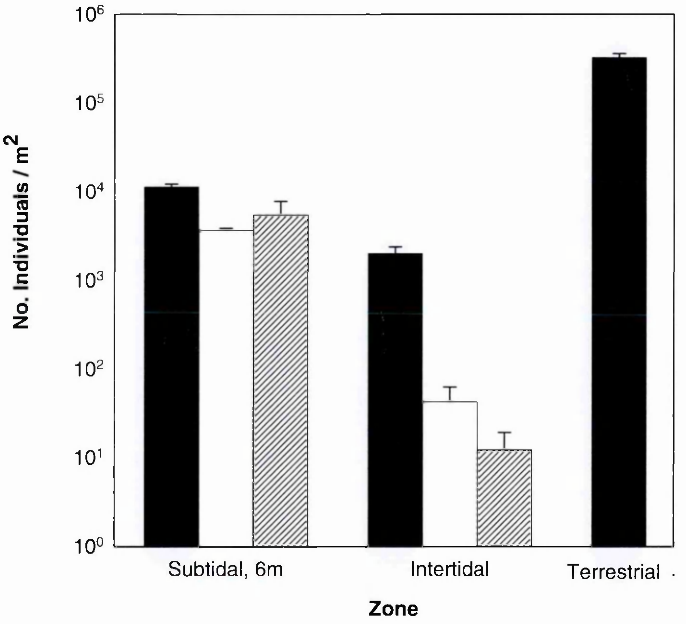


Fig. 3.7. Mean faunal abundance (+SE) of both encrusting and non encrusting species per zone for 2003, 2001and 1999. (Each bryozoan colony was counted as 1 individual) (2003 data black; 2001 white; 1999 shaded).

Table 3.4. Results of 2 way ANOVA for variability in overall faunal abundance by site and zone.

Source	DF	Adj MS	F	P
Zone	2	35.086	26.46	<0.001
Site	2	8.283	6.65	0.009
Zone*site	4	1.872	1.41	0.270
Error	18	1.326		

Individual size

Of the six species where comparison of individuals across the marine and intertidal zones was possible, intertidal individuals of three species were significantly larger, one was not significantly different and two were significantly smaller than individuals from 6 m depth (Fig. 3.8).

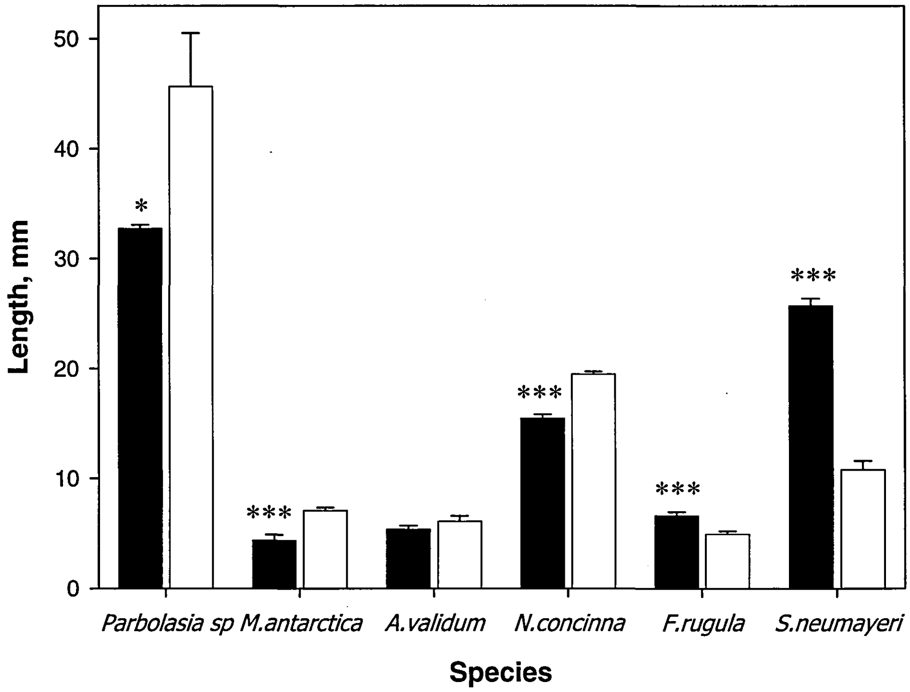


Fig. 3.8. Comparison of mean sizes of subtidal (black) and intertidal (white) individuals of 6 species found in both zones.(n>36 in each case) (+SE). * $p< 0.05$ ** $p< 0.01$ *** $p<0.001$

Age

Bryozoan colonies ranging from one to three years of age were found at all sites in both sub and intertidal zones, while 4 year age class colonies were found only in the intertidal zone. The mean number of colonies in each age class was not significantly different between zones however there was a tenfold reduction with each year from 1 to 3 years old in both zones (Fig. 3.9).

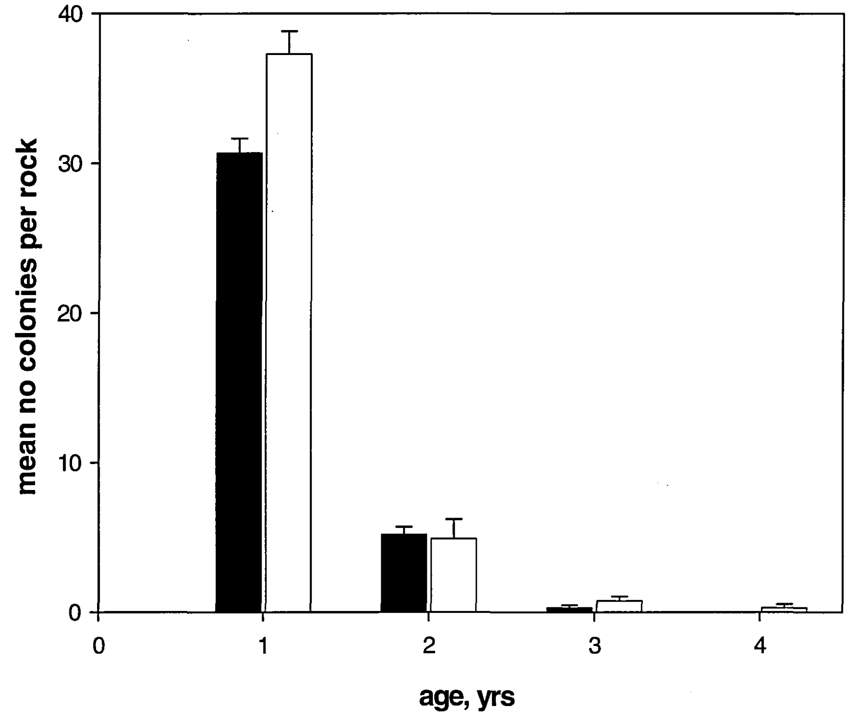


Fig. 3.9. Ages of cheilostome bryozoan colonies from subtidal (black) and intertidal (white) zones (data are from 2003-4 samples).

DISCUSSION

This study focussed on quantifying community differences across one of the most extreme and least studied transitions between adjacent environments anywhere on Earth. However, here as elsewhere in the globe, marine and terrestrial ecologists and their studies have remained separate.

Though patchily distributed, life in coastal terrestrial and marine Antarctic habitats is normally visually obvious, if small in the former, but this is not the case in the narrow intertidal zone that separates them. However, far from being lifeless, the intertidal zone of Adelaide Island was found to be one of genuine transition between the two better-studied realms. In contrast with the initial hypothesis and the prevailing view, the lower section of the intertidal can support similarly high numbers of species to the subtidal, while the middle of the zone had similarly low numbers of species to the adjacent terrestrial habitats (Fig 3.3). It is likely that the few previous reports of life in the Antarctic intertidal have been restricted to that visible at the substratum surface or, at best, in accessible crevices. The current study sampled below the exposed surface layer of intertidal substratum. Almost all the taxa found were not present on the upper surfaces of the outer layer of boulders (exposed to regular ice scour), but in protected microhabitats on lower boulders and in the interstices between. Although not previously quantified in a single study, the finding of greater species richness in the marine relative to the terrestrial zone is not surprising and is consistent with general biodiversity studies in both zones. The diversity levels found to be present in the intertidal - on average 14 species of 7 classes in a $0.25m^2$ study quadrat - an area previously considered to be populated only occasionally by limpets is, however, both surprising and striking. Most species present in the intertidal zone were of marine origin, an observation consistent with the general pattern found at lower latitudes. Indeed the two higher taxa found in both the intertidal and the terrestrial zone, mites and springtails, are also common to these environments at temperate latitudes. So in terms of richness, Antarctica's land-sea interface is not always the depauperate environment that has been reported or assumed in previous studies.

Biomass measurements in the immediate study region have been reported from the subtidal only by Barnes & Brockington (2003). The subtidal biomass values obtained in the current study were temporally variable with data from 2001 being lower but of the same order of magnitude to those reported by Barnes & Brockington (2003). In contrast data from 2003 were an order of magnitude less. Biomass values reported from other Antarctic and sub-Antarctic studies also show strong variability (see Blankley & Grindley 1985, Gambi et al. 1994) probably due to patchiness in ice scour

(Barnes 1999, Gutt 2001, Brown et al. 2004). Terrestrial faunal biomass found in the current study is comparable with that reported by others from the surrounding area, with the population density values reported by Convey & Smith (1997) equating to a mean value of ~11.7 g m^{-2}. When compared with temperate and tropical regions Antarctic terrestrial biomass values are strikingly low, likely a function of permanently resident terrestrial communities at these high latitudes consisting entirely of small invertebrate species. To date virtually no biomass data are available from the Antarctic intertidal however the biomass values reported here are at least 1 to 2 orders of magnitude lower than are found at low latitude regions (see McQuaid & Branch 1985, Bustamante & Branch 1996, Ricciardi & Bourget 1999). Most (74%) of the intertidal biomass present in the current study was accounted for by mobile species, e.g. the limpet *N. concinna*, a pattern also common to sub-Antarctic islands such as Marion Island, where the limpet *Nacella delesserti* accounted for 78% of intertidal biomass (Blankley & Grindley 1985).

Quantitative estimates of (total) faunal abundance or population density in the shallow sublittoral, intertidal and even terrestrial habitats of Antarctica are scarce. The densities of terrestrial fauna found in the current study were similar to those reported at neighbouring Lagoon Island by Convey & Smith (1997), but an order of magnitude higher than they reported on Rothera Point itself. Such differences are likely to be a function of the specific habitat sampled in the terrestrial environment. Abundance levels of subtidal fauna measured in the current study are comparable with values reported from other polar localities (Jazdzewski et al. 1986, Sejr et al. 2000, Beckley & Branch 1992). Typically, the few published data for Antarctic intertidal sites are limited to the most abundant species present (e.g Picken 1980, Brethes et al. 1994, Smith & Simpson 2002). Barnes & Brockington (2003) reported 0 to 30 individuals of 9 species m^{-2} in their study at Rothera Point, which, whilst two orders of magnitude lower than found in 2003-4 samples in the current study, corresponds with the 2001 findings at the same site. As at the more intensively studied temperate and tropical localities, while both spatially and temporally variable, these data clearly establish that it is possible for the intertidal zone at southern Antarctic Peninsula sites to support relatively rich and abundant communities.

The data also illustrate that under conditions encountered at this locality on the Antarctic Peninsula, intertidal individuals can persist over longer timescales than the seasonal, as live 4 year old bryozoan colonies were found at two of the three sites (Plate 3.1) This indicates that animals can survive throughout the winter, even whilst this zone appears from the surface to be encased in an icefoot. Furthermore, this study has demonstrated that some animals may be as large and live as long as those in the shallow subtidal. In that the Antarctic intertidal is almost entirely populated by species that also occur in the subtidal, it contrasts with the pattern seen in this zone elsewhere in the world, where the presence of terrestrial, marine and obligate intertidal species is typical. It is clear that the intertidal is not always the uninhabitable environment that is currently portrayed, and that within protected microhabitats in the boulder matrix, communities can persist not only seasonally but over longer timescales.

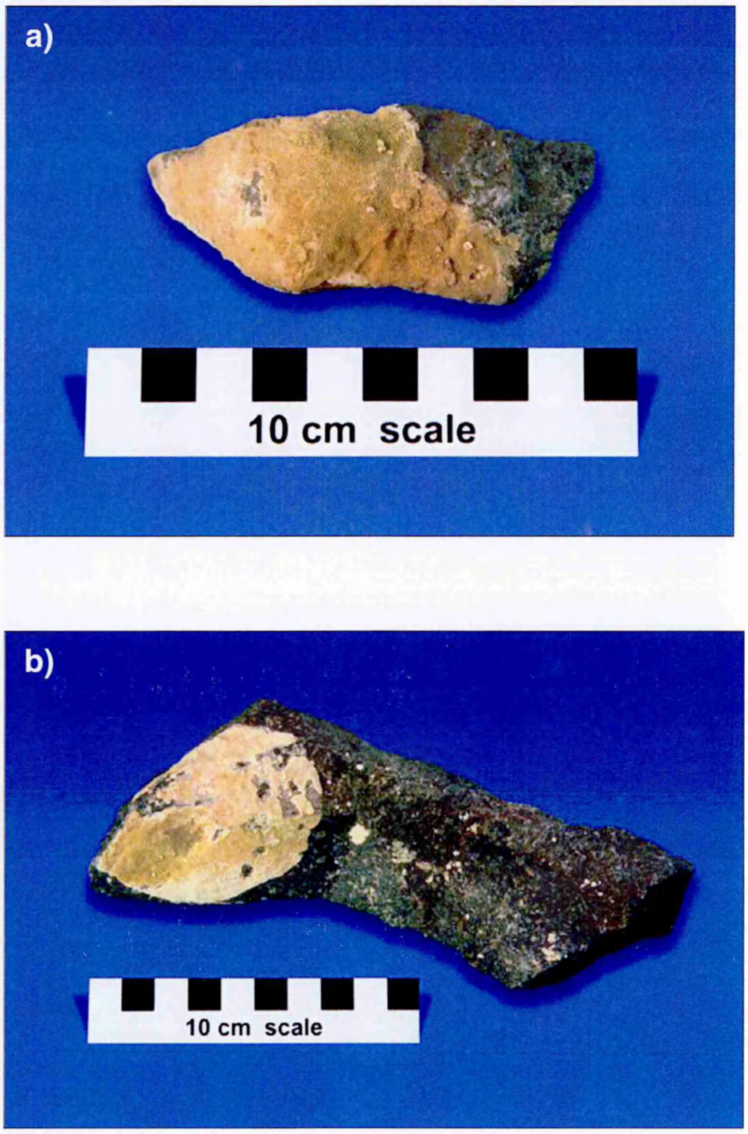


Plate 3.1 a,b. Four year old bryozoan colonies (*Inversiula nutrix*) found alive in the intertidal zone in summer 2003-4

Chapter 4 – Cryptic intertidal community structure

Chapter 4 – Cryptic intertidal community structure

INTRODUCTION

Raffaelli and Hawkins (1997) describe four major environmental gradients common to intertidal environments. These are (i) the vertical, unidirectional stress gradient from sea to land (increasing emersion and the resultant problems of desiccation and variable osmotic stress, and exposure to highly variable temperatures); (ii) the horizontal gradient of exposure to wave action (from sheltered bays to exposed headlands); (iii) the particle size gradient (from mudflats to boulder shores and bare bedrock) and (iv) the marine-freshwater gradient in salinity (typically seen in estuarine systems, although variation in salinity may also occur along the vertical gradient with hyper and hypo saline conditions occurring in pools). The interplay of these factors has been proposed as the major structuring force on intertidal communities, resulting in visually obvious zonation patterns (e.g. Southward 1958, Sousa 1979, Paine & Levin 1981).

From superficial observation the Antarctic littoral environment would appear to be virtually lifeless, with nothing more than small numbers of the relatively mobile limpet *N.concinna* being apparent, and no visible zonation - otherwise one of the most obvious and defining features of rocky shores globally. The barren appearance of Antarctic and many sub-Antarctic shores is entirely due to the influence of ice scouring (Gutt et al. 1996, Barnes 1999), which removes nearly all macroflora and fauna from the surface of the intertidal zone. However the physical characteristics of the intertidal environment at sites around Adelaide Island (and elsewhere in Antarctica) may permit the existence of cryptic communities that are richer and more diverse than previously anticipated (Waller et al. 2006a, Chapter 3). As described in the previous chapter whilst being both spatially and temporally patchy, intertidal communities at this locality on the Antarctic peninsula can be as rich and diverse as the contiguous shallow sublittoral. Zonation as a concept is not applicable to the Antarctic intertidal surface zone, and indeed the intertidal zone globally is perceived as a two dimensional environment extending between high water spring level and low water spring level along a surface gradient, despite the fact that on both rocky (except bedrock) and sedimentary shores there is a three dimensional factor. This has been recognised by community ecologists studying soft sediment communities (Raffaelli & Hawkins 1997 p.87), primarily because the majority of their fauna are buried in the habitat rather than attached to the surface. Temperate boulder shores are variable in complexity and surface rugosity. The three dimensionality of this surface environment has been recognised, as upper surfaces of large boulders are emersed for longer than those of smaller ones (McGuinness & Underwood 1986). However this obvious three dimensionality is in contrast with much of the Antarctic littoral zone (around the current study area), a large proportion of which consists of smoothed and compacted areas of densely packed "pavements", often with virtually no sediment within the matrix (Plate 4.1).

Habitat structure and complexity have been proposed as important factors in structuring many biological communities, with more complex habitats providing refuges from physical extremes and predation (Menge et al. 1986, Raffaelli & Hawkins 1997). Although there are many studies of community structure on boulder shores (e.g. Rios & Mutschke 1999, Barnes & Lehane 2001, Le Hir & Hiley 2005, Kuklinski et al. 2006) and adaptive physiology of intertidal animals (e.g. Hargens & Shabica 1973, Shabica 1976, Nolan 1991, Davenport & McAllister 1997, Davenport et al. 1997, McAllen & Block 1997, Davenport & Davenport 2005) to date there have been no studies of possible zonation and community structure through a vertical section of an intertidal cobble boulder matrix.

The current chapter considers the influence of depth within the cobble boulder matrix on the diversity, abundance and distribution of taxa present within the low shore Antarctic intertidal zone. The hypothesis being examined is that diversity, species richness and abundance of taxa will increase with depth within the matrix.

Plate 4.1. Examples of compacted cobble pavement (circled).

MATERIALS AND METHODS.

Sample sites and protocol

Samples were collected from Lagoon Island, close to Rothera Research Station (Fig. 4.1) over two consecutive days in early January 2004, approximately one hour either side of spring tide low water (~ +0.44m above chart datum). The general physical and environmental characteristics of the study site are described in detail in Chapter 2.

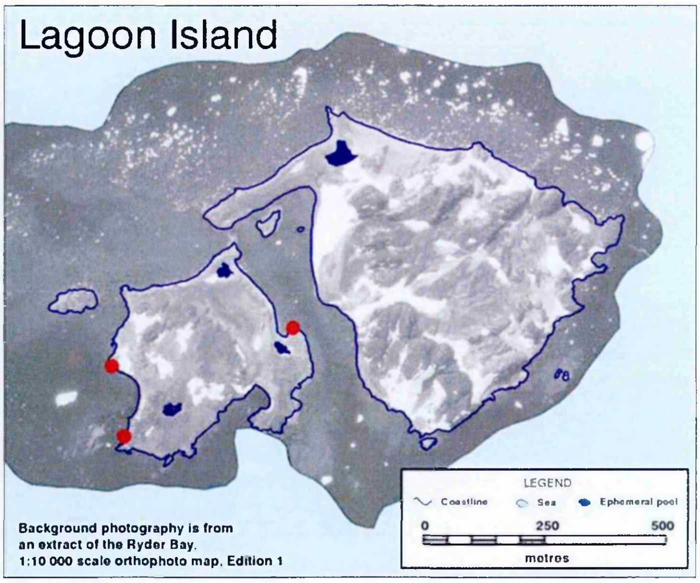


Fig. 4.1. Location of sampling points on Lagoon Island (red dots).

The sample stations were characterised by compacted cobble pavements, with virtually no sediment within the matrix. Three randomly placed quadrats 300-500 m apart were excavated to a level where water was encountered (as described in Chapter 2). Bedrock was not encountered at any of the three locations. Rocks were considered to be within the quadrat if over 50% of their volume was encompassed. The rocks were collected, upper surface marked, and then bagged and labelled by depth and sampling station. Depth classes were defined as Layer 1: 0-0.12 m; Layer 2: 0.13-0.24 m; Layer 3: 0.25-0.36 m and Layer 4: 0.37-0.48m (the maximum depth attained before water was encountered). On occasions rocks were encountered that encompassed more than one depth class. In these circumstances the depth of the upper, mid point and under-surface of the rock were recorded. The rocks were then returned to the laboratory where tube-dwelling polychaetes (excluding Spirorbids and serpulids) and samples of hydroids and sponges were removed and preserved. The rocks were then dried, allocated a unique reference number and the encrusting taxa present identified to lowest taxonomic level possible, in most cases to species. A similar process was applied to mobile taxa, which were collected in plastic pots filled with seawater, labelled according to the depth and surface on which they were found, and then returned to the laboratory where they were identified and counted. For highly abundant, mobile, species (e.g. *Tigriopus angulatus*) an estimate of the percentage collected was made *in situ*.

Analyses of collected rocks:

Ten random 2.5 cm^2 areas on each surface of all rocks were analysed for abundance of species present within the selected area. The areas analysed were determined by generating a pair of random numbers (Microsoft Excel), which were then related to a numbered grid on transparent acetate, overlaying the rock surface, the numbers giving the bottom left-hand corner of the box to be analysed. The surface area of each rock was estimated using a non-elastic mesh of 1 cm^2 grid size following Barnes et al. (1996). All encrusting fauna were counted on each rock and the abundance of each taxon calculated by using the relative proportions estimated from the grid subsamples. These values were then standardised to $1m^2$. Sizes of 50 randomly selected cheilostome bryozoan colonies from both upper and lower surfaces of cobbles in each layer were measured to an accuracy of 0.1 mm using digital callipers. The method of selection of colonies followed the random number protocol described above, the colony closest to the co-ordinates being measured. In cases where the colony was irregularly shaped, the maximum and minimum dimensions were recorded and the mean calculated.

Data analysis

The DIVERSE routine within the PRIMER ecological software package (Primer-e Ltd. Plymouth, UK) was used to calculate indices of species richness, abundance, diversity (Shannon H' log e) and evenness (Pielou J'). Data were transferred to the Minitab statistical software package, checked for normality (using the Kolmogorov-Smirnov test) and homoscedacity and transformed where necessary (fourth root transformations were applied to abundance and cheilostome bryozoan colony size data to stabilise variance). These data were then subjected to GLM ANOVA with depth class and surface (top or bottom) as fixed factors. Where differences were found, *post hoc* Tukey pair-wise comparisons were made to identify the surface and layers contributing to the difference. Non-metric multidimensional scaling (nMDS) ordination was used to visualise the similarities of assemblages between layers and surfaces.

Analysis of community structure (i.e. generating a species by site matrix), using GLM ANOVA is generally inappropriate, as the assumptions of homoscedacity and normality are rarely met (Clarke & Warwick 2001). However ANOSIM, which is a non parametric analogue of the standard ANOVA makes fewer assumptions as to the normality or variance of the data and is therefore a more robust and appropriate means of analysing these data. ANOSIM and SIMPER routines within the PRIMER package were applied to Bray Curtis similarity matrices of square root transformed data of species distribution within the intertidal zone in order to ascertain whether there were significant differences between assemblage composition between rock surfaces and layers and if so which species and trophic groups contributed most to the dissimilarity.

RESULTS

A wide range of both encrusting and mobile taxa was found to be present in the intertidal zone at the study sites selected. In the current study a total of 40 species, representing 22 orders and 9 phyla, were identified within the cobble/pebble matrix that formed the substratum. The species accumulation curve approached an asymptote (Fig. 4.2), indicating that, despite the relatively small sampling area, the sampling protocol used was appropriate to provide a representative description of the taxa present in the intertidal zone at this site. Overall the intertidal community comprised 57.5% vagile and 42.5 % sessile taxa, however the proportions of each varied significantly with layer (depth) and rock surface (ANOVA $F_{3,1}$=13.21, P<0.001). The dominant (i.e. the most frequently occurring and numerically most abundant) groups were all encrusting (cheilostome bryozoans, hydroids and spirorbid polychaetes) (Table 4.1, Fig 4.3), but mobile taxa, whilst numerically less abundant, were more speciose with totals of 17 encrusting and 23 vagile species found. Upper surfaces were dominated by spirorbid polychaetes and the cheilostome bryozoan *Celleporella antarctica.* Lower surface communities were more diverse, with a greater number of species contributing to the within-surface similarity. Analysis by trophic groups revealed that both upper and lower surface communities were predominantly composed of suspension feeders.

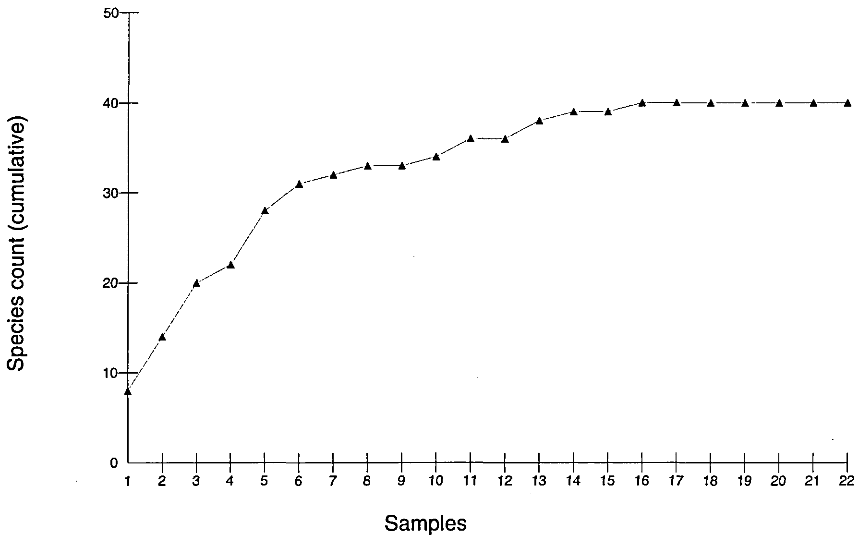


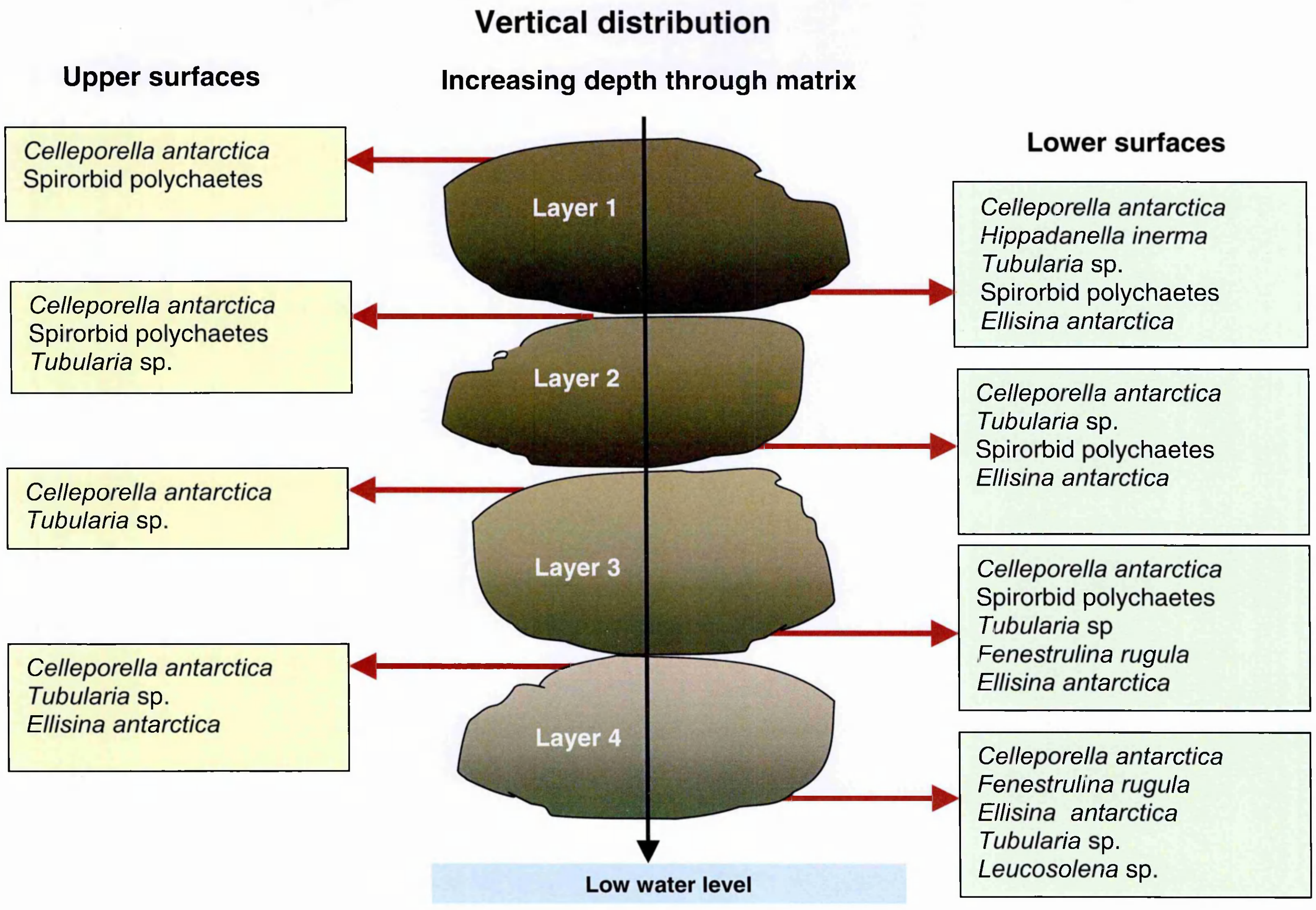
Fig.4.2. Taxon accumulation curve by sample point (layer and surface)

Table 4.1. Full taxon list and mean abundance per $0.25m^{-2}$ of each species by layer (1-4) and surface (upper, U and lower, L)

				Mean abundance by layer and surface							
Phylum	**Class**	**Order**	**Species**	**1U**	**1L**	**2U**	**2L**	**3U**	**3L**	**4U**	**4L**
Arthropoda	Copepoda	Harpaticoida	*Tigriopus angulatus*	0	33	15	8	2	4	0	12
	Chelicerata	Pycnogonida	*Achelia communis*	0	2	1	13	7	19	6	9
	Malacostraca	Amphipoda	*Prostebbingia gracilis*	0	0	10	0	2	0	4	0
		Amphipoda	Stenothoidae	0	10	22	8	5	1	0	0
		Amphipoda	*Cheirimendon femoratus*	0	0	1	0	0	0	0	0
		Amphipoda	*Gondogeneia antarctica*	0	0	4	0	1	0	0	0
		Amphipoda	*Cymodocella* sp.	0	0	0	0	0	1	0	0
		Isopoda	*Notasellus sarsi*	0	0	0	0	1	0	0	0
		Isopoda	*Munna antarctica*	0	0	2	1	1	0	0	0
Mollusca	Gastropoda	Sorbeoconcha	*Laevilittorina caliginosa*	0	39	31	26	8	15	1	0
		Docoglossida	*Nacella concinna*	3	4	3	0	1	0	0	0
		Vetigastropoda	*Margarella antarctica*	0	1	4	3	1	0	2	0
		Nudibranchia	*Eubranchus* sp.	0	0	0	1	0	0	0	0
		Sorbeoconcha	*Onoba luvqueti*	0	1	0	1	1	1	0	0
Nemertea	Anopola	Heteronemertea	*Antarctonemertes validum*	0	2	2	4	0	2	1	1
			Parbolasia sp.	0	0	0	4	0	0	0	0
Platyhelminthes	Turbellaria	Polycladida	*Pseudoceros* sp.	0	0	0	0	1	0	1	0
			Unknown flatworm	0	0	0	0	0	1	0	0
Echinodermata	Echinoidea	Echinoida	*Sterechinus neumayeri*	0	0	4	0	1	0	0	0
	Asteroidea	Phranerozonida	*Odontaster validus*	0	0	0	0	1	0	0	0
Cnidaria	Hydrozoa	Trachylina	*Gonionemus* sp.	0	0	18	0	24	0	7	0
		Leptothecata	*Tubularia* sp.	2	57	57	197	146	132	240	287
Bryozoa	Gymnolaemata	Cheilostomatida	*Celleporella antarctica*	48	139	164	295	266	372	287	469
			Celleporella bougainvillei	0	0	0	0	0	12	0	46
			Hippadanella inerma	0	51	19	79	3	56	14	108
			Aimulosia antarctica	0	3	5	0	4	3	5	127
			Arachnopusia inchoata	0	0	0	0	0	3	0	0
			Fenestrulina rugula	2	15	5	43	2	120	63	418
			Ellisina antarctica	2	40	11	97	10	81	154	325
			Inversiula nutrix	0	3	0	0	0	4	8	12
			Xylochotridens rangifer	0	1	2	0	0	39	0	11
			Chaperiopsis quadrispinosa	0	0	0	0	0	0	0	12
	Stenolaemata	Cyclostomatida	Cyclostome bryozoans	0	14	0	11	11	48	5	118
Annelida	Polychaeta	Spirorbidae	Spirorbid 1	37	54	39	119	92	220	70	120
			Spiroid 2	2	4	0	6	3	8	0	12
		Capitellidae	Unknown tubeworm	0	0	0	0	1	32	0	71
		Serpulidae	Serpulidae	0	0	0	0	0	0	0	1
		Aciculata	*Barrukia cristata*	0	0	0	0	1	0	0	0
		Terrebellidae	Unknown terrebelid	0	0	0	1	1	1	1	0
Porifera	Calcarea	Leucosolenida	*Leucosolenia* sp.	0	0	0	63	0	44	5	240

Next page.

Fig. 4.3. Schematic diagram of distribution of dominant species by surface and layer (i.e. species that comprise>75% of the total faunal abundance for each layer)


Vertical distribution
Upper surfaces
Increasing depth through matrix
Lower surfaces
Celleporella antarctica
Spirorbid polychaetes
Layer 1
Celleporella antarctica
Hippadanella inerma
Tubularia sp.
Spirorbid polychaetes
Ellisina antarctica
Celleporella antarctica
Spirorbid polychaetes
Tubularia sp.
Layer 2
Celleporella antarctica
Tubularia sp.
Spirorbid polychaetes
Ellisina antarctica
Celleporella antarctica
Tubularia sp.
Layer 3
Celleporella antarctica
Spirorbid polychaetes
Tubularia sp
Fenestrulina rugula
Ellisina antarctica
Celleporella antarctica
Tubularia sp.
Ellisina antarctica
Layer 4
Celleporella antarctica
Fenestrulina rugula
Ellisina antarctica
Tubularia sp.
Leucosolena sp.
Low water level

1. Univariate measures of community structure with depth and surface.

i. Abundance

At the study site there was a significant difference in overall faunal abundance between both layers and cobble surfaces within layers (ANOVA $F_{3,1}$= 8.04, and $F_{3,1}$= 25.29, P<0.001 in both cases). Upper surfaces had significantly lower abundances than lower surfaces of rocks (Tukey T= -5.029 P<0.001). There was also a significant difference between layers. Layer 1 had significantly lower faunal abundance than all other layers (Table 4.2). Mean faunal abundance on the upper surface of the top layer of the matrix was 97 individuals $0.25m^{-2}$ (range 15 to 212), an order of magnitude lower than the mean of 2400 individuals $0.25m^{-2}$ on the lower surface of the bottom layer of rocks (Fig. 4.4). The cheilostome bryozoan *Celleporella antarctica* and spirorbid polychaetes accounted for an average of 90% of the animals present on upper surfaces of rocks.

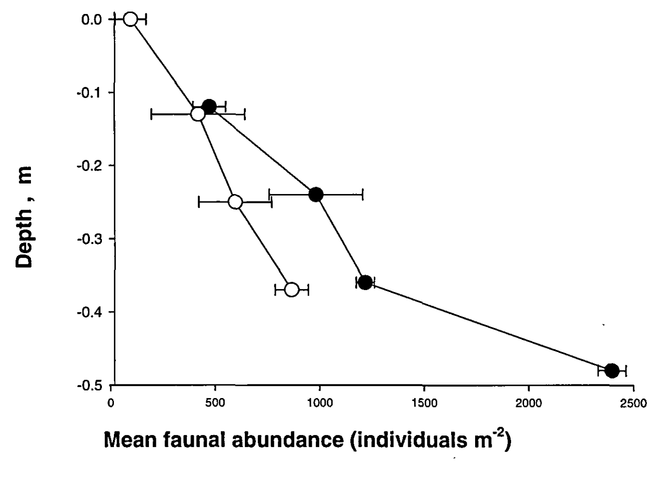


Fig. 4.4 Mean faunal abundance (± SE) found on upper (○) and lower (●) surfaces of rocks found at increasing depth through the intertidal cobble matrix.

Table 4.2. Summary of significant results obtained from *a posteriori* Tukey pairwise comparisons of means, after application of GLM ANOVA on abundance, richness, evenness & diversity data. Significance of result is denoted as * P<0.05; **P<0.01 ***P<0.001.

	Richness, S	**Abundance, N**	**Evenness, J'**	**Diversity, H'**
Layer	1 & 2 **	1& 2 *	1 & 3 *	1& 2 **
	1 & 3 **	1 & 3 **		1 & 3 *
	1 & 4 ***	1 & 4 ***		1 & 4 **
		2 & 4 ***		
Surface	U & L**	U & L***	U & L***	U & L***

ii. Diversity and evenness

Shannon (H') diversity differed significantly between both surfaces and layers (ANOVA $F_{3,1}$= 5.70 and 39.01, $P<0.001$ in both cases) and ranged from 0.84 on the outer face of the upper layer of the intertidal to 2.18 on the lower surface of the bottom layer of rocks (Fig. 4.5a). *Post hoc* Tukey pair-wise comparisons revealed that the differences were predominantly caused by the low diversity of taxa found on upper and lower surfaces of the initial layer of rocks (Table 4.2). Lower surfaces had significantly higher diversity than upper with the exception of the initial layer of the matrix (Tukey T=-6.246 $P<0.001$). Evenness (which describes the relative abundance with which each species are represented in an area) was not as variable as diversity at the study sites. The main difference in evenness was between surfaces, with lower values obtained on upper surfaces (Fig 4.5b).

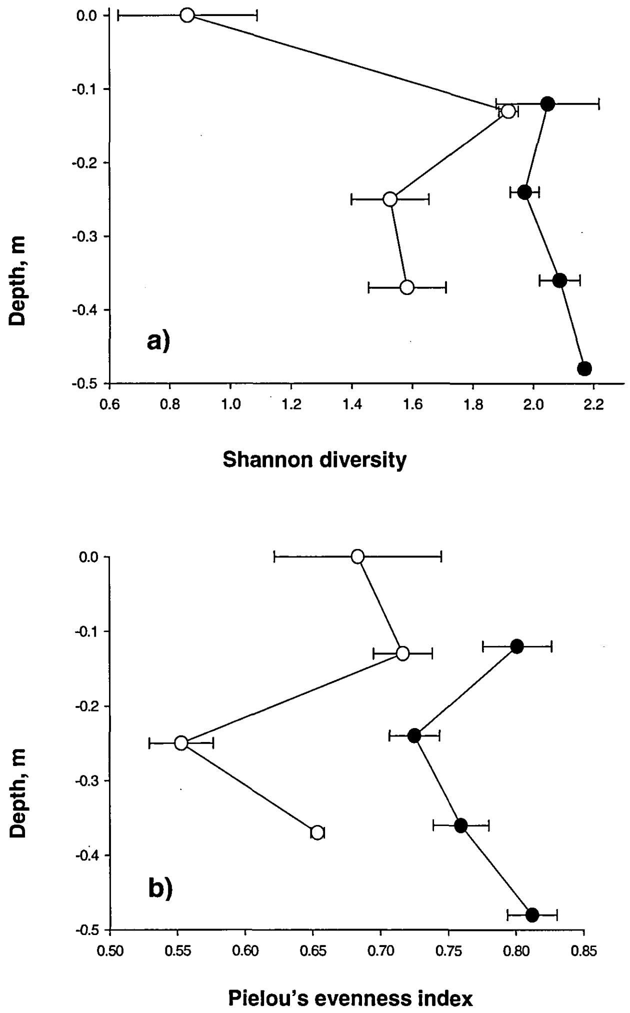


Fig. 4.5 a,b. Mean diversity (± SE) a) and evenness (± SE) b) found on upper (○) and lower (●) surfaces of rocks in the intertidal zone.

iii. Richness

Overall there were significant differences in species richness with both surface and layer (ANOVA $F_{3,1}$= 5.60, P <0.001). However *post hoc* Tukey comparisons again revealed that this was due to the difference between the upper surface of the top layer of rocks (i.e. the visible intertidal environment) and all other points (Table 4.2). The mean richness of the outer (exposed surface of Layer 1) surface of the intertidal at these Lagoon Island sites was only 4.3 species (Fig. 4.6) compared with lower layers, which had a mean across the layers of 14.5 species. The maximum richness (a mean of 16 species) was found on the upper surface of layer three.

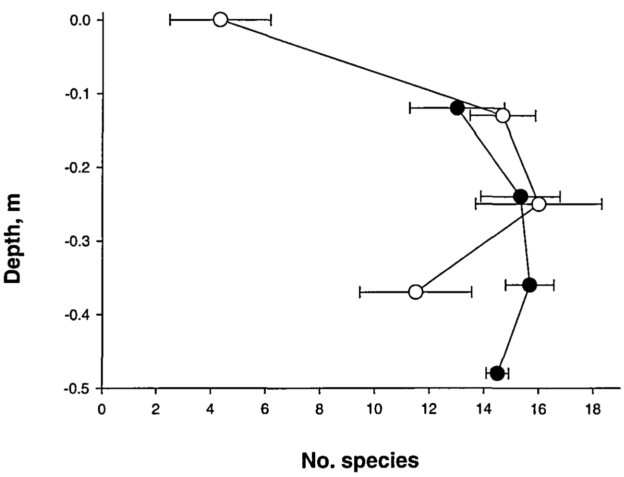


Fig. 4.6. Mean species richness (± SE) on upper (○) and lower (●) surfaces of rocks in the intertidal zone.

v. Size of residents: cheilostome bryozoan colonies as an example

Cheilostome bryozoan colonies were significantly larger on lower surfaces, with the exception of the uppermost layer of rocks. Mean size ranged from ~2mm on the exposed upper surface of the intertidal zone to ~6.4mm at the bottom of the matrix (Fig.4.7). The maximum colony size recorded was 28.5mm and was found on the lower surface of layer 4. The maximum size colony found on upper surfaces was a colony of 14.0mm diameter on the second layer of the matrix.

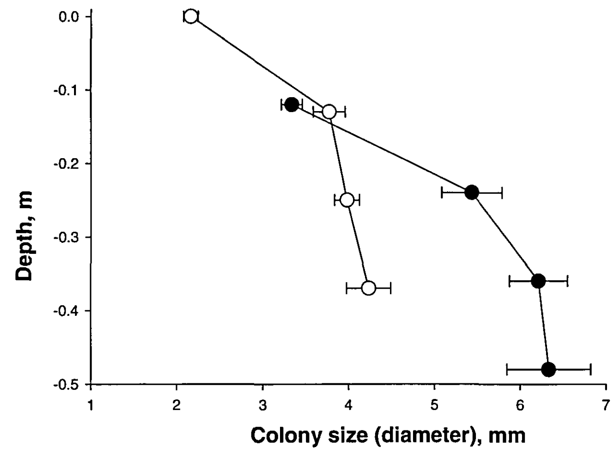


Fig. 4.7. Mean cheilostome bryozoan colony size in mm (± SE) found on upper (○) and lower (●) surfaces of rocks in the intertidal zone.

2. Variability of community structure with depth and rock surface.

Community composition varied with layer and surface through the intertidal matrix, with much greater variability in assemblage structure present in comparisons between the upper surface communities of different layers. The top layer community was significantly different from those of all other layers (Table 4.3). Communities on lower surfaces were similar, both within and between layers, and showed a distinct gradient of similarity with depth. Visualisation of underlying trends using nMDS ordination showed that the upper surface communities were more variable than those on lower surfaces (Fig. 4.8), with average similarities of around 50% for upper surfaces of all layers except layer 4 (68%) and around 68% for lower surfaces (Table 4.4). SIMPER analysis revealed that the species contributing most to within group similarity were *C. antarctica* and Spirorbid polychaetes for layers 1 to 3, accounting for 96 % of the similarity between samples on the outer layer of rocks (Table 4.4). The dissimilarity between layers was due to a wider range of taxa with no clear patterns emerging. The dissimilarities between surfaces were predominantly due to several cheilostome bryozoans and Spirorbidae.

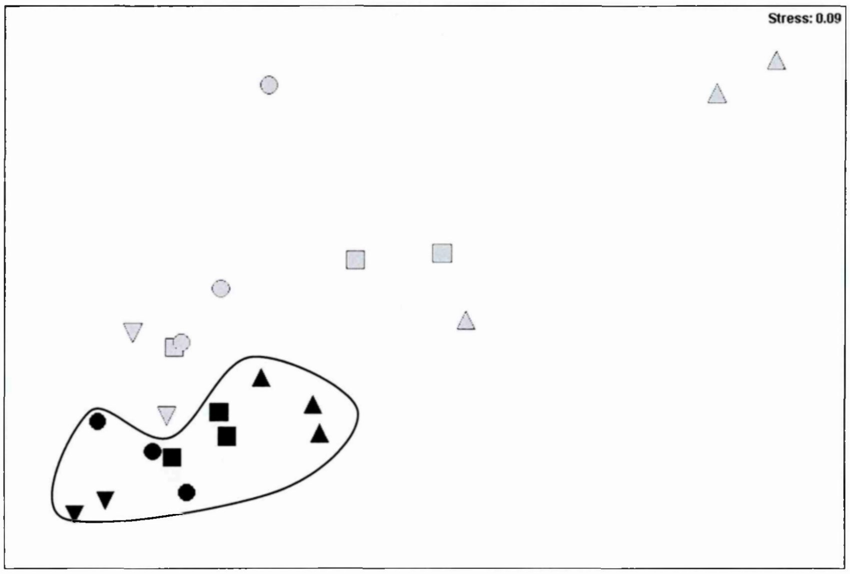


Fig. 4.8. nMDS ordination plot showing of similarities within layers and surfaces. The symbols are lower surfaces (black), upper surfaces (grey), layer 1 (upright triangle), layer 2 (squares), layer 3 (circles)and layer 4 (inverted triangles)

Table 4.4. SIMPER analysis of within group (layer) similarities. Species contributing most (75% cut off) to the similarity within the layer are listed. Group (layer) 1 is the uppermost layer and group 4 the lowermost layer. upper and lower refer to the surface of the rocks within each layer

Group 1 upper

Average similarity: 50.70

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	25.67	28.81	2.26	56.82	56.82
Spirorbid 1	23	19.96	1.75	39.37	96.19

Group 1 lower

Average similarity: 64.18

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	116.47	12.3	7.88	19.16	19.16
Hippadanella inerma	50.66	10.84	7.93	16.89	36.05
Tubularia sp.	56.83	9.77	16.04	15.22	51.27
Spirorbid 1	44.06	9.48	7.1	14.77	66.04
Laevilittorina caliginosa	39.33	6.7	1.83	10.44	76.48

Group 2 upper

Average similarity: 47.75

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	164.13	13.02	4.64	27.27	27.27
Spirorbid 1	48.52	7.81	2.83	16.35	43.61
Laevilittorina caliginosa	27.67	7.59	4.14	15.89	59.51
Tubularia sp.	38.47	5.88	2.92	12.3	71.81
Hippadanella inerma	18.85	3.09	3.13	6.48	78.29

Group 2 lower

Average similarity: 69.93

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	295.13	13.61	10.13	19.46	19.46
Tubularia sp.	196.96	11.57	6.93	16.55	36
Spirorbid 1	132.37	9.9	12.3	14.16	50.16
Ellisina antarctica	97.41	9.78	9.7	13.99	64.15
Fenestrulina rugula	43.42	6.13	6.69	8.76	72.91
Hippadanella inerma	79.26	5.91	2.14	8.45	81.35

Group 3 upper

Average similarity: 47.10

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	248.7	16.71	2.84	35.48	35.48
Spirorbid 1	85.47	12.45	7.59	26.43	61.91
Tubularia sp.	145.75	6.42	0.58	13.63	75.54

Group 3 lower

Average similarity: 68.05

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	296.87	12.07	2.54	17.74	17.74
Spirorbid 1	219.63	11.77	14.48	17.29	35.03
Tubularia sp.	131.81	8.88	19.5	13.05	48.08
Fenestrulina rugula	119.84	8.79	12.47	12.92	61
Ellisina antarctica	80.68	5.32	3.41	7.81	68.81
Hippadanella inerma	55.91	4.91	5.67	7.22	76.03

Group 4 upper

Average similarity: 67.96

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Tubularia sp.	239.7	19.99		29.42	29.42
Celleporella antarctica	257.02	19.72		29.01	58.43
Fenestrulina rugula	63.23	10.16		14.94	73.37
Spirorbid 1	69.8	9.86		14.51	87.88

Group 4 lower

Average similarity: 68.54

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Celleporella antarctica	469.35	13.01		18.98	18.98
Fenestrulina rugula	417.89	11.28		16.46	35.43
Tubularia sp.	286.72	9.21		13.44	48.87
Ellisina antarctica	324.53	7.51		10.96	59.83
Cyclostome bryozoans	118.3	7.28		10.62	70.45
Hippadanella inerma	108.25	4.6		6.72	77.17

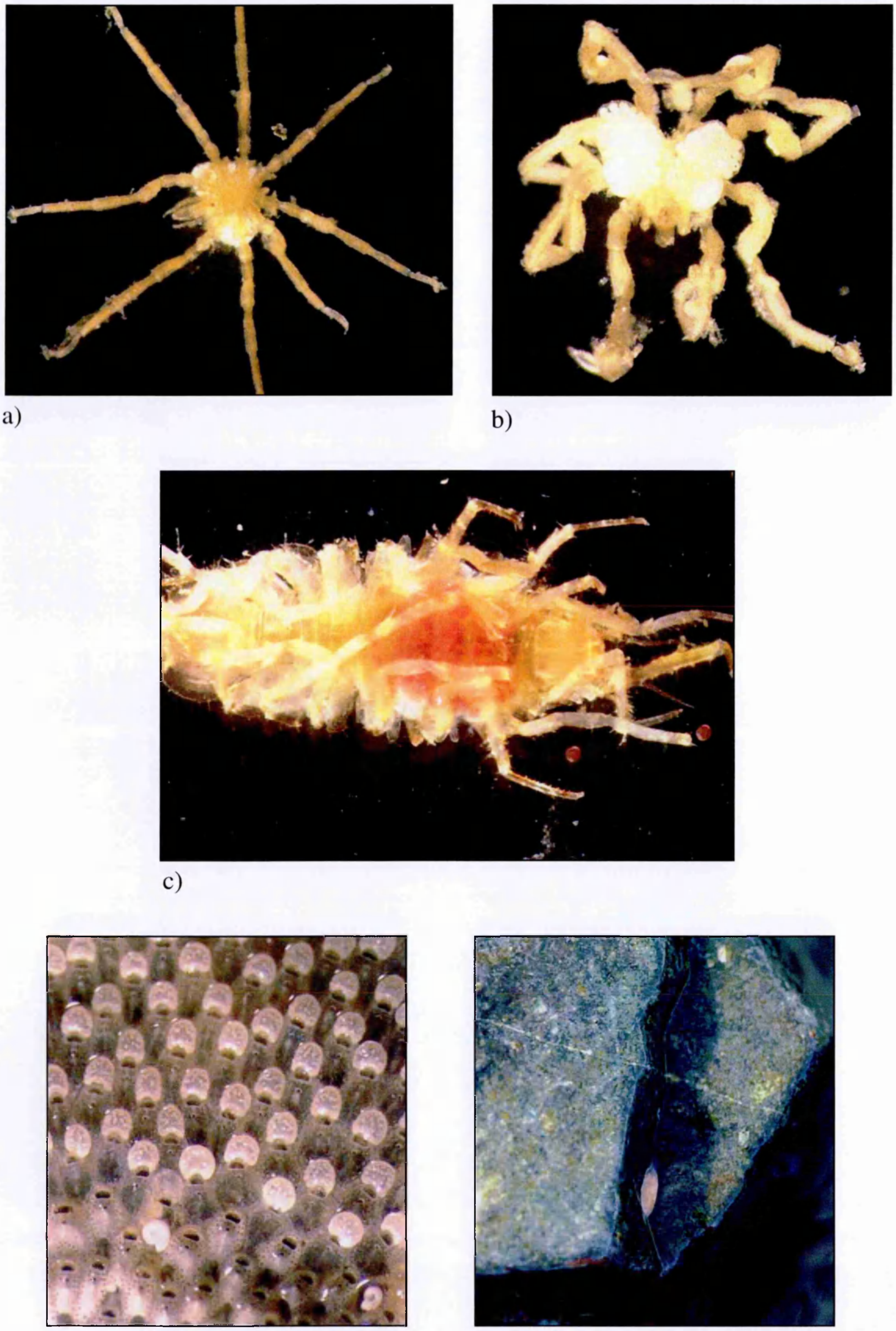
DISCUSSION

The concept of a three-dimensional environment and attenuated distribution of taxa is an accepted phenomenon within the study of soft sedimentary habitats (Raffaelli & Hawkins 1997). Typically, this is associated with meio- and macro-organisms living within the surface few cm of sands and muds. In principle, many organisms may live in the spaces made available amongst substrata of much larger grain sizes, such as the boulders of the study environment examined here. Studies of temperate rocky shores have compared variability in various metrics of their communities (e.g. diversity, richness, abundance, biomass) with habitat characteristics, including heterogeneity at differing scales (see Benedetti-Cecchi & Cinelli 1997, Le Hir & Hiley 2005, Kuklinski et al. 2006), degree of exposure (McQuaid & Branch 1985, Bustamante & Branch 1996) and position along intertidal gradients (Benedetti-Cecchi et al. 2003, Davidson et al. 2004), but these studies generally have not considered depth within the matrix *per se*. Temperate rocky shores vary dramatically when compared with southern polar littoral environments, as all but the most exposed temperate localities have obvious signs of macrobiota, from macroalgae to dense aggregations of mussels and barnacles. In contrast, Antarctic (and sub-Antarctic, see Chapter 6) intertidal zones superficially appear to support little more than small populations of mobile species such as the limpet *N.concinna* and Spirorbid polychaetes. Colonisation of the intertidal zone at localities around the current study area can be both temporally and spatially patchy (Barnes & Brockington 2003, Bowden 2005, and see also Chapter 2). Such patchiness, the relatively limited number of previous studies and the fact that previous sampling protocols at the current study site only collected the outer layer of rocks, (DKAB pers. comm.) go some way to explaining why so few macrobiota have previously been found. The few reports from Antarctic sites generally cite richness levels similar to the mean of 7.5 species found on the upper layer of rocks in the current study. However in the current study a total of 40 species were recorded, which is higher than any other study published to date from both Antarctic and sub-Antarctic localities (Blankley & Grindley 1985, Smith & Simpson 1985, Lawrence & McClintock 1987, Barnes et al. 1996, Pugh & Davenport 1997, Smith & Simpson 2002).

The physical appearance of much of the intertidal at this site and others around Adelaide Island is also notable. In addition to large areas of bare bedrock and unconsolidated boulderfields on bedrock, the effect of persistent summer ice scour and winter encasement (in ice) has resulted in many places in a characteristic "pavement" effect (plate 4.1). This comprises a flat densely packed mosaic of ice-smoothed boulders and cobbles. Such morphological characteristics are common throughout maritime Antarctic and sub-Antarctic islands as well as at sites along the Antarctic Peninsula (Hansom 1983; pers. obs.). These structures are highly resistant to wave and ice disturbance (Hansom 1983) and may offer a stable and protected environment for community development within the protected matrix. Deliberate disturbance of a 4 m^2 area of a morphologically similar pavement in the South Shetland Islands (the upper layer of rocks were removed and left lying at random) remained almost unaltered after a month in which there was a storm event and several periods of ice inundation (Hansom 1983). The current study found similar results after removing boulders then replacing them to monitor temperature in the intertidal zone over an annual cycle (described in chapter 2). After a period of 11 months the boulders had not been further moved or inverted despite winter encasement and several prolonged periods of summer ice scour. Furthermore radiocarbon dating of pavements in both the South Shetland Islands and South Georgia suggests that it may take up to 300 years for these pavements to form. Pavements in South Georgia are well developed on glacial till dated at over 9000 years whereas they stop abruptly at the limit of similar till dated at 200 years (Hansom 1983). These pavements could therefore be highly stable over thousands of years, supporting the proposition that populations of subtidal taxa with sufficiently wide physiological tolerances are able to colonise these protected habitats on a permanent basis. The current study showed at least 17 macrofaunal species to be present in the intertidal boulder matrix in winter (Chapter 5) and also live four year old bryozoan colonies have been found to be present (see previous chapter). It would seem, therefore that in contrast with the long held view that few macro-organisms would survive winter in this environment, intertidal communities are persistent over annual cycles. It seems likely that intertidal communities elsewhere on the Antarctic Peninsula and at sub-Antarctic island localities are more likely to be found in these conditions rather than on more disturbed shores where the boulder matrix is very loose and unconsolidated and hence more likely to be affected by the influence of ice.

The most obvious differences in all diversity metrics (except species richness) were found between the surfaces of boulders in each depth layer examined. Lower surfaces of all boulder layers had significantly higher values than upper surfaces (the exception being the lower surface of layer one and upper of layer two). Although there appear to be no directly comparable Antarctic intertidal studies available in the literature, the findings of the current study are similar to those of Barnes et al. (1996) who reported that approximately 80% of the (fauna and) bryozoans present on rocks at Signy I. were found on the undersurfaces (although that study only sampled the surface layer of rocks). A previous study in the sublittoral of Adelaide I. (Bowden 2005) reported that over 15-21 months, recruitment was almost exclusively to the underside of settlement plates attached to rocks. These rocks were placed on the outer surface layer of the immediate sublittoral zone (0.2 to 0.4m below chart datum). Bowden (2005) found that, despite the environment being highly impacted by ice (see Brown et al. 2004), only two of the 20 cyclostome bryozoan recruits recorded after an initial 3 months immersion failed to survive his 15 month study period. This high survivorship pattern was also found in Spirorbid polychaetes and all cheilostome bryozoans other than the fragile pioneer species *C. antarctica.* However, the latter species was the most abundant on all surfaces of all layers of rocks in the current study. The contrast between the dominance of this pioneer in the current study, and its low survival rate in previous studies, highlights the highly heterogeneous spatio-temporal nature of the intertidal environment at this locality and the difficulty of inter study comparisons as most of the taxa including bryozoans were found below the surface layer. The highest abundances and greatest diversity of fauna were found on the lower surface of the lowest layer of rocks (Plate 4.2). Intuitively this seems reasonable as this environment will be exposed to air for the shortest duration, is protected from ice scouring and is closest to the sublittoral communities which may provide a larval recruitment pool. However, as well as evidence suggested by the age/size of fauna present, it is also plausible that the intertidal community may be self-sustaining and not reliant on external recruitment from lower tidal levels, as there is also evidence of reproduction (Plate 4.3 a,b,c,d,e), predation (Plate 4.4a), commensalism (Plate 4.4 b) and both intra- and inter- specific competition (Plate 4.5) within the intertidal zone involving both encrusting and mobile taxa. That such processes occur provides evidence that the Antarctic intertidal, in contrast to a current paradigm, can support a true community. If so, it may be argued that this hitherto largely ignored Antarctic habitat is less inhospitable than has previously been thought, as it is protected from the worst of ice scouring and UV irradiation. However, animals that populate this habitat have to deal with a combination of the extremes faced in both the adjacent terrestrial and sublittoral marine environments. These include the often sub zero air conditions characteristic of the terrestrial environment, (as described in Chapter 2), and marine extremes of ice encasement in winter, and highly variable salinity in spring and summer (Peck et al. 2006). The cold tolerance mechanisms and life history strategies employed by intertidal taxa under these extremes remain to be thoroughly investigated and would seem a key area deserving of scrutiny. In a region undergoing rapid warming and ice retreat (Cook et al. 2005), and with a fauna considered to be highly stenothermal (see Peck 2005), understanding survival capabilities of taxa in one of the fastest changing Antarctic environments (the intertidal zone) is clearly an important next step.

Plate 4.2. Underside of boulder from depth of ~0.4m below surface of intertidal matrix. 17 taxa have been annotated, including ?calcareous sponge (1); polychaetes (2,12); gastropods (4,5,7); cyclostome bryozoans (6,10,14) cheilostome bryozoans (8,9,11,16); isopod (13); pycnogonids (15) and hydroids (17).



a) b)

c)

d) e)

Plate 4.3 a, b, c, d, e. Intertidal taxa found in summer samples with eggs or ovicells . a, b) pycnogonids (*Achelia communis*) males carrying eggs. c) Isopod (*Notasellus sarsi*) d) *Fenestrulina rugula* with ovicells e) nemertean *Antarctonemertes validum* in protective cocoon with eggs

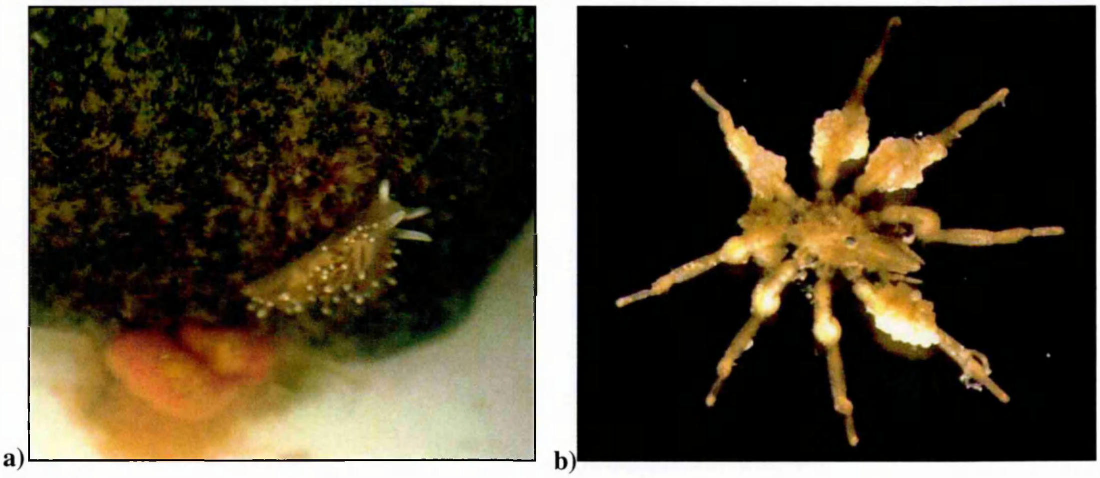


Plate 4.4 a, b.
a) Intertidal aeolid nudibranch predating on hydroids;**b)** *A.communis* with bryozoan cells

Plate 4.5 Inter- and intra- specific interactions. Interspecific interaction between colonies of *Arachnopusia inchoata* (brown colony upper right quadrant) and *F.rugula* (bottom left quadrant). Intraspecific interaction can be seen between 2 colonies of *F.rugula* in the lower left quadrant. The boundary is indicated by the dashed line.

Chapter 5 – Cold tolerance of intertidal invertebrates

[The data in this chapter are also presented in: Waller C.L., Worland M.R., Convey P. & Barnes D.K.A. (2006) Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. Polar Biology **29:**1077-1083]

Chapter 5 – Cold tolerance of intertidal invertebrates

INTRODUCTION

Although thermal conditions in the Antarctic marine environment remain relatively stable, terrestrial and intertidal species have to deal with wide fluctuations over diurnal, seasonal, decadal and even evolutionary timescales (Clarke 1991, Convey 1996 a,b). For animals that cannot avoid exposure to sub-zero temperatures two basic alternative strategies for survival exist: to avoid freezing by extensive supercooling (freeze avoidance) or to tolerate the formation of ice in body fluids (freeze tolerance) (Salt 1961, Aarset 1982, Cannon and Block 1988, Block 1990, Sinclair et al. 2003). These basic strategies have been developed into various more ecologically realistic groupings, primarily to recognise different intensities of "pre-freeze" injury up to and including death (e.g. Bale 1993). Notwithstanding this point, it is generally accepted that supercooling points (SCPs, the temperature at which ice first forms) provide a useful measure both of cold tolerance itself, and in changing patterns of cold tolerance under natural conditions and experimental manipulations. On a global scale, in contrast to many terrestrial invertebrates, intertidal taxa are thought to show negligible use of supercooling strategies, with most of those studied to date tolerating the formation of ice in their extracellular fluids (Murphy 1983, Block 1984, Loomis 1995, Davenport and MacAlister 1996, Storey and Storey 1996, Pugh and Davenport 1997, Ansart and Vernon 2003, 2004, Sinclair et al. 2004). Other survival strategies have also been proposed, such as the production of mucus to isolate tissue from inoculative freezing as proposed for the limpet *Nacella concinna* (Hargens & Shabica 1973).

Terrestrial biodiversity in contemporary Antarctica is very low (Convey 2001a,b). Until recently, the combination of extreme terrestrial and marine environmental stresses faced in the Antarctic intertidal has been widely thought to have led to an even more depauperate faunal representation (Peck et al. 2006). However, recent studies have revealed both that a previously unanticipated number of (predominantly marine) phyla and species are present in the Antarctic littoral (Chapters 3, 4, Waller et al. 2006a) and that many of these are permanent residents surviving year-round rather than being wiped out at the onset of winter as had previously been thought (Chapter 3 and current chapter results).

Thus, it is now appropriate to examine the ecophysiological strategies adopted by the inhabitants of the Antarctic intertidal zone, in order to further understand the features of their biology that permit them to survive in one of the most extreme environments on the planet. In the marine environment, it could be argued that invertebrates, whose body fluids are isosmotic with seawater, may have little need for further cold tolerance strategies in a medium that remains in the liquid state and which very rarely cools below –1.9°C (Clarke 1991). In contrast, rapid changes of temperature are likely to be experienced frequently in intertidal environments, particularly when exposed to the rapid and unpredictable fluctuations typical of air temperature that are already known to dominate the thermal regime of the terrestrial environment (Convey 1996b, and see Chapter 2).

Previous studies have shown that some intertidal invertebrates do have the ability to acclimate to colder conditions and lower their supercooling points under experimental conditions (see Ansart & Vernon 2003, and references therein). Therefore, the long-term residence of some taxa in the respective zones leads to the hypothesis that subsamples of intertidal and subtidal populations of such species would have different mean supercooling points (SCPs), as a reflection of the different levels of environmental thermal stress faced. The current chapter presents a preliminary investigation of the levels of cold tolerance typical of a range of intertidal and subtidal invertebrates under summer conditions. The possibility of winter survival was examined by sampling in the intertidal zone under winter conditions, in order to determine if any live animals were present. Finally, several species were examined in order to assess whether antifreeze proteins (also known as Thermal Hysteresis Proteins, THPs) contributed to their cold tolerance strategy. THPs (high molecular weight glycoproteins) lower freezing point of water in a noncolligative manner, such that the temperature at which a seed ice crystal starts to grow is depressed below the melting point. THPs have been shown to be present in several Antarctic Nototheniid fishes (DeVries et al. 1969, DeVries 1971). THPs have also been found in many over-wintering insects (Duman et al. 1982). To data there is only one report of THPs being present in marine invertebrates, the mussel *Mytilus edulis* (Theede et al. 1976), a finding that was later questioned (Loomis 1995).

MATERIALS AND METHODS

Environmental conditions

Intertidal temperatures were recorded over the period 9 April to 20 December 2004 using Thermochron DS1921G-F5 i-button data loggers (Maxim/Dallas Semiconductors, Sunnyvale, California). 12 loggers were deployed, but one was lost as one boulder from the high subtidal subset was not relocated. Subtidal temperatures (15m depth) are recorded on a routine year round basis under the Rothera oceanographic Time Series (RaTS) long-term monitoring programme of the British Antarctic Survey as described in Chapter 2.

Study sites and species

Animals were collected from the intertidal and subtidal (6m depth, by SCUBA) zones around Rothera Research Station, Adelaide Island, Antarctic Peninsula (67°34'20"S, 68°07'50"W) during summer (December - January) 2004-5. The study animals were chosen to include a wide diversity (11 species of nine classes) and range of size (spanning five orders of magnitude) (Table 5.1). Of the 11 species investigated eight were found in both subtidal and intertidal zones. Individuals were collected on an *ad hoc* basis whenever they were encountered and held in tanks of aerated seawater at ambient temperature (~1.5°C, typical of local summer seawater temperatures at this location) and synchronous photoperiod for summer conditions, in the aquarium facility of the Rothera Bonner Laboratory until used for measurement (normally within 24 hours of collection).

Table 5.1 Summary of number of individuals and mean individual mass of species examined in the current study

Class	Species	No. of Intertidal individuals	No. of Subtidal individuals	Mean individual wet mass (g)
Enopla	*Antarctonemertes validum*	11	6	0.025
Malacostraca	*Prostebbingia gracilis*	31	8	0.008
Copepoda	*Tigriopus angulatus*	90	32	0.00012
Gastropoda	*Laevilittorina caliginosa*	12	22	0.0026
Echinoidea	*Sterechinus neumayeri*	12	8	2.80
Polychaeta	*Barrukia cristata*	4	20	0.212
Gastropoda	*Margarella antarctica*	8	11	0.118
Gastropoda	*Nacella concinna*	24	16	1.273
Arachnida	*Rhombognathus gressitti*	32	0	0.00002
Pycnogona	*Achelia communis*	8	0	0.006
Asteroidea	*Odontaster validus*	0	7	2.39

Supercooling point measurement protocol

Supercooling Points (SCPs) of small (< 3mm) species were measured using a Mettler Toledo DSC820 Differential Scanning Calorimeter (DSC, Mettler Toledo Ltd, Leicester, UK). The standardised protocol was to place up to 25 animals in an aluminium sample pan that was then hermetically sealed and cooled at 1°C/min^{-1} from +2 to -30°C. This protocol allows differentiation between the individual SCPs of each animal (see Worland and Convey 2001 for full details). Larger species were placed in tubes with a fine wire thermocouple (cu/con 0.2mm diameter) held against their bodies. After plugging the neck of the tube with tissue paper, tubes were placed in a low temperature cryo-bath (Thermo Haake P2 circulator) and cooled as per the DSC protocol. The SCP of individual animals was taken as the beginning of the exotherm produced by the release of the latent heat of freezing of the animal's body fluids (Fig. 5.1).

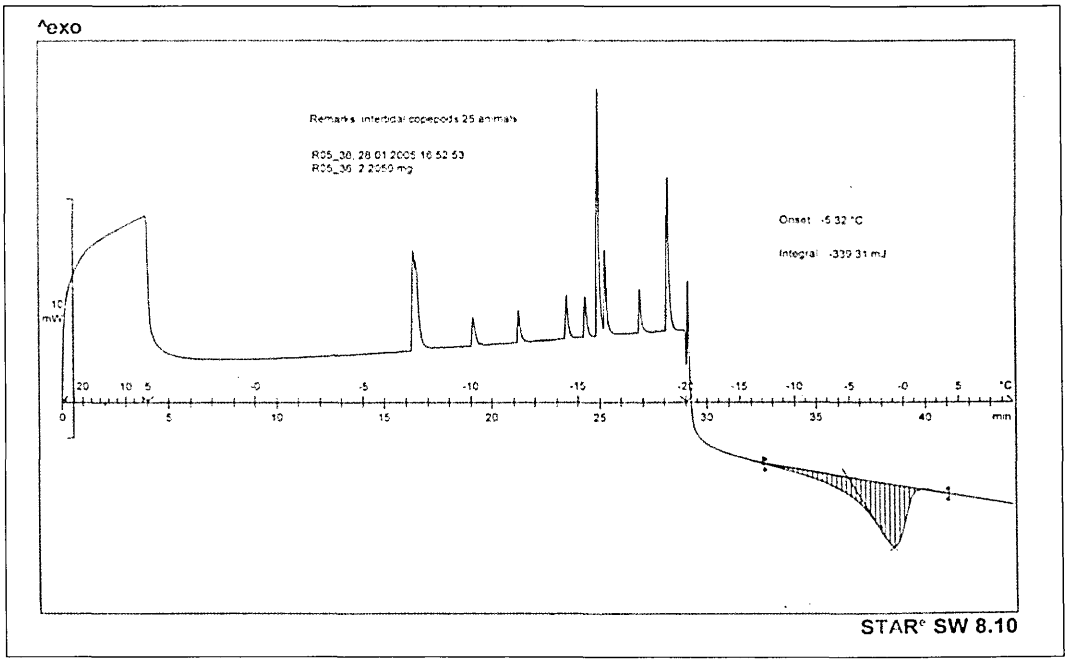


Fig. 5.1. DSC plot showing SCPs of multiple animals, in this example 25 intertidal specimens of *Tigriopus angulatus*.

Survival of *Nacella concinna* after freezing stress, experimental protocol

To investigate the summer acclimated supercooling ability and subsequent recovery of the limpet *N. concinna*, batches of 8 individuals were each attached to a separate thermocouple and placed in suitably sized tubes as described above. On immersion in the cryo-bath, batch 1 (intertidal animals) were cooled at 1°C min^{-1} from + 1.5 °C (ambient temperature) to –10 °C followed by immediate re-warming at the same rate, in order to establish whether *N. concinna* can survive ice formation within its tissues. A second batch of intertidal individuals was cooled at a rate of 0.1°C min^{-1} to –9°C, held at this temperature for 60 minutes and then re-warmed at the same rate, in order to investigate the effect of cooling rate on survival ability. As the mean SCP of this species was found to be -5.6°C subsequent batches of both intertidal and sublittoral animals followed the same cooling and re-warming protocol but were held at –6°C for 60 minutes. After these experimental exposures the animals were transferred to labelled 200ml beakers of seawater held at the aquarium ambient temperature (*c.* +1.5°C). Individuals were placed upside down i.e. foot uppermost, and those that were able to right themselves (i.e. complete a normal behaviour, cf. Peck et al. 2004) and were exhibiting normal behaviour 48 hours after exposure were recorded as having survived.

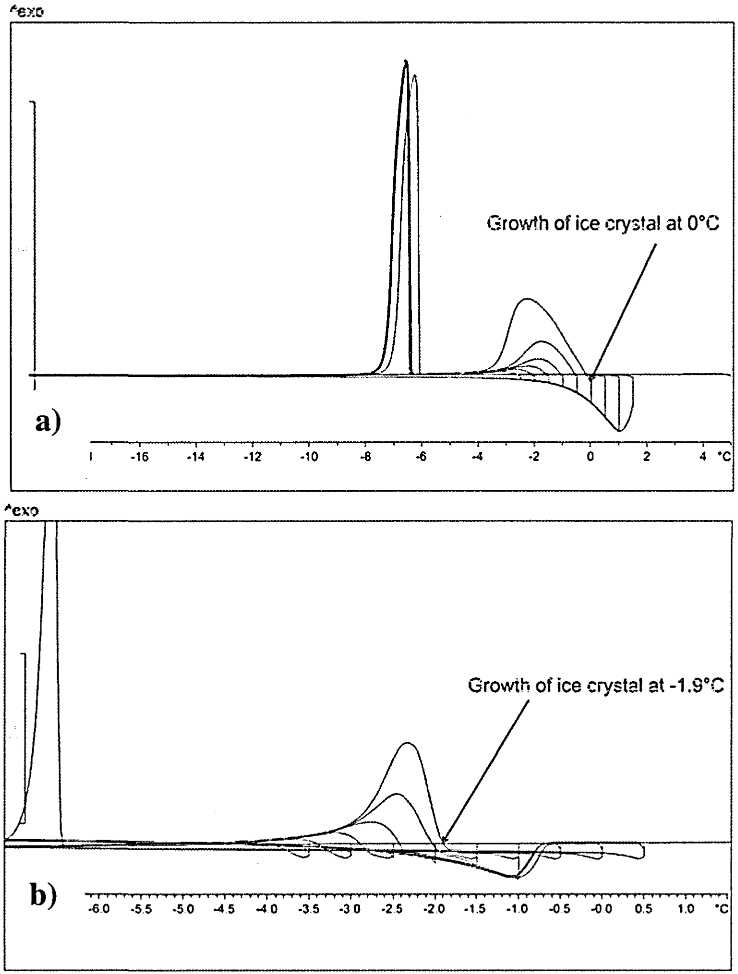
Overwinter survival in the intertidal zone

Three $1m^2$ quadrats were excavated towards the end of an Antarctic winter (September 2004) to investigate the presence of living macrofauna in situ in the intertidal zone (Plate 5.1) Taxa present were identified to the lowest possible taxonomic level and abundances recorded. No SCP measurements could be performed on these individuals, as the necessary equipment or expertise were not available at Rothera Research Station during the Antarctic winter.

Plate 5.1 Winter intertidal quadrat excavation, South Cove. Sampling was carried out on 04 September 2004 at low water spring tide (0.47m above chart datum).

Presence of thermal hysteresis proteins

One method commonly used to test for the presence of thermal hysteresis proteins is to freeze a sample of body fluid (haemolymph) then thaw it until only a very small ice crystal remains (Hansen and Baust 1988). If THPs are not present, the ice crystal will start to regrow immediately the sample is then cooled below 0°C. The presence of THPs will cause a delay in the initiation of growth of the ice crystal until the temperature of the sample is a few degrees (typically 2 - 5) below 0°C. In order to establish whether THPs were present we measured the changes in heat flow using the DSC (for a similar method see Worland and Lukesova (2000)). Samples were sealed in a 40µl aluminium sample pan and cooled (1°C min^{-1}) to –20°C (to ensure complete freezing). The sample was then warmed at the same rate to approximately +0.5°C and the melt endotherm observed. This cooling and warming temperature cycle was repeated several times, but each time the upper temperature was reduced by 0.5°C. As the upper temperature falls below zero, melting is incomplete (i.e. an ice crystal remains in the sample). Any delay in growth of the ice crystal (thermal hysteresis) is measured as the delay (in degrees centigrade) of the exotherm produced by the latent heat of freezing. Example data of a sample containing no THP activity (water) and a sample of haemolymph from *Tenebrio molitor*, a beetle known to produce THPs (Tomchaney et al. 1982) are included in Fig 5.2 a and b.



British Antarctic Survey

Fig. 5. 2. Cooling and warming cycle of a) of pure water b) haemolymph of larvae of the beetle *Tenebrio molitor*, which is known to produce THPs. Temperature scale,°C is shown below each plot

Data Analyses

Mean and median SCPs were calculated for each species. Data were tested to check compliance with assumptions for ANOVA (normality and homoscedacity) and $\log_{10}$ transformed where appropriate (*Tigriopus angulatus, Laevilittorina caliginosa* and *Prostebbingia gracilis*). Student's t tests were used to test for significant difference in mean SCP between intertidal and subtidal subsets of each species. Histograms of SCP distribution of each the study species were used to identify any bimodality in SCP distributions (typically present in many terrestrial arthropods, see Rothery and Block 1992, Worland and Convey 2001). In order to investigate the relationship between measured SCP and animal size, mean SCP and wet mass values were log transformed to permit the construction of a line of best fit and mathematical description.

RESULTS

Environmental variability

Mean intertidal temperatures ranged from -4 to +11.8°C over the collection period (December- January 2004/5). Mean winter minima of -15°C in the high intertidal were recorded while the low intertidal varied less and for much of winter temperatures remained relatively constant at around –5°C (Chapter 2)

SCP variability within and between species

There were statistically significant differences in SCP across the study species (ANOVA $F_{7,\,289} = 65.11$, $P<0.001$) and between species in each zone (ANOVA $F_{7,\,289}=9.91$, $P<0.001$) (Table 5.2)

Table 5.2 Results of GLM ANOVA comparing SCP by species and zone.

Source	**DF**	**Adj MS**	**F**	**P**
Zone	1	0.01715	1.13	0.289
Species	7	0.98757	65.11	<0.001*
Species*Zone	7	0.15032	9.91	<0.001*
Error	289	0.01517		

Supercooling data for the study species are presented in Fig. 5.3. No study species showed evidence of bimodal distributions in SCP. Mean SCPs of the study species varied from –5.5°C (*N. concinna*) to –23.1°C (*R. gressitti*). The highest SCP was -2.9°C (*N. concinna*) and lowest -27.6°C (*R. gressitti*). The smallest species, *R. gressitti* and *T. angulatus* had the lowest SCPs and *T. angulatus* also showed the widest variation in SCP (Fig. 5.3). There was an inverse correlation between the mean body size ($\log_{10}$ wet-mass) of a species and its mean SCP ($y = -0.0981 + 0.801$ $r^2 = 0.838$, $p < 0.001$). Three species (*Margarella antarctica*, *N. concinna* and *T. angulatus*) had significantly different SCPs in subtidal and intertidal populations (Table 5.3), with those of subtidal *T. angulatus* being significantly lower and more variable, while those of *M. antarctica* and *N. concinna* were higher in the subtidal than the intertidal zone.

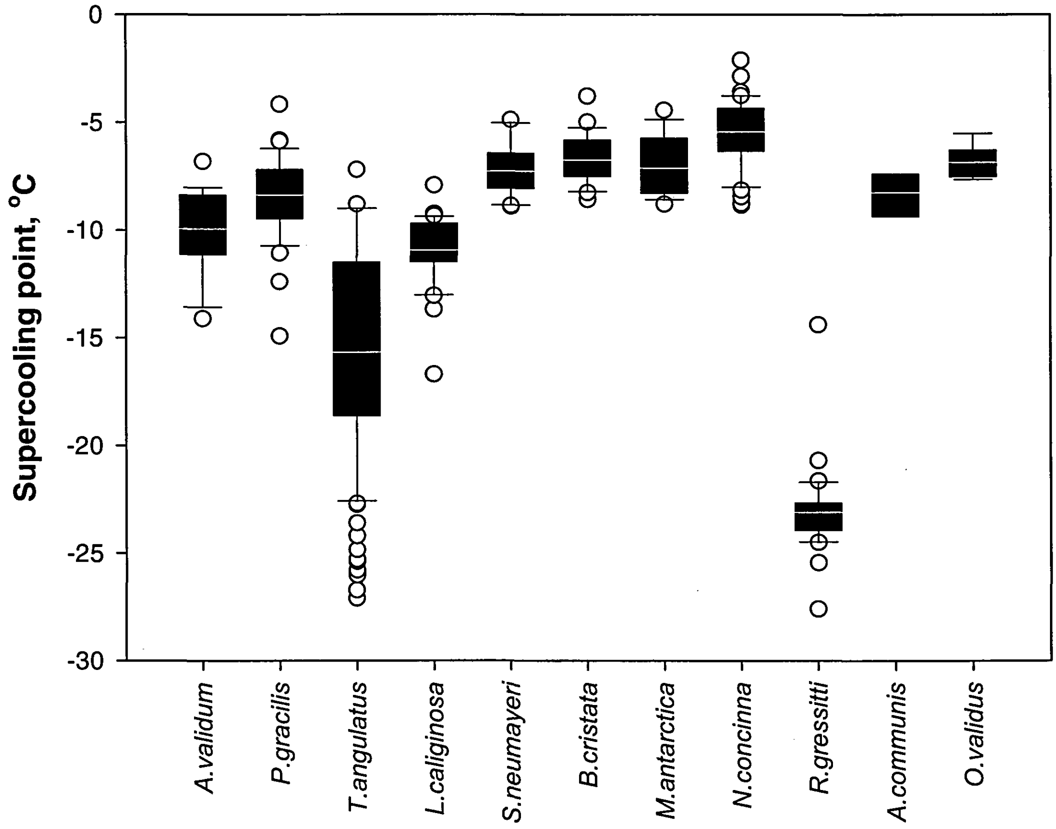


Fig. 5.3. Box whisker plot showing median (white line), 25th, 75th percentiles (upper and lower limits of box) of SCP values for each species. Whiskers (error bars) above and below the box indicate the 10th and 90th percentiles. Open circles denote outliers.

Table 5.3 Comparison of mean SCPs of intertidal and subtidal populations of eight species.* $p<0.05$

Species	Mean Intertidal SCP, °C	Mean Subtidal SCP, °C	DF	T	P
Antarctonemertes validum	-9.68	-10.50	7	0.65	0.53
Prostebbingia gracilis	-8.24	-8.91	18	1.46	0.16
Tigriopus angulatus	-14.96	-17.73	48	2.24	0.03*
Laevilittorina caliginosa	-10.83	-11.01	14	0.50	0.63
Sterechinus neumayeri	-7.57	-6.86	12	-1.24	0.24
Barrukia cristata	-6.80	-6.75	5	-0.18	0.87
Margarella antarctica	-7.93	-6.56	12	-2.84	0.015*
Nacella concinna	-5.52	-4.75	16	-2.11	0.05*

Nacella concinna survival

The mean SCP for *N. concinna* measured in this study was -5.6 °C. The first batch of intertidal individuals (cooled to -10°C at 1°C min^{-1} and then warmed at the same rate) all showed complete freezing exotherms at temperatures above -8.4 °C. These individuals had a 75% recovery rate after a period of 48 hours. The second batch of intertidal animals (cooled to -9°C at 0.1°C min^{-1} and held at this temperature for 60 minutes) also showed complete exotherms. Here the survival rate after 48 hours was reduced to 5%. Further subtidal and intertidal batches of animals, cooled to -6°C at a rate of 0.1°C min^{-1} and held for 60 minutes, had survival rates of 67% and 95% respectively after 48 hours (7 of 8 animals in subtidal and 6 of 8 in the intertidal subset showed complete exotherms). Intertidal individuals had significantly ($t_{18} = -4.5$, $p<0.01$) higher rates of survival following this cooling regime than those in the subtidal.

Survival in the Antarctic littoral zone in winter

The survey data showed that a number of taxa clearly have the ecophysiological capability to survive year-round temperature conditions in situ in the Antarctic intertidal zone. Within the three 1m^2 intertidal quadrats excavated, a total of 11 species (7 classes) of mobile taxa and 6 species (3 classes) of encrusting taxa were found to be present and alive under the top layer of cobbles (Table 5. 4).

Table 5.4. List of the 17 species found in winter samples. • denotes mobile taxa.

Class	Family/Genus species	
Gastropoda	*Nacella concinna*	•
	Margarella antarctica	•
	Laevilittorina caliginosa	•
Echinoidea	*Sterechinus neumayeri*	•
Asteroidea	*Odontaster validus*	•
Malacostraca	*Prostebbingia gracilis*	•
	Notasellus sarsi	•
	Munna antarctica	•
Polychaeta	*Barrukia cristata*	•
	Protolaeospira levinsi	
Anopla	*Antarctonemertes validum*	•
Turbellaria	*Pseudoceros* sp.	•
Hydrozoa	*Tubularia* sp	
Gymnolaemata	*Celleporella antarctica*	
	Fenestrulina rugula	
	Ellisina antarctica	
	Inversiula nutrix	

Presence of Thermal Hysteresis Proteins

Of the three species tested for the presence of THPs (*N. concinna*, *Achelia communis* and *Antarctonemertes validum*) only *A. validum* showed evidence for the presence of THPs, with c.1.4 degrees of thermal hysteresis in the haemolymph (Fig. 5.4).

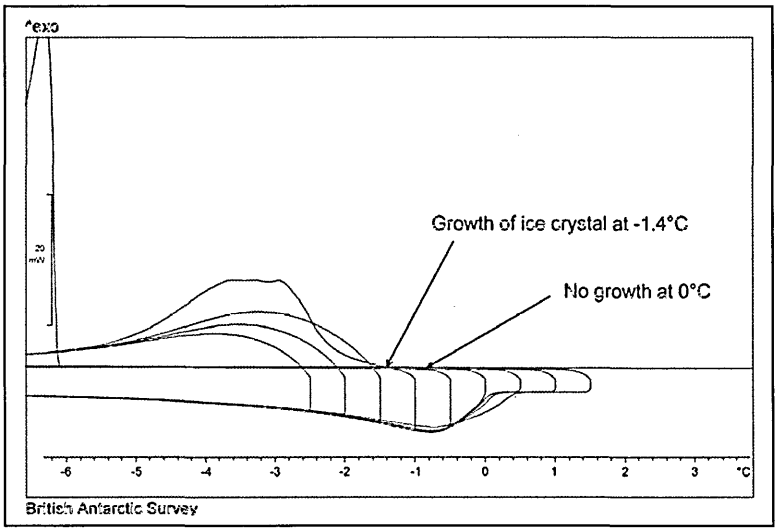


Fig. 5.4. Enlargement of section of DSC plot for *Anatrctonmertes validum* showing depression of freezing point to –1.4°C

Model fitting.

Models were constructed and tested to describe the relationship between SCP and body mass (m). This involved fitting a power law model of the form $SCP = a + b/m^c$, giving estimates of a, b and c: $SCP = -6.29 - 0.6534/m^{0.299}$. The fit of this model (Fig. 3) was very good ($r^2 = 0.97$).

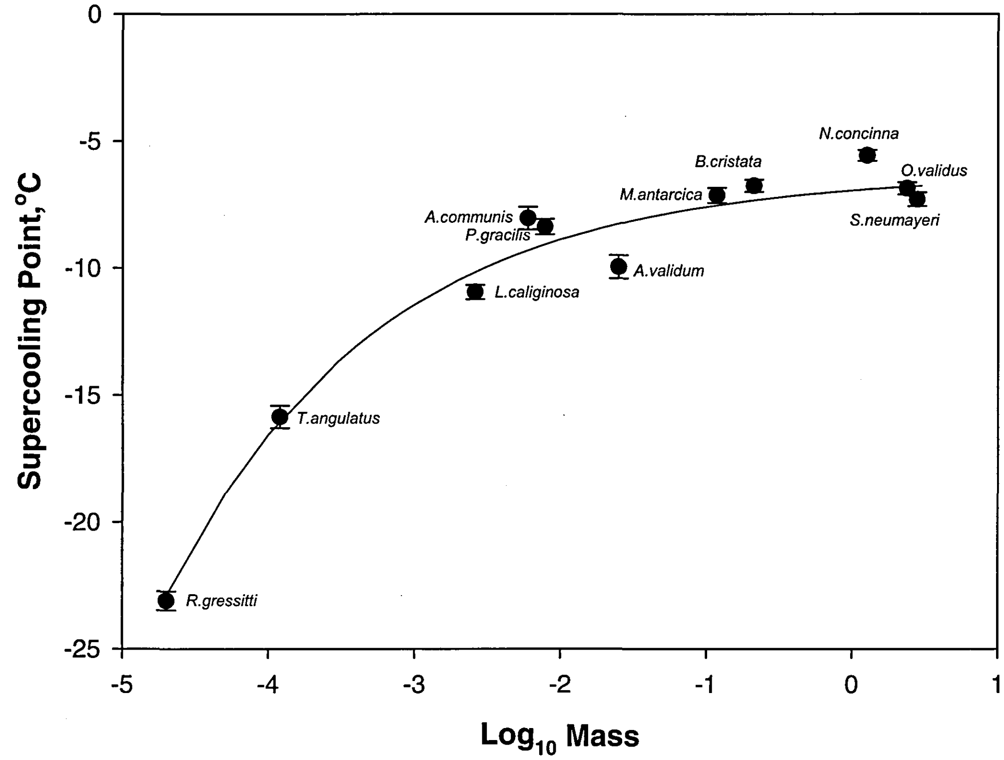


Fig. 5.5. Fitted power law model of relationship between supercooling point and wet mass (m) of the invertebrates studied. $SCP = -6.29 - 0.6534/m^{0.299}$ ($r^2 = 0.97$).

DISCUSSION

The current study presents summer cold tolerance data for the widest phylogenetic and size ranges of invertebrates published to date from the Antarctic intertidal zone (11 species of 9 classes ranging in size over 5 orders of magnitude) and is the first to report data from several major taxa. The data indicate that a range of Antarctic intertidal and subtidal invertebrates have cold tolerance characteristics (lowered freezing points) well below those of their surrounding seawater. While it is clear that SCP values alone may not give a full picture of the cold hardiness of a species (Bale 1993, Sinclair et al. 2003), it is also the case that those Antarctic species that have been studied in detail generally show little or no evidence of significant pre-freeze damage or mortality (e.g. Convey, 1996b, Worland and Convey, 2001). However, these findings are preliminary and should now be strengthened by, first, more detailed studies of the individual species responses to sub-zero exposure above their "classical" SCP and, second, studies across the annual cycle.

Clear and significant differences in levels of cold tolerance between the study species were found (Fig. 5.3, Table 5.3). While a general inverse relationship between body mass and supercooling capacity in ectothermic animals is recognised (Lee and Costanzo 1998), this study appears to be the first attempt to quantify this relationship. A scaling exponent of approximately 0.3 suggests a relationship between an animal's linear dimensions and its SCP. Modelling of SCP distributions of Antarctic mites has shown that they behave like supercooled water droplets (Rothery and Block 1992), smaller droplets supercooling to lower temperatures (Bigg 1953). Separately, it has also been shown that body water content is related to SCP in mites, with small animals (containing less water) being less likely to freeze at higher sub-zero temperatures (Pugh 1994). The addition of SCP data reported from a range of previously published studies also fit this model well ($r^2 = 82.7\%$, Fig 5.6), suggesting the existence of an underlying general principle

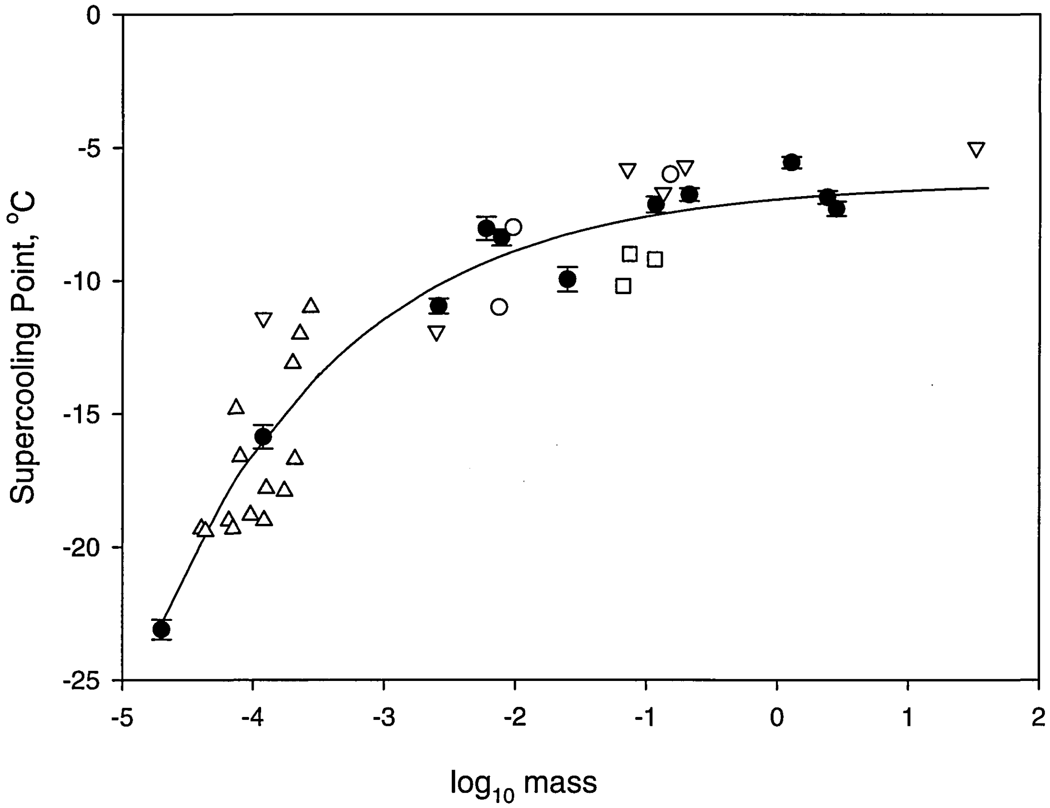


Fig. 5.6. Fitted power law model of relationship between supercooling point and wet mass (*m*) of taxa investigated in the current study (●) and reports from previous studies. Data are taken from Sinclair et al. 2004 (□); Pugh 1994 (△); Block 1984 (▽); Miller 1982 (○) (r^2= 0.827).

Differences in SCP between intertidal and subtidal populations of eight species were not significant in five cases, and significant in three, with examples of intertidal animals with both higher and lower mean SCPs than subtidal representatives of the same species. It is clear, therefore, that the initial hypothesis (of systematic differences in SCP patterns between occupants of the intertidal and subtidal) does not apply generally across species. The subtidal and intertidal environments typically have very different thermal characteristics with seasonal fluctuations in the sea temperature ranging from ~-1.8°C to +2°C compared to summer fluctuations in the intertidal varying from >15°C to -3°C. During winter, even more extreme intertidal temperatures can be experienced, occasionally reaching a minimum of –12°C in the low intertidal and –16°C near the high spring tide level. Given the potential for local acclimation. (Murphy 1983, Ansart and Vernon 2003, Sinclair et al. 2004) it is surprising that we did not find intertidal individuals to have lower SCPs than those in the warmer subtidal.

No previous studies have investigated Antarctic intertidal faunal richness during winter, and only one study (at the current site) has documented evidence of possible permanent intertidal colonisation, with 4 year old bryozoan colonies present on intertidal rocks (Chapter 3, Waller et al. 2006a). The summer SCPs of taxa measured in the current study were sufficiently low to allow these animals to avoid freezing with the minima experienced during the summer period, but also insufficient to allow most species to cope with winter extremes. However, it is also clear that some species can tolerate winter conditions in situ in the intertidal, although no data are yet available on winter cold tolerance characteristics. It is likely that the taxa studied will be able to vary their supercooling or cold tolerance ability on a seasonal timescale (a feature well known in studies of Antarctic terrestrial invertebrates (Cannon and Block 1988, Block 1990, Convey 1996 b)), a factor that it was not possible to address in the current study. Our data demonstrate that the limpet *N. concinna* is capable of freeze tolerance and can survive all of the osmotically active water freezing. Although similar studies have not been carried out on other species, the utilization of a freeze tolerance strategy obviously allows animals to survive to temperatures below measured SCPs.

It is known that some temperate intertidal molluscs and barnacles can seasonally alter their freezing resistance. The barnacle, *Semibalanus balanoides*, can cope with extremes ranging from –6°C in summer to –17.6°C in the winter (Crisp et al. 1977). The summer SCPs of most species in the current study were nearly all lower than that of *S.*

balanoides, but not low enough to enable freezing avoidance at minimum winter temperatures at this locality. The small intertidal halacarid mite, *R. gressitti,* had SCPs more similar to those achieved by similar-sized terrestrial arthropods than by the marine taxa found in the lower intertidal zone. It is well known that many terrestrial arthropods can lower their SCP in response to factors such as the onset of winter conditions (cold hardening) moulting (Worland et al. 2006) or starvation (Cannon and Block 1988, Block 1990), often giving rise to bimodal SCP distributions (Rothery and Block 1992, Worland and Convey 2001). However, *R. gressitti* does not appear to follow the pattern typical of terrestrial mites, lacking a subgroup with relatively high sub-zero SCPs (with only one individual of 32 measured having an SCP of -14°C, all others falling in the range -21 to –27°C). Even under summer conditions, mites in Antarctic terrestrial habitats (Cannon and Schenker 1985) and South Georgia (sub-Antarctic) intertidal environments (Sømme and Block 1982, 1984, Pugh 1994) are found to have bimodal distributions with both high and low groups of SCPs. *R. gressitti* may have been forced to adopt a different cold tolerance strategy from those more typical of terrestrial Antarctic mites, through a combination of the requirement to feed and its existence in a permanently wet habitat with inherent risk of inoculative freezing. The individuals taken from the field and analysed in this study were active and feeding on algae growing on the surface of intertidal rocks and cobbles. This species may exhibit permanent cold tolerance, thereby overcoming the problems associated with ice nucleation caused by particles of food and bacteria in its gut (Worland and Lukesova 2000) and inoculative freezing from external ice nucleation. Sømme (1986) described an analogous instance of permanent cold tolerance in the continental Antarctic springtail, *Cryptopygus sverdrupi*, an inhabitant of inland nunataks where air temperatures are almost permanently below freezing and there is a likelihood of microhabitat temperatures crossing the freezing boundary frequently even during the species' very short period of activity during the summer.

Although there have been previous studies investigating the presence of THPs in polar fish (Duman & DeVries 1972, DeVries 1984), there is only one previous report of THPs being found in an Antarctic terrestrial arthropod, the oribatid mite *Alaskozetes antarcticus* (Block & Duman 1989) and to date *Mytilus edulis* from Norway appears to be the only intertidal invertebrate for which antifreeze proteins may play a role in freezing tolerance (Theede et al. 1976). There is some question over the generality of this report, since no antifreeze proteins were found in *Mytilus* sp. Subsequently collected from temperate east coast USA sites (Loomis 1995). Of the three species of intertidal invertebrates tested for the presence of THPs in the current study, only the nemertean *A. validum* showed any evidence of thermal hysteresis, with 1.4 degrees of freezing point depression in its haemolymph. As such, this is the first Antarctic, and only the second marine, invertebrate likely to possess THPs.

Chapter 6 – Community variability along a latitudinal gradient

Chapter 6 – Community variability along a latitudinal gradient

INTRODUCTION

More than 100 million years ago Antarctica was part of the supercontinent of Gondwana. In the early Cenozoic (100- 60 million years ago (Ma)) the supercontinent began to fragment into the familiar continents of today, and Antarctica drifted south towards the pole. The opening of the Drake Passage and formation of the Antarctic Circumpolar Current (ACC) around 30-35 million years ago resulted in the isolation of Antarctica and the removal of the last intercontinental land bridge. These factors have long been thought to form a highly effective barrier to dispersal of most species (Bergstrom & Chown 1999, but see Clarke et al. 2005, Barnes et al. 2006b). The movement of the Antarctic continental plate and resultant volcanic activity has been responsible for the formation many of the peri-Antarctic islands including those of the Scotia Arc (the archipelagos of South Georgia, South Sandwich Islands, South Orkneys and South Shetlands, although South Georgia contains continental elements) (Bergstrom et al. 2006). These archipelagos provide the most likely 'stepping stones' for the dispersal of organisms both into and away from western Antarctica (Picken 1980, Barnes et al. 2006b). Studies of the Magellan – Antarctic region have been providing important insights into the presence and nature of latitudinal clines in diversity (Clarke & Johnston 2003). The progressive isolation, cooling and periodic glaciations of Antarctica has lead to an attenuation of (terrestrial) groups of taxa along the Scotia Arc (Convey 2001a, Chown & Convey in press b), although these patterns are largely on a geological timescale, or in the marine realm (Moe & DeLaca 1976, Crame 2000, Boschi & Gavio 2005, Linse et al. 2006) However the classical pattern of declining diversity from the tropics to the poles (as seen in terrestrial biomes and

Antarctic macroalgae) is much less clear in the few marine animal taxa for which strong data exist (Barnes & De Grave 2000, Crame 2000, Clarke & Johnston 2003, Linse et al. 2006 but see Boschi & Gavio 2005). This is particularly evident in the southern hemisphere where, south of 45 degrees latitude, there are few landmasses other than small remote islands until the Antarctic continent is reached. Patterns of intertidal community diversity in this region are poorly documented. The only previous study, on encrusting communities, found decreasing dominance of Bryozoa with increasing latitude, high latitude communities being almost exclusively (98% of taxa present) composed of spirorbid polychaetes (Barnes & Arnold 1999).

Strikingly, balanomorph crustaceans (acorn barnacles) are almost absent from the Antarctic littoral zone, and rocky shores seem denuded by comparison with non-polar localities. However, until recently, very few quantitative investigations of diversity or community structure had been undertaken on Antarctic shores, primarily due to the long held view that it is too extreme an environment to support more than a transient summer population of a few vagrants (Shabica 1972, Convey et al. 2000) or the occasional encrusting species in more sheltered rock pools (Barnes et al. 1996). Peck et al. (2006) recently reviewed environmental constraints on life history strategies in Antarctic subtidal, intertidal and terrestrial environments. New investigations of the Antarctic coastal regions are revealing very strong structuring forces of iceberg scouring in the shallow subtidal and even much deeper water (Gutt 2001, Brown et al. 2004) and daily frequencies of impacts on the lower shore (Smale et al. in press). Despite this, and rapid and considerable temperature variability, a recent study of a single locality on the Antarctic Peninsula, reported previously unanticipated levels of species richness, biomass and diversity in cryptic intertidal habitats (Chapters 3, 4, Waller et al. 2006a).

In the current study, which aimed to extend the coverage achieved from this single locality, patterns of intertidal species richness and diversity were investigated at several locations along the Scotia Arc, and also at the Falkland Islands on the South American continental shelf, in order to provide an initial assessment of the generality of the findings. This study effectively provides a latitudinal or environmental transect from a southern cold temperate oceanic location (Falkland Islands), through the sub-Antarctic (South Georgia) to the northern maritime Antarctic South Orkney Islands and the Antarctic Peninsula, and forms the first comparative study of intertidal organisms across this region.

METHODS

Sampling Protocol

Sampling was carried out at locations between the Falkland Islands (51°S, 59°W) and Adelaide Island, Antarctic Peninsula (67°S, 68°W) (Fig. 6.1.) during November and December 2004. Samples of fauna were collected in both intertidal and supralittoral terrestrial environments at a minimum of two separate sites at each location (see Fig.6.2. for schematic protocol). Unlike the studies described in the preceding chapters, conducted exclusively at Rothera Research Station, where subtidal sampling was possible, logistical constraints precluded this at Falkland Island and Scotia Arc localities.

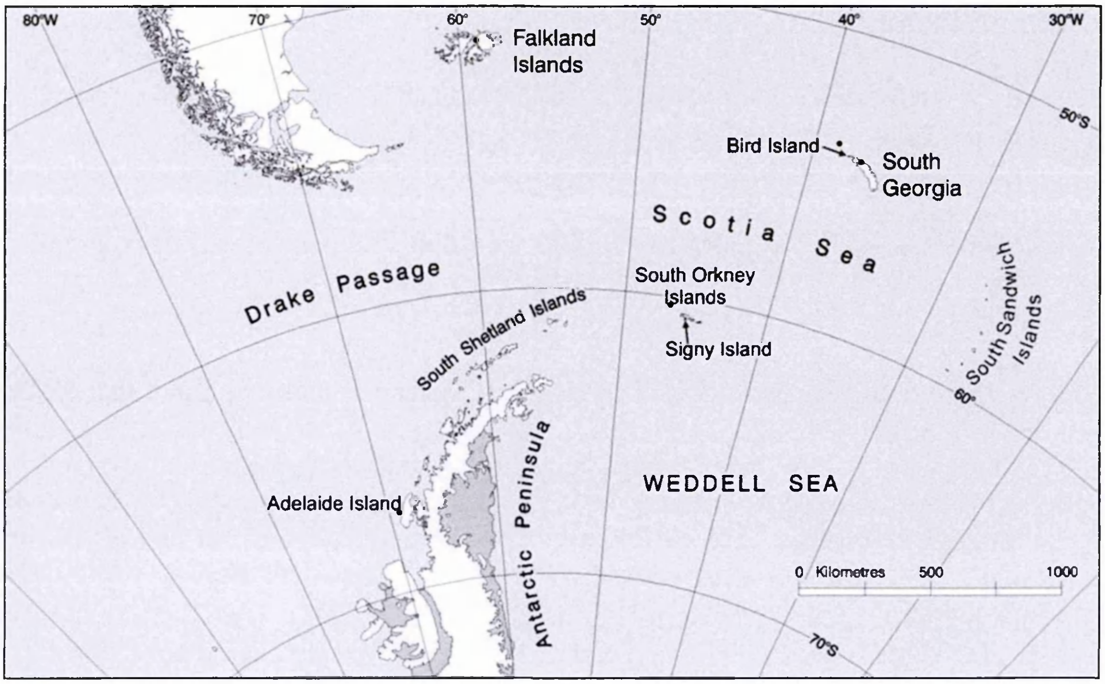


Fig. 6.1. Sites sampled (from north to south): Falklands, Bird Island, South Georgia, Signy Island, Adelaide Island.

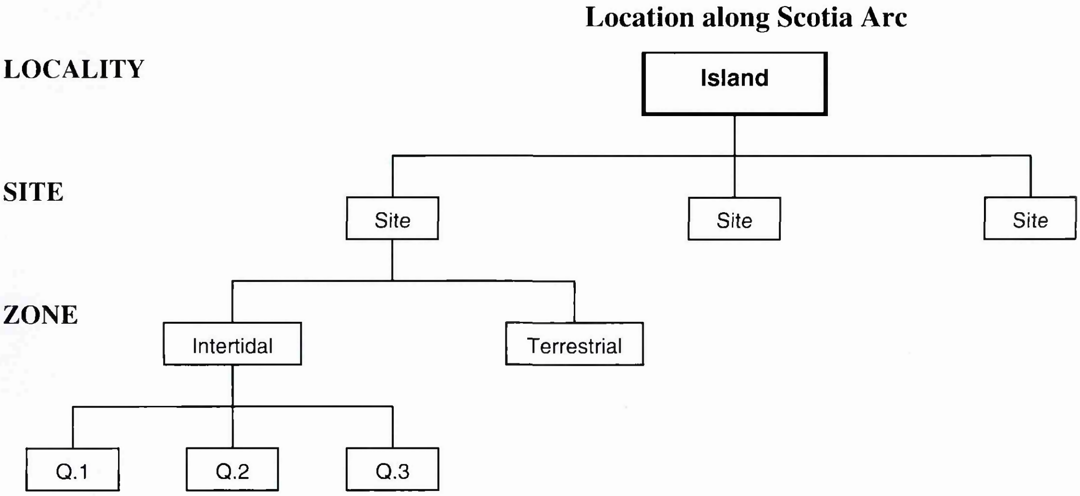


Fig. 6.2. Schematic representation of sampling protocol. 3 replicate quadrats (Q.1, Q.2 and Q.3) were completed for each zone at each site at each locality.

Intertidal sampling protocol

Three randomly placed 0.25m^2 replicate quadrats were used to collect samples at each intertidal site. Within each quadrat, all mobile taxa were collected and returned to laboratory for identification. Where dense aggregations of ecologically dominant species were found, care was taken to check for cryptic mesofauna within these biogenic microhabitats. Rocks with encrusting fauna present were collected from each quadrat in order to identify and estimate abundances of taxa present. On occasions where this was impractical (e.g. where sessile taxa were attached to bedrock), identification and estimates of abundance were completed *in situ*. Abundances of encrusting fauna on rocks were estimated by counts on sub-samples of 5 randomly selected rocks from each site. All taxa were identified to the lowest taxonomic level possible, and the number of individuals of each taxon counted. Colonies of animals, such as Bryozoa (Gymnolaemata), were each recorded as one unit. The surface area of each rock was estimated using a non-elastic mesh of 1 cm^2 grid size following Barnes et al. (1996).

Terrestrial sampling protocol

A similar overall protocol was followed to that of the intertidal sampling. Terrestrial samples typically consisted of very high numbers of small organisms, so samples from each quadrat were sub-sampled and the data scaled up to represent unit area. Samples of ~ 25 cm^2 were collected and the percentage cover of each habitat (grass, moss and /or algae) in each 0.25m^2 area was estimated. All visible animals within the sample were collected using forceps and samples of moss, algae and grass / soil were also removed to the laboratory and checked for fauna using a binocular microscope. Specimens were preserved in 80% ethanol for later identification. Habitat samples from Signy Island were stored in plastic boxes for planned subsequent Tullgren extraction of animals following transport by ship to Rothera Research Station. Unfortunately, these samples were lost, heavy sea ice delaying their arrival by approximately 8 weeks. In order to address this, additional samples were collected by staff at the Signy base, frozen and returned to Cambridge at the end of the field season. These samples were sorted by hand, but no live extractions were possible.

Taxon identification.

Fauna (both intertidal and terrestrial) were typically identified to a minimum of order level. Within problematic groups, taxa were separated into 'morphotypes' and designated as species 1, 2 etc. All species were conservatively identified i.e. where there was any uncertainty in differentiating between individuals they were classed as one taxon not two. Species designations within each taxonomic group in both intertidal and terrestrial zones were consistent within each locality but non comparable between locations. Thus for example "Collembola sp. 1" identifies a single species across sites at South Georgia but is not assumed to be identical to Collembola sp. 1 at sites on Adelaide island. As a result of this sampling approach, application of a gradient diversity index (e.g taxonomic distinctness (Clarke &Warwick 1998)) was not possible at species level. Univariate diversity measures such species richness, Pielou's evenness and Shannon H' diversity (Magurran 2003) were therefore used.

Study Sites.

Environmental factors such as solar radiation, temperature and sea ice cover/ice impact vary reasonably predictably with latitude (see Peck et al. 2006). For example, with increasing latitude, light climate becomes more extreme in duration. Ice impacts increase drastically with latitude south of ~53°S, decreasing again at ~72°S because of the lack of coastline and presence of icesheets. (The general environmental characteristics of the Falkland Is., South Georgia and Signy I. are summarised in Table 6.1 and Plates 6.1 and 6.2), and those of Adelaide I. are described in Chapter 2.

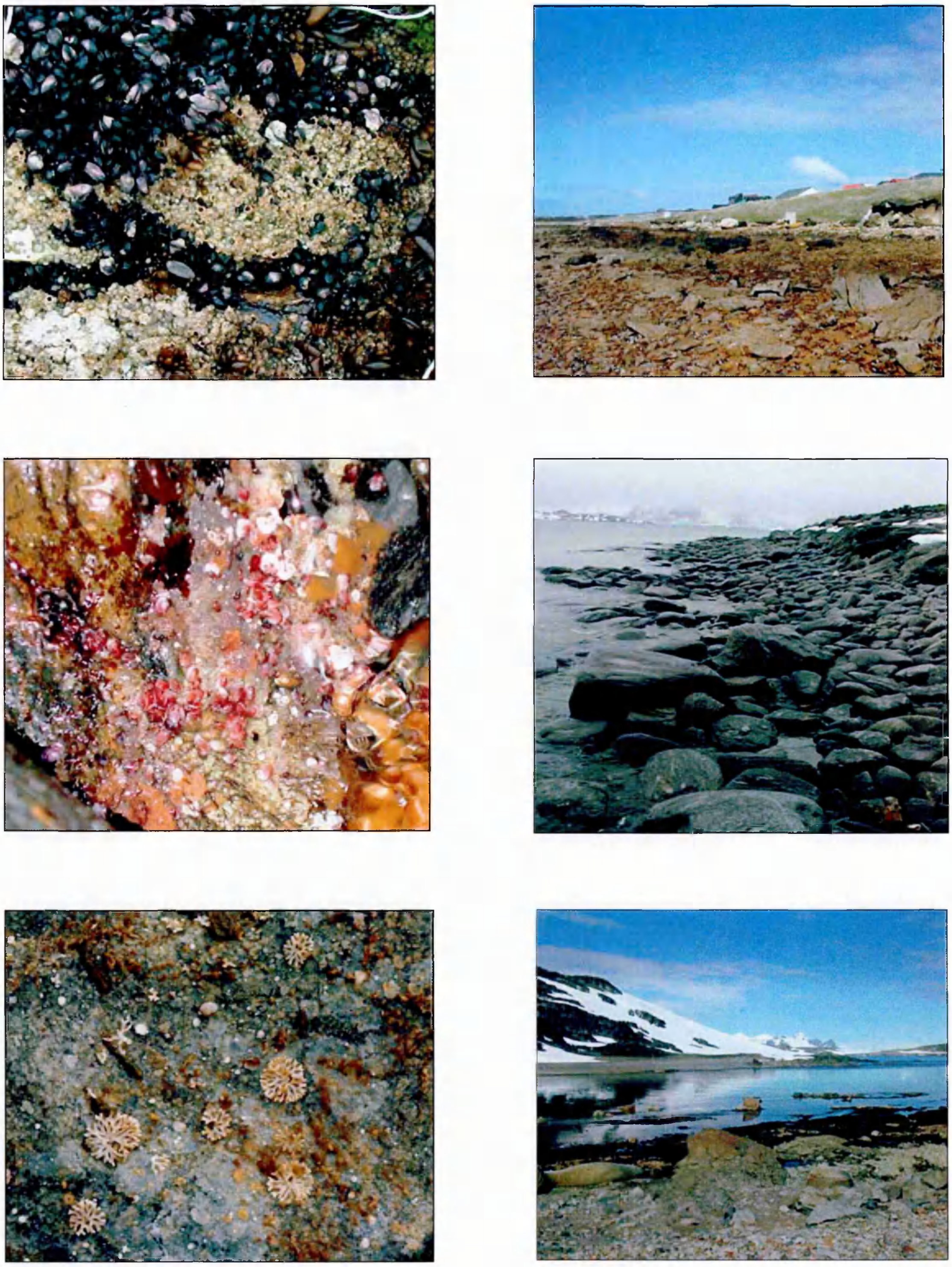
Tidal cycles, durations and ranges vary across the localities from the Falkland Is. with a regular semi diurnal cycle (Atlantic tidal regime) and tidal range of approximately 0.5m at neap tides to 2m at spring tides to a complex mixed diurnal / semidiurnal cycle at Rothera (Pacific tidal regime) with tidal ranges of ~ 0.3 to 2.0m at neap and spring tides respectively (Fig. 6.3).

Next page: Table 6.1. Overview of physical characteristics, environmental conditions and flora and fauna of sites on East Falkland and the Scotia Arc islands sampled in the current study. Sites on Adelaide Island are described in chapter 2.

Locality		Intertidal	Terrestrial
East Falkland	**Habitat description** i) physical characteristics	Substrata consist of a variety of habitats ranging from pebbles and cobbles interspersed with silt to bedrock and boulders.	Supralittoral habitats consisted of grasses and mosses over soil pebbles and bedrock. Sites were immediately adjacent to their intertidal counterpart.
	ii) Flora and fauna	Numerous species of large macroalgae common, including the giant kelps *Macrocystus pyrifera* and *Durvillea antarctica*, Filamentous green algae, *Ulva* sp. Rhodophytes inc. encrusting coralline *Lithothamnion* sp. and foliose species e.g *Iridea*	Numerous species (approximately 171) of vascular plants inc. grasses, sedges and mosses (Broughton & McAdam 2005).
		Obvious sessile faunal communities on upper and lower surfaces of substratum dominated by cirripedes and *Mytilus edulis chiliensis*. Other common species include the gastropods *Patiniger deayrata* and *Nacella mytilina* and gammarid amphipods.	Invertebrate taxa include ca. 18 species of spider, 250 species of insects with 39 families and 132 genera. (Pugh 2004, McDowell 2005)
	Temperature range	Sea temperature range from >12°C to 6 °C (Barnes et al. 2006b).	Mean air temperatures range from ~7°C to ~10°C but can be significantly warmer on west side of islands. (McDowell 2005)
	Disturbance due to ice/snow	Minimal / none due to ice encasement or scour.	Minimal, brief and localised cover snow in winter months.
	Disturbance due to marine mammals/ other	Impact of marine mammals negligible. Disturbance due to wave action/ degree of exposure – low to medium at sites sampled	Negligible

Locality		**Intertidal**	**Terrestrial**
South Georgia & Bird Island	**Habitat description** i) physical characteristics	Bedrock interspersed with boulders. Some areas of pebble and cobbles (South Georgia). Bedrock and boulders interspersed with compacted mud (Bird Island).	Supralittoral sites consisted of grasses, mosses and lichens over soil and bedrock (Plate 6.2)
	ii) Flora and fauna	Cumberland West Bay (S.Georgia) macroalgae including phaetophyes *Macrocystis pyrifera*, *Durvillaea antarctica* (giant kelp), rhodophytes (*Bostrychia* sp., *Ceramium rubrum, Cladonata* sp., *Iridaea cordata, Lithothamnion* sp. and filamentous green algae. No encrusting algae present in the intertidal zone. Fur seals *(Arctocephalus gazella)* and elephant seals *(Mirounga leonine)* seasonally abundant. King Edward Point (KEP) and sites on Bird Island had little macroalgae, mainly consisting of small rhodophytes and filamentous green algae *Enteromorpha* sp.	145 species of moss (Ochyra et al. 2002) and >30 vascular plants including 26 native, 2 endemics. 85 liverworts, 150 lichens. Invertebrates include 148 arthropods, 40 insects, 50 endemics, 4 spiders, 1 earthworm, enchytraeid worms, 1 land snail, 10 freshwater crustacea (Gressitt 1970, Smith 1984).
	Temperature range	Sea temperature range from >4°C to -0.5 $^{\circ}$C (Barnes et al. in press).	Small annual temperature range. Mean monthly air temperatures over the period 2002 to 2006 varied from a maximum of +6.75°C (February) to a minimum of -1.1°C (BAS meteorological database).
	Disturbance due to ice/snow	Intermediate. Some ice scour especially around glaciers (Pugh & Davenport 1997). Winter snow cover of intertidal zone but no icefoot.	Much of terrestrial environment covered by snow for ~ 4-6 months of year.
	Disturbance due to marine mammals/ other	High. Current estimates of fur seal *(Arctocephalus gazella)* populations around South Georgia and Bird I are in the region of five million. Breeding beaches on Bird Island in breeding season can hold 10,000 fur seals (D.Briggs pers comm.).	Can be high at some nearshore sites, especially around breeding beaches on Bird Island, and penguin colonies.

Locality		Intertidal	Terrestrial
Signy, S.Orkney Is.	**Habitat description** i) physical characteristics	Bed rock, boulder and cobble beaches (mainly quartz mica schists), negligible sediment content in interstices at sample sites.	Moss banks, lichens, alga (*Prasiola crispa*). Some areas of grass.
	ii) Flora and fauna	Some red algae. No obvious fauna on upper surfaces of rocks. High concentrations of the bivalves *Kidderia bicolor K.pusilla Mysella charcoti* and *Lissarca* sp. (Plate 6.1a)	Range of microarthropods and smaller inverts (Block 1984, Convey 2001a)
	Temperature range	Mean sea temperatures range from –1.86°C (winter) to + 1.6°C (summer) (Clarke & Leakey 1996)	Mean monthly air temperatures 1990-1999 ranged from –11.5 (August) to +0.6 (January) (BAS meteorological database)
	Disturbance due to ice/snow	High. Winter encasement in fast ice (mean duration 119 days (Clarke & Leakey 1996)) and scour in summer.	Summer ~40 years ago ~50% of surface free from snow (Holdgate 1967). Snow/ice cover has rapidly decreased since then Smith 1990 estimated ~30-40% summer snow cover. Precipitation 35-50 cm per annum, with much falling as rain in summer (Smith 1984).
	Disturbance due to marine mammals/ other	Can be high in places. Fur seal population has increased from less than 3000 individuals in 1977 to over 20 000 in 1995 (Hodgson et al. 1998).	Can be high in places.



a) **b)**

Plate 6.1. Typical intertidal assemblages, (a) and sites, (b). From top: Stanley, East Falkland Island (lat 51 ° 42'S), Middle, Signy I., South Orkney Is., (lat 60° 43'S), no encrusting and few vagile taxa found on upper surfaces of habitat but undersurfaces have relatively high cover. Bottom, Lagoon Island Marguerite Bay, Adelaide Island, latitude (67° 35'S), spatially variable assemblages present on undersurfaces of cobbles and boulders. Site substrata show increasing effect of the impact of ice scour and encasement with high latitude sites exhibiting typical "cobble pavement" structure and having few or no macrophytes present .

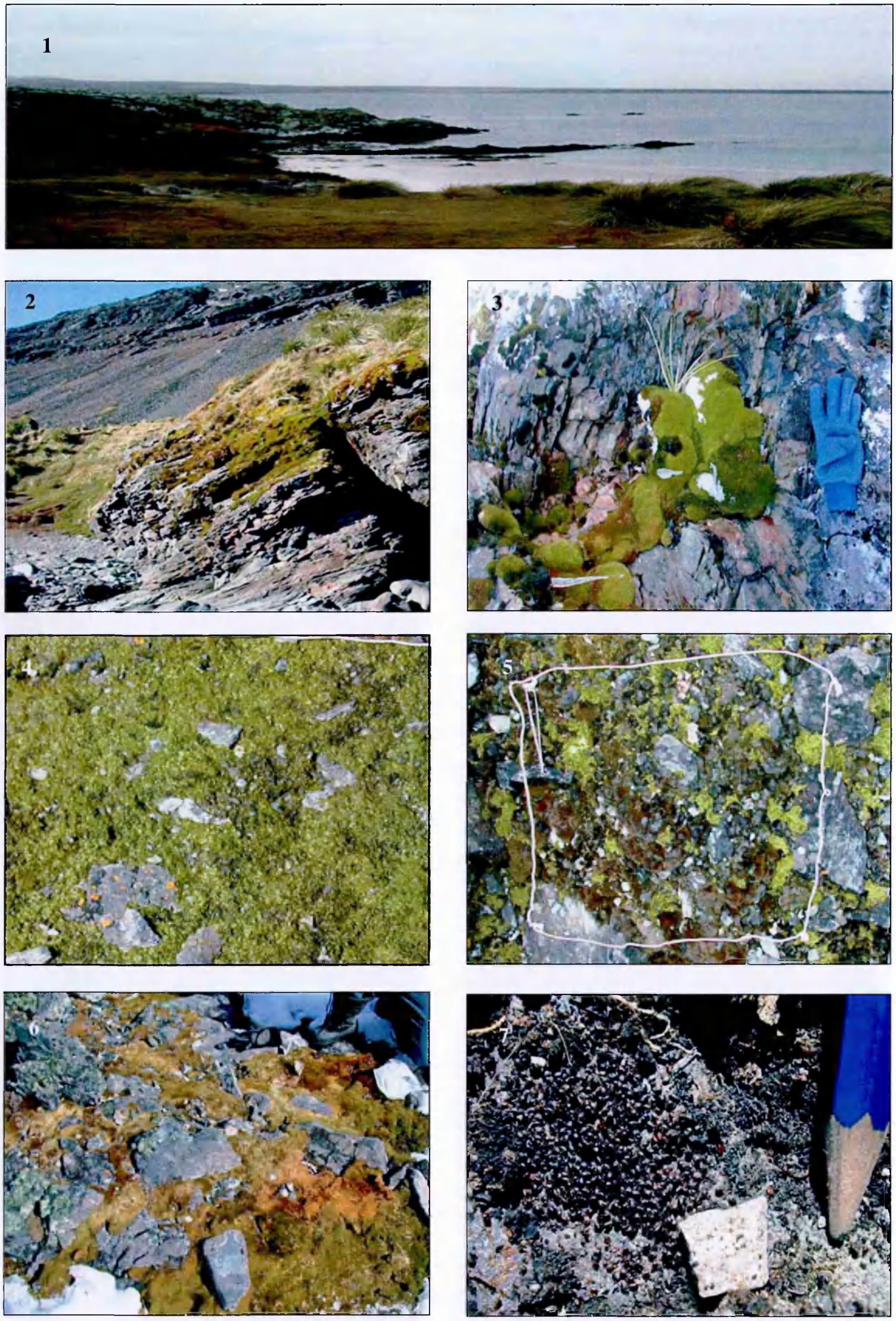


Plate 6.2. Typical nearshore terrestrial sites: From top: 1 Stanley, East Falkland Island (lat 51 ° 42'S);

2,3 Hope Point, Cumberland Bay East, South Georgia;

4,5 Signy , South Orkney Islands, (lat 60° 43'S).

Bottom 6,7, Lagoon Island Marguerite Bay, Adelaide Island, (lat 67° 35'S)

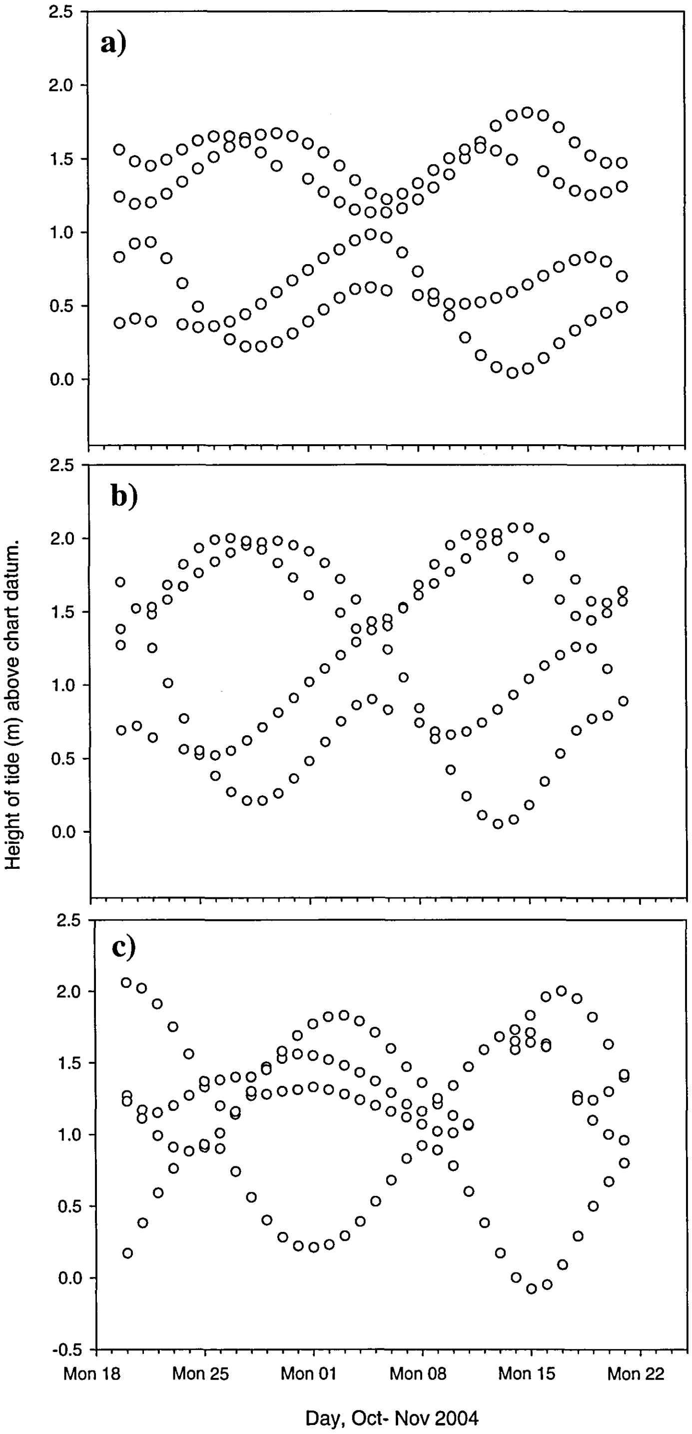


Fig. 6.3. Illustration of tidal cycles showing heights of high and low water at a) Stanley, Falkland Islands, b) Borge Bay, Signy Island and c) Rothera Point, Adelaide Island for mid October to mid November 2004.

Data Analyses.

Univariate and multivariate analyses using routines within the PRIMER software package (Clarke and Warwick 2001) were utilised to examine community variability and structure at species and order levels. Abundance (N), richness (S), evenness (Pielou's J') and diversity (Shannon H') values were calculated for both intertidal and terrestrial environments at each site and locality (island) using the DIVERSE routine. These results were transferred into the statistics package, Minitab. Data were checked for compliance with the assumptions for ANOVA (normality and homogeneity of variance) and transformed where appropriate (Ln(x+1) transformations were performed on abundance data from both intertidal and terrestrial environments to stabilise variance). GLM ANOVAs with site and locality as fixed factors were then calculated. Where a significant difference in the test variable was found, *post hoc* Tukey pairwise comparisons were made in order to determine where the differences occurred. Comparisons of community similarities were visualised using nMDS ordination on Bray-Curtis similarity matrices of intertidal and terrestrial data at each site within each locality. The differences between latitudes were then compared using the one-way ANOSIM routine (a non parametric test applied to a rank similarity matrix, testing the null hypothesis that there is no difference in community composition between sites (Magurran 2004)). Finally the percentage similarities within and between groups (islands) and the taxa contributing most to dissimilarities between them were identified using the SIMPER routine within the PRIMER software package. In all multivariate analyses, data were fourth-root transformed in order to down-weigh the effect of highly abundant species.

RESULTS

At the study sites selected, a wide range of macrofauna was found inhabiting the littoral fringe. These communities, although generally cryptic and occupying predominantly the undersides of boulders and protected interstices, at some locations and sites were rich at multiple taxonomic levels and included certain taxa that were, patchily, highly abundant.

Community richness, abundance, evenness and diversity:

Across the study locations, species richness in the intertidal zone ranged from 7 to 30 species, 5 to 13 orders and 4 -11 phyla. This compared with a maximum of 11 species, 6 orders and 2 phyla at sites in the adjacent terrestrial sites sampled (Table 6.2a,b). The highest overall richness in the intertidal occurred in the vicinity of Rothera Research Station, Adelaide Island with a cumulative total of 34 species pooled across all sites (Fig 6.4a). GLM ANOVA showed that within latitude (location) variability was not significant but that there were significant differences in intertidal richness between latitudes at phylogenetic levels of species and order (ANOVA, $F_{4,31}$=13.36, *P*<0.0001 and $F_{4,31}$=5.14, *P*=0.023, respectively). A posteriori comparisons of means (Table 6.3) revealed significantly lower intertidal richness in the South Georgia and Bird Island sites than those at other localities. In contrast, in the terrestrial environment richness at species level was not significantly different between any pairs of groups. At order level there was a significant difference in richness (ANOVA $F_{4,30}$=14.95, *P*= 0.003), with Adelaide I. having significantly lower richness than all other localities with the exception of Signy I. However the unavoidable loss of samples taken at during the study and the possible sampling bias this causes means that any results from this location need to be interpreted with caution.

Table 6.2 a,b. Supralittoral a) and Intertidal b) richness, evenness and diversity at Species and Order level analysed by site.

a) supralittoral	Richness, S	Pielou's evenness, J'	Shannon, H' (log$_e$)	Richness S	Pielou's evenness, J'	Shannon, H' (log$_e$)
Species				**Order**		
Rothera 1	6	0.40	0.72	2	0.81	0.56
Rothera 2	10	0.59	1.35	2	0.74	0.51
Rothera 3	11	0.42	1.00	3	0.20	0.22
Signy	4	0.43	0.60	3	0.54	0.59
Bird Island 1	10	0.50	1.15	5	0.43	0.69
Bird Island 2	11	0.88	2.12	6	0.90	1.61
S. Georgia 1	9	0.85	1.86	5	0.73	1.18
S. Georgia 2	11	0.45	1.09	5	0.12	0.20
Falklands 1	10	0.21	0.48	7	0.19	0.37
Falklands 2	8	0.33	0.69	5	0.25	0.40
Falklands 3	8	0.85	1.76	7	0.87	1.70

b) Intertidal	Richness, S	Pielou's evenness, J'	Shannon, H' (log$_e$)	Richness S	Pielou's evenness, J'	Shannon, H' (log$_e$)
Site	**Species**			**Order**		
Rothera 1	27	0.46	1.51	13	0.49	1.25
Rothera 2	20	0.56	1.69	8	0.72	1.50
Rothera 3	26	0.67	2.19	11	0.71	1.71
Signy 1	19	0.31	0.93	10	0.33	0.75
Signy 2	23	0.66	2.08	10	0.58	1.33
Signy 3	30	0.72	2.47	12	0.70	1.74
Bird Island 1	8	0.57	1.19	5	0.67	1.07
Bird Island 2	7	0.76	1.48	6	0.81	1.46
S. Georgia 1	10	0.67	1.55	7	0.67	1.31
S. Georgia 2	13	0.53	1.37	9	0.52	1.14
Falklands 1	22	0.28	0.86	10	0.33	0.75
Falklands 2	28	0.36	1.20	13	0.43	1.12
Falklands 3	28	0.36	1.20	13	0.44	1.13

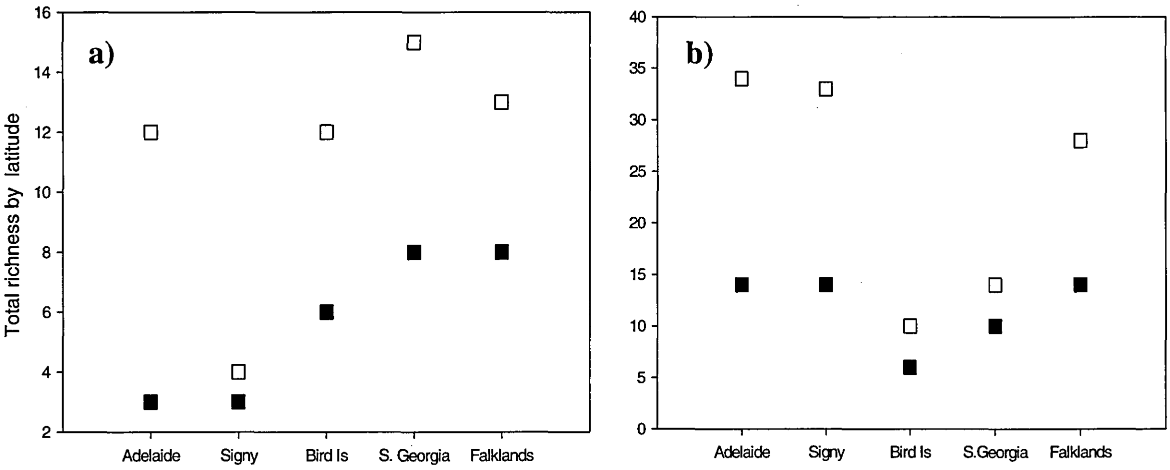


Fig. 6.4. Total community richness of a) terrestrial and b) intertidal communities, by class (solid squares) and species (open squares) level, at locations along the Scotia Arc and the Falkland Islands, from left 67°S, to right 51°S.

Table 6.3. Summary of significant results obtained from *a posteriori* Tukey pairwise comparisons of means, after application of GLM ANOVA to abundance, richness & diversity data at species (sp.) and order (o) levels. Abbreviations are F- Falklands; BI- Bird Island; SG- South Georgia. Si-Signy; Ad-Adelaide Island. Significance of result is denoted as * P<0.05; **P<0.01 ***P<0.001.

	Richness, S	Abundance, N	Evenness, J'	Diversity, H'
Supralittoral	Ad/BI* (o) Ad/SG* (o) Ad/F*** (o) Si/F * (o)	Ad/F ***	No significant differences in evenness between any sites at either species or order level.	No significant differences in diversity between any sites at either species or order level.
Intertidal	Ad/BI *** (sp.) Ad/SG ** (sp.) Si/BI ** (sp.) Si/SG ** (sp.) BI/F *** (sp.) SG/F *** (sp.)	Ad/BI*	No significant differences in evenness between any sites at either species or order level.	Ad/B.I* Ad/F **

Faunal abundance values were variable, with very high abundances at some sites. Across the study locations, abundance in the intertidal zone ranged from 1758 to 7358 individuals m^{-2} and in the supralittoral terrestrial study areas from 337 to 39856 individuals m^{-2}. There was a significant difference in the mean faunal abundances of individuals in both intertidal and terrestrial zones between islands (latitudes), (ANOVA $F_{4,8} = 4.22$, $P = 0.04$ and $F_{4,6} = 7.85$, $P = 0.015$ respectively) (Fig.6.5). Typically representatives of some orders and phyla were much more abundant than others, e.g. the patchy super-abundance of bivalve molluscs in the South Georgia area.

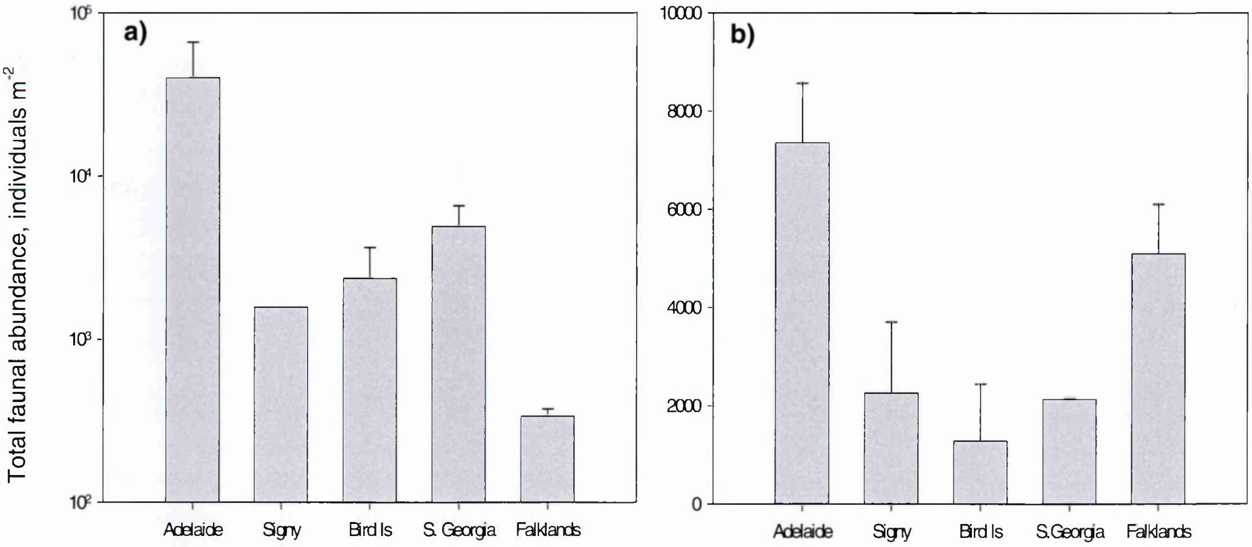


Fig. 6.5. Mean faunal abundance (individuals m^{-2}) of a) supralittoral (note: logarithmic scale) and b) intertidal individuals of all taxa (± SE) at localities sampled along the Scotia Arc and Falkland Islands.

Diversity (Shannon H') was significantly different between locations at species level in the intertidal zone (ANOVA $F_{4,31}$=7.65, P=0.001) (Table 6.2, Fig. 6.6), the assemblages at Adelaide I. being significantly more diverse than those at Bird I. and the Falkland Is. (Table 6.3). Terrestrial diversity was not significantly different at either taxonomic level across the latitudinal gradient.

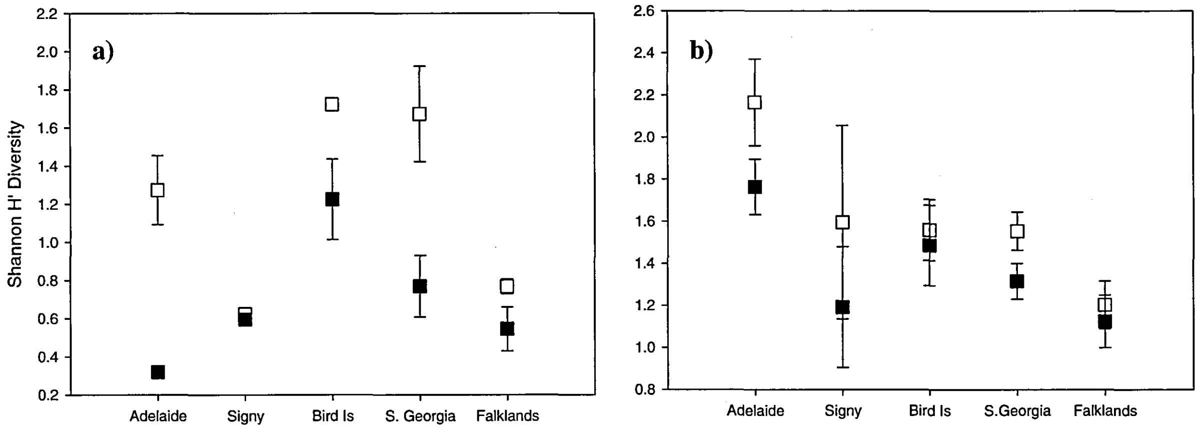


Fig. 6.6 Mean diversity (± SE) of (a) supralittoral and (b) intertidal taxa at species (white) and order (black) levels at localities along a latitudinal gradient across the Scotia Arc. Shannon H' is given in Log $_e$.

Similarities in assemblage structure with geography.

Visualisation of the similarities between sites and groups (islands) using nMDS showed clear island-specific clustering in the intertidal communities. Similar, although slightly less pronounced, patterns were found in the terrestrial assemblages (Fig. 6.7. a,b). Investigation of trends using ANOSIM with islands as a factor showed that there were significant differences in both intertidal and terrestrial community assemblages between islands (ANOSIM, Global R=0.85 and 0.88 respectively, P= 0.001).

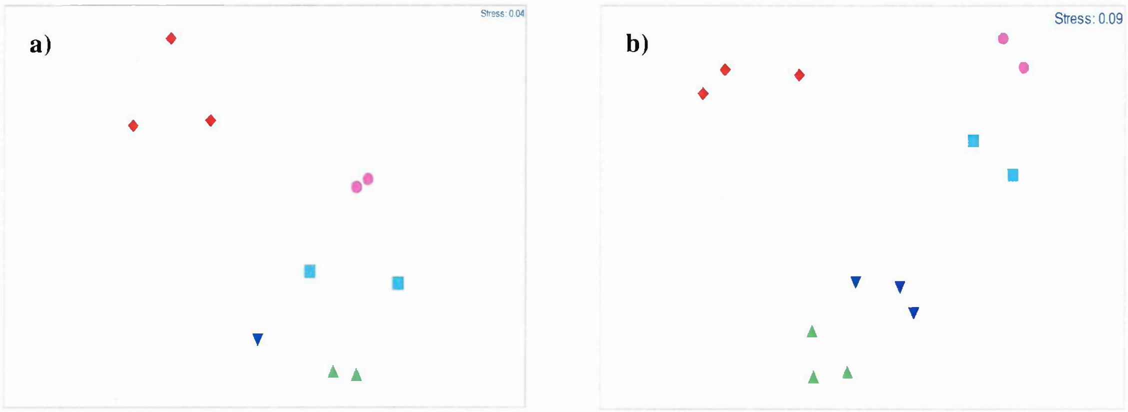


Fig. 6.7. nMDS ordination based on Bray-Curtis similarity matrices (fourth root transformations of abundance data at order level) of a) terrestrial taxa and b) intertidal taxa at localities along the Scotia Arc, stress = 0.04 and stress = 0.09 respectively. (Symbols denote: ▲ Rothera, Adelaide Island; ▼ Signy, S.Orkneys.; ● Bird Island, S.Georgia; ■ King Edward Point, S. Georgia; ◆ Stanley, Falkland Islands). (Note: Rothera terrestrial sites 1 & 2 overlay each other).

SIMPER analysis was used to identify the taxa which contributed most to the overall similarity within island groups and the differences between them. It revealed little similarity between intertidal assemblages at sites within locations (islands), ranging from 2.9 % at Bird I. to a maximum of 64.1% at South Georgia. The lowest between site similarity, at Bird Island was caused by the differences in abundance of oligochaete worms and bivalve molluscs, which accounted for 86.2% of the dissimilarity. There was also a high degree of inter-location dissimilarity, all groups showed > 73% dissimilarity of community composition after pairwise comparisons. Assemblage composition varied between islands with Adelaide and Signy sites having high proportions of polychaetes (33.4% and 47.0% respectively). Sites at Adelaide also had a high proportion of cheilostome bryozoans (28.2 %) which was almost 5 times higher than the next highest locality, Signy I. at 6.1% (Fig. 6.8a). In contrast to Adelaide I., assemblages at Signy I. had a similar proportion of bivalves to that found at Bird Island. Gastropods were a dominant part of the community in the South Georgia archipelago sites (King Edward Point and Bird I.) accounting for 25.5% and 38.6% of the overall abundance at each locality. The Falkland Is. sites had high proportions of cirriped crustaceans, accounting for on average 65% of the community, which was the primary contributor to the dissimilarity between this locality and all others, with the exception of Adelaide Island where the high proportion of cheilostome bryozoans was the main influence.

Antarctic terrestrial study assemblages at the study locations were dominated by Acari, primarily the species or genera *Halozetes belgicae, Tydeus, Globoppia* and *Alaskozetes antarcticus.* Inter island comparisons highlighted a high degree of dissimilarity between Adelaide Island and all other localities, ranging from 74% (South Georgia) to 99.7 % (Falklands). This is primarily due to the high proportion of Acari present in the Adelaide Is. samples (a total of 90.3% of the taxa at these sites (Fig. 6.8 b)). South Georgia and Bird Island assemblages showed an average dissimilarity of 76.1%, the differential abundances of Collembola and Acari accounting for 81.6% of the difference.

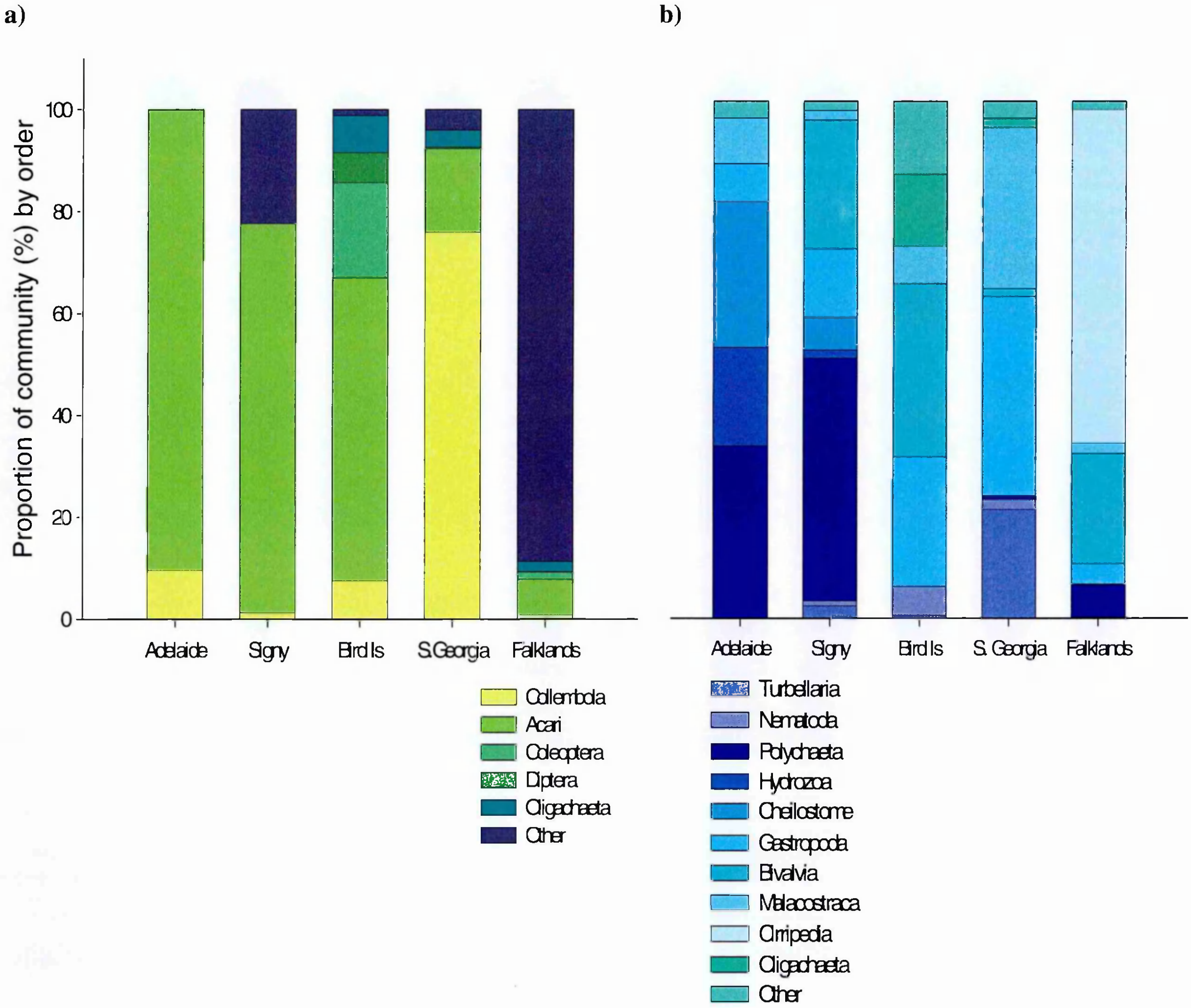


Fig. 6.8. Composition of a) terrestrial and b) intertidal communities (pooled data for sites at each locality) expressed as a percentage of the total population. The "other" taxa of the terrestrial Falkland Is sites are predominantly amphipods.

DISCUSSION

Within the southern polar intertidal zone, at all island localities sampled, there are areas that appear to be lacking in macrofaunal life. The intertidal zone at polar latitudes experiences locally variable environmental stresses, due to the increasing impacts of ice (scour and encasement) with increasing latitude, disturbance due to wave exposure decreasing with latitude, and localised trampling and increased organic input associated with marine mammals and birds. In addition to these stresses the shores at these latitudes are subject to a contemporary combination of regional warming, coastal ice-shelf retreat and increased UV irradiation (due to stratospheric ozone depletion). The structure and organisation of intertidal (and to a lesser extent supralittoral) communities of southern cool temperate, sub-Antarctic and Antarctic localities is little known and poorly understood. Most of the limited literature available focuses on the limpet *N. concinna* (Hedgpeth 1969a, Shabica 1972) or encrusting communities (Barnes et al. 1996, Barnes & Lehane 2001, Bowden 2005, but see Waller et al. 2006a).

Barnes & Brockington (2003) postulated that, with increasing latitude, the intertidal zone progressively supports fewer visually obvious biota and reduced zonation of macrobiota. The data reported here support the contention that life in the intertidal becomes less visually obvious at higher latitudes. The typically temperate communities, dominated by barnacles and mussels, found in the Falkland Is. study sites contrast sharply with the apparently depauperate communities of the more southerly sites investigated (Plate 6.1). However at both the Antarctic locations (Signy I. in the South Orkney archipelago and Adelaide I. west of the Antarctic Peninsula) an unanticipated and wide range of taxa was found to be resident in protected pockets between cobbles and the undersides of boulders. Indeed, the Adelaide I. samples obtained in the current study showed the highest species richness and diversity yet reported from any study of Antarctic or sub-Antarctic island shores. All reports of latitudinal clines in the southern ocean have considered specific groups of taxa (Moe & Delaca 1976, Clarke 1992, Roy et al. 1998, Boschi 2000) from benthic communities at varying depths from the continental shelf to the slope. The few intertidal studies to date have focussed on encrusting communities (Barnes & Arnold 1999, 2001), with the result that total community diversity across the full range of taxa has not been estimated at each study location. The data reported here represent the first intertidal study of community structure across a latitudinal gradient and, in contrast to many of benthic studies, indicate a significant cline of decreasing intertidal diversity with progression from higher to lower latitude locations.

The macrobiota found in the current study at intertidal sites on sub-Antarctic South Georgia of were similar in composition, if slightly higher in richness, to those reported on this island at Cumberland West Bay and Husvik by Pugh & Davenport (1997). Of the locations sampled in the current study, those on South Georgia (including Bird Island) were the least diverse and numerically abundant. The compositions of these assemblages were more similar to each other (nMDS, Fig 6.7) than to those of any other locations. There are various factors that may have contributed to the impoverished nature of these sub-Antarctic shores, but in particular it is significant that South Georgian shores are the most remote from other polar intertidal communities (1300km from the nearest land – Table 6.4), separated to the north from cold temperate shores by the Polar Frontal Zone 'barrier' (as well as considerable distance), as well as being geologically young (neighbouring terrestrial habitats have been estimated at ~10,000 – 14, 000 years since emergence from the last glacial maximum (van der Putten &

Verbruggen 2005)). They also experience seasonally high disturbance from large marine mammals and the consequent effects of increased nutrient input (Smith 1988b). Contemporary summer abundances of fur seals have been estimated at in excess of 5 million around the South Georgia archipelago and in the breeding season individual beaches on Bird Island can support populations of 10 000 individuals (D.Briggs pers. comm.). Species richness in the subtidal around South Georgia can be very high (Barnes et al. 2006a), while the shallows are also significantly warmer than 'normal' conditions for the polar fauna found there (Barnes et al. 2006b). It is possible that the more extreme conditions of the intertidal zone exceed the viable thermal range for many Antarctic species, many of which have been shown to be highly stenothermal. At higher temperatures some taxa have been shown to become incapable of performing essential survival behaviours such as reattachment to substratum or burying (Peck et al. 2004). In comparison with many continental Antarctic localities, shores on South Georgia (and to a lesser degree some sites on Signy I.) may also experience high freshwater runoff from melting snow, ice and glaciers (Pugh & Davenport 1997). South Georgian shores can be subject to strong wave action and some ice scour (although more limited than at maritime Antarctic localities). Unlike maritime Antarctic shores, the intertidal zone supports several species of macroalgae, including the giant kelps *Macrocystis pyrifera* and *Durvillea antarctica*, rhodophytes and filamentous green algae (Table 6.1). The few other remote cold temperate or sub-Antarctic islands where intertidal studies have been carried out also have depauperate faunal assemblages (Blankley & Grindley 1985, Smith & Simpson 1985, Lawrence & McClintock 1987, Smith & Simpson 2002). In contrast to the relatively rich and diverse assemblages found to be present in the current study at Adelaide Island, Barnes and Brockington (2003) reported a total of only nine species representing eight orders on the uppermost layer of rocks and their interstices at a site adjacent to Rothera Research Station. Barnes et al. (1996) found six species in 2 square meters on the lower shore of Signy Island (Table 6.4) (increased by a further four by unquantitative searches, Barnes unpublished data). Earlier investigations of some Antarctic Peninsula sites typically reported only one or two species (e.g. Shabica 1972). The highly heterogeneous tempero-spatial nature of cobble-boulder intertidal environments may explain the contrasting diversity and richness measures obtained across such studies. It seems likely that the variability reported between studies is influenced strongly by factors including sampling methods and effort, point of sampling within the tidal cycle (spring or neap tides) and position within the intertidal zone (low, mid or high shore). In the current study, sites were sampled at low water spring tides wherever possible, and boulders below the outer surface layer were included, to a level where bedrock was encountered or the rocks were immersed in water (i.e. the low water level). In contrast (where a sampling protocol has been described) previous studies only considered the taxa found on the top layer of boulders.

Disturbance plays a major role in defining and structuring intertidal communities, with intermediate levels of disturbance generally generating communities with highest diversity (Connell 1979, Huston 1979, Sousa 1979, McGuinness 1987a, Menge & Sutherland 1987). It seems surprising, therefore, that in the current study the highest species richness and diversity were found at localities which experienced the highest physical disturbance due to ice scour, and appeared superficially to be denuded of life (Plate 6.1). However the fact that virtually all taxa present at high latitude sites were found below the surface layer of boulders (i.e. the layer most directly impacted by ice scour) suggests that the level of disturbance changes significantly within localities, being high at the surface but low below the initial layer of cobble pavement, the compacted and relatively stable nature of which may enhance the protection afforded to species inhabiting the lower layers. Little is known about the intertidal fauna on Falkland Is. shores. The study sites were clearly exposed to considerable wave action but only rarely to trampling by large marine mammals and very rarely if at all to ice scour. The low diversity found here may be in part due to smothering by dense aggregations of a few ecologically dominant species (mussels and barnacles).

Waller et al. 2006b (and see also Chapters 3, 5) showed at a single study site, that the widely held view that the Antarctic intertidal zone cannot support a truly permanent community of species seems to be largely unfounded. The current study expands on this earlier but localised finding by documenting analogous, if somewhat lower, intertidal diversity at a range of Antarctic sites. There is much literature suggesting biological diversity (of specific taxonomic groups) decreases from tropics to the poles (Moe & Delaca 1976, Clarke 1992, Roy et al. 1998, Boschi 2000, Crame 2000 and Willig et al. 2003 for review). However, within some taxa, this certainly does not seem to be the case (Barnes & DeGrave 2000, 2001, Clarke & Johnston 2003, Linse et al. 2006).

In the current study of terrestrial diversity, only supralittoral environments of the islands were sampled, and as such do not reflect the full complexity of all terrestrial habitats along the latitudinal gradient. However they are comparable within this study and no consistent trend of decrease in supralittoral species richness along the Scotia Arc islands was found. Studies that compare wider data, such as Convey & Smith (1997), show similar patterns within an Antarctic region such as the maritime Antarctic, while various reviews suggest that the trend is strongest between regions as distinct from within

(Chown & Convey in press b). As in the marine environment the picture is not clearly defined as there are some data supporting reverse trends (eg Maslen & Convey 2006). However comparisons are complicated by area, e.g. there is much more snow free area in the Falkland Is. for exploitation than in more southerly locations such as Adelaide Is., where only small pockets of suitable habitat generally support large numbers of a few species (e.g. *Prasiola* (alga) habitats can support collembolan populations in the order of >100k individuals m^{-2} (Convey & Smith 1997)). Furthermore, northerly sites have recently been invaded by many non-indigenous species (NIS) thus increasing their apparent richness, largely as a result of human activity (Frenot et al. 2005, Barnes et al. 2006b). South Georgia is known to support 12 non-indigenous terrestrial invertebrate species, with 10% of the springtail fauna being alien (Frenot et al. 2005). Larvae of the beetle *Oopterus soledadinus* were found at Maiviken in the current study, a distance of 6 km from the only previously recorded location at Grytviken (P.Convey pers. comm.) The related carabid beetle *Trechisibus antarcticus* has also been found to have established and spread in the area around Husvik (Ernsting et al. 1995) suggesting that NIS are benefiting from increasing anthropogenic disturbance.

Prior to this study almost nothing was known of the littoral diversity south of the Falklands, although there has been much discussion of subtidal and terrestrial diversity by separate groups of ecologists. The current study demonstrates that Maritime Antarctic and Peninsula intertidal habitats can be significantly more diverse than study sites at lower latitude (sub–Antarctic) and closer in richness levels to the cold temperate Falkland Is. This suggests that richness and abundance in the littoral zone appear to be more influenced by the isolation of localities from other continental landmasses than by the “harshness” of the environmental conditions.

Table 6.4. Intertidal species richness and abundance values taken from current study and literature. Distances from and location of nearest landmasses have been calculated using great circle distances on Southern Polar Azithmul Equidistant Projection. * Collected from 0.05m depth. Only Amphipoda and Gastropoda identified to species (total of 14) all other fauna identified to class (total of 6) ** from immediate sublittoral (0.5 m below chart datum).

Island / Region	Lat/ Long	Distance, km from nearest continental landmass	Richness, S (species)	Mean faunal abundance m^{-2}	Reference
Magellan Str. Chile	54° 00'S 70° 10' W	n/a	43	1677	Rios & Mutschke 1999
Falklands	51° 42'S 57° 51' W	483km S.America	29	5096	Current study
Marion I.	46° 54'S; 37° 45'E	1750 km South Africa	16	7663	Blankley & Grindley 1985
Macquarie I.	54° 38'S 158° 53'E	1034 km New Zealand	18	~4000	Simth & Simpson 2002
Kerguelen Is	53° 05' S 73° 30' E	3317 km Madagascar	6	n.d	Lawrence & McClintock 1987
South Georgia	54° 14'S 36° 41'W	1451 km Falklands	9	~300	Pugh & Davenport 1997
South Georgia	54° 14'S 36° 30'W	1451 km Falklands	14	2133	Current study
Bird I.	54°00' S 38°03' W	1451 km Falklands	10	1284	Current study, Barnes et al. 1996
Heard I.	53° 05' S 73° 30' E	3811 km Madagascar	13	n.d	Smith & Simpson 1985
Signy	60° 43'S 45° 36'W	565 km Joinville Is.	5 31	n.d 2261	Barnes et al. 1996, Current study
King George I.	62° 08'S 58° 26'W	139.km Trinity Pen	>20*	13,000	Jazdzewski et al. 2001
Anvers I.	64° 46'S 64° 05'W	50km Graham	n.d n.d 32	n.d n.d	Hedgpeth 1969a, Stout & Shabica 1970, Stockton 1973
Adelaide I.	67° 34'S 68° 08'W	90km Grahamland	9 34	n.d 7358	Barnes & Brockington 2003, Current study
Terra Nova Bay, Ross Sea	74° 45' S 164° 10' E		2**	n.d	Gambi et al. 1994

Chapter 7 – General discussion

Chapter 7 - General discussion

Globally the intertidal is arguably one of the most studied environments (area for area), and has been pivotal in the development and testing of ecological theories over the past half century. The steep environmental gradient of the eulittoral has been key to concepts of zonation (Southwood 1965, Stephenson & Stephenson1945), intermediate disturbance hypothesis, the relative influences of predation competition, succession, supply side ecology, top-down and bottom-up regulation (Connell 1961, Paine 1966, 1969, Dayton 1971,1972, Menge 1976, 2000). These concepts have almost exclusively been developed on accessible temperate rocky shores. To a lesser extent tropical shores have also been a focus for ecology, mainly with respect to mangrove swamps, seagrass beds and crab or mollusc behaviour (see Luxton 1967, Acker 1972, Long & Manson 1984, McGuiness 1990, Sheaves 1992, Lee 1999). Arctic shores have received much less attention but are still relatively well studied in places (e.g. Gurjanov 1968, Green et al. 1983, Weslawski et al. 1993, 1997, 1999, McKindsey & Bourget 2001, Sokolova & Portner 2003, Barnes & Kuklinski 2004, Urban-Malinga et al. 2004, Kuklinski et al. 2006). In contrast virtually nothing is known of southern polar shore communities, either simply in terms of their general composition and structure or whether the generally accepted theories defining patterns on temperate shores are globally applicable. This is likely to be due to the fact that the Arctic landmasses are divided between a number of countries and many Arctic shores are close (relatively) to permanent human populations, contrasting with the extreme isolation of the Antarctic continent and the absence of any indigenous populations.

The low and high water levels are relatively arbitrary demarcations in a gradient of physical environmental conditions. The intertidal zone represents the interface between two vastly different environments, and this contrast in polar regions is probably the most pronounced to be found worldwide due to the extreme variability in temperature, light and primary production. However investigation of the changes in environmental stresses and community composition from terrestrial through intertidal to marine conditions has rarely been undertaken. Peck et al. (2006) were the first to attempt a synthesis / review of similarities and contrasts across the land-sea interface in an Antarctic context based on findings from separate ecological studies of terrestrial ecologists and marine ecologists.

The original aim of the current research was founded on the prevailing view of the Antarctic intertidal as a zone largely devoid of life. with that present in virtually all cases simply being a result of the transient movement of individuals from their adjacent permanent marine or terrestrial habitats. Thus, in order to characterise the Antarctic intertidal environment there was a need to compare the species present and environmental conditions experienced across the three zones and to investigate ecophysiological responses and life history strategies of a range of taxa, from both what was expected to be their "natural" environment (terrestrial or marine) and the transient and more "stressful" or "extreme" conditions of the intertidal zone. However, during the first season of study the true extent of intertidal communities rapidly became apparent, and the study emphasis evolved into a broader ecological study of these communities and their biota within the intertidal. The four main questions addressed in this thesis were:

1. Is there such a thing as an Antarctic intertidal community?

2. How does life in the Antarctic intertidal compare to that in the adjacent supralittoral and sublittoral zones?
3. What strategies do taxa utilise to survive in this environment in summer and can macro-biota survive winter conditions *in situ*?
4. How similar or different are these intertidal communities to those present at lower latitudes?

As such this study is the first detailed report investigating Antarctic intertidal community ecology.

Main Findings of the study

Although appearing to be inhospitable, detailed studies of the intertidal, at sites around Rothera Research Station on the west Antarctic Peninsula, found it to support unexpectedly rich and diverse communities both when compared with the only previous study there (Barnes & Brockington 2003), and with results reported from brief examinations of other Antarctic and Sub- Antarctic locations (Ch. 6). Perhaps unsurprisingly the great majority of species found were of marine origin, however unlike intertidal communities at other latitudes only one suspected obligate intertidal animal was found (the mite *Rhombognathus gressitti*) (P.Pugh pers. comm.) and no terrestrial species were observed, although they have been reported in previous studies (Convey & Block 1995, Convey et al. 2000). A total of 57 species were found over the two summer seasons (Appendix 1) compared with 9 reported in the same general locality by Barnes & Brockington (2003). This nearly doubles the total number of intertidal species recorded from the continent of Antarctica and surrounding islands within the Polar Front. Brief observations at some areas along the Peninsula north of the current study sites suggest patchy occurrences of even more abundant or richer intertidal macro-biota such as at Thorgersen I. (Palmer Archipelago) and various shores around the South Shetland Islands (D.Barnes pers. comm.).

Many of the taxa found in the current study at sites around Rothera were not merely transient occupants, but were clearly successfully exploiting a habitat that would also have become available in warm interglacial periods over the last 800 000 years (EPICA 2004). Nor was residency mere survival; reproductive and other activities occurred within this environment at all study sites (see Chapters 4, 5). The hydrozoan *Gonionemus* sp. and the nemertean *Antarctonemertes validum* were observed aggregating and reproducing in large numbers at locations around Adelaide Island, while in a single 0.25m^2 quadrat 96 individuals of the pycnogonid *Achelia communis*, many of which were males carrying eggs, were found feeding on bryozoan colonies (pers obs). The current study also showed that residence time of individuals in the intertidal may span several years, as 3-4 year old bryozoan colonies were found at the study sites (Chapters 3). Indeed colonies of the cheilostome bryozoan *Inversiula nutrix* in the intertidal were older than any of those found in the immediate sublittoral at the same site (Chapter 3). Residency of both sessile and mobile species was confirmed by a winter excavation of only 3 m^2 of the intertidal zone (in September 2003), which revealed 17 species of both encrusting and non-encrusting taxa alive under the first layer of rocks (Chapter 5, Waller et al. 2006 b).

In the Antarctic terrestrial environment very specific strategies such as cold hardening (Worland & Convey 19xx) aid survival and exploitation of their extreme situation. It is unclear if specific survival or ecophysiological strategies are used by species living in the Antarctic intertidal zone, and if so what these are, to maximise chances of surviving winter conditions. A preliminary study of summer cold tolerance levels of Antarctic intertidal individuals at Adelaide I. showed that most species did not possess cold tolerance levels at that time that would be capable of coping with winter extremes (Chapter 5, Waller et al. 2006b). However, much more work is required throughout the year in order to describe these tactics.

The Scotia Arc chain of islands represent the only transition zone for terrestrial, intertidal and shallow shelf biotas between the peninsula and the nearest continental landmass. The inevitably less detailed, investigation into the intertidal and supralittoral communities across the wide environmental gradient between locations from the Falkland Islands to Adelaide Island (Chapter 6) found that the highest richness and diversity occurred in what was perceived to be the most disturbed / extreme conditions at the highest latitude location (sites around Rothera, Adelaide Island). This was also the first southern polar study to compare communities along a latitudinal cline, within a short time period (all sites were sampled within a matter of weeks), and using a consistent sampling strategy. Thus the possible effects of variability with time (Clarke 1988, 2001) and sampling inconsistencies, which affect comparisons from literature, were minimised. However, as with Barnes (2006) study of subliitoral communities around the Scotia Arc, the main limitation is the small size of the study.

Discussion of results in a broader ecological context

How different are Antarctic intertidal conditions /stresses from those encountered on lower latitude shores?

Intertidal habitats are subject to 4 main environmental stresses (the unidirectional emersion gradient from sea to land, horizontal wave exposure gradient, salinity from marine through estuarine to freshwater and the gradient in particle size from fine muds to bedrock). Clearly these environmental stresses have different levels of impact on temperate, tropical and Antarctic intertidal environments. As at other latitudes, Antarctic intertidal environments range from bedrock through boulder shores to sedimentary shores (although these are rare at the study sites). Antarctic intertidal shores contrast with lower latitude sites in that there is very little in the way of biogenic sedimentary input and no permanent salinity gradient (i.e. no rivers), although they can experience freshwater run off due to melting glaciers / ice sheets and precipitation. Clearly Antarctic intertidal conditions are different in many respects from those at lower latitudes, but does this mean they are more extreme for biota, and if so how much more extreme? Winter ice encasement has previously been considered as killing surface colonists, rendering the intertidal zone uncolonisable and restricting any primary production developing there (e.g. Barnes 1999). However the icefoot protects the intertidal from storm events and disturbance, due to wave action moving boulders, which can devastate communities on temperate shores. The summer influence of ice (specifically scouring) becomes more obvious with increasing latitude and the surface of the intertidal environment is effectively scoured clean of life. However this raises the question of how to quantify disturbance, as below this outer surface and within protected interstices a rich and diverse assemblage of species was found to be present. It could be argued that the shallow sublittoral environment, at least at the sites investigated around Rothera research station, is more disturbed than many parts of the adjacent intertidal zone. Icebergs and brash ice have a more direct impact in the sublittoral (Brown et al. 2004) where similar protected stable pavements do not seem to occur. Both temperate and Antarctic high intertidal zones are challenging places to survive, with few species having the capacity to survive in either.

Are Antarctic intertidal assemblages true communities?

Despite an extensive literature focussing on community ecology, there is no single unambiguous definition of what an ecological community is. Most definitions include the idea of a collection of species found in a particular place that interact in some way and have some form of long-term presence (e.g. Elton 1927, Whitaker 1975, Price 1984). These definitions encompass aspects such as predator-prey interactions, mutualism and interspecific competition (Morin 2003). Other factors that can influence these interactions include seasonal or spatial dynamics related to recruitment and dispersal of taxa.

The findings presented in this thesis clearly show that by these definitions Antarctic communities do exist, albeit in a more cryptic manner than on temperate shores, with examples of predator prey interactions (nudibranchs and hydroids, pycnogonids and bryozoans), intra and interspecific competition between bryozoan species, bryozoans and spirorbid polychaetes and between sponges and hydroids) (Chapter 4). Unlike intertidal communities at other latitudes only one possible obligate intertidal species was found and no terrestrial taxa. At other Antarctic locations similarly low numbers of obligate intertidal species are known such as the collembolan *Archisotoma brucei* (Wise 1971, Holdgate & Barker 1979) and *Neohyadesia signyi*, endemic to Signy I. (Schenker 1986).

How will global climate change affect these communities?

Global climate is currently changing rapidly especially in the Arctic and Antarctic Peninsula. Climate change is now considered to be one of the major issues facing the human race (King 2005). At the current rate of anthropogenic carbon emissions, global air temperatures are predicted to increase by 2°C by 2035 and in the longer term there is a greater than 50% chance that the temperature rise might exceed 5°C (which is equivalent to the total change in average temperatures from the last ice age to today) (Stern 2006). The mean air temperature of the peninsula has already warmed by 2.5°C since 1945 (Vaughan & Doake 1996) and substantial effects of this are being observed, with 87% of the ice shelves and glaciers measured in a recent study retreating (Cook et al. 2005). Consequently, more of the shore is becoming ice free and available for colonisation, while the existing environment is being exposed to increasing temperatures and potentially scouring due to increased summer floating ice. It is accepted that climatic regimes influence species' distribution (McCarty 2001, Walther et al. 2002) therefore it is likely that there will be a southwards shift as new habitats become available and temperatures increase. This zone is one of the most likely environments which southern temperate species can travel to and establish, via fouling of marine debris or ships hulls, though whether they are alien or returning may be hard to establish.

In addition to these environmental changes, seal populations are both increasing dramatically (Smith 1996) and extending their range south (750 seals were counted on Rothera Point in late summer 2004 (D.Smale pers.comm.) compared with tens reported 10 years ago (B.A.S. unpublished data). The resultant increased nutrient levels may enhance algal growth and biomass and propagate to higher trophic levels as has been reported in areas of high seabird guano (Menge 2000). Under present environmental conditions few macro-algae other than high intertidal filamentous green algae (possibly *Enteromorpha* sp.). can survive in this zone due to the effects of ice. It is likely that excessive nutrient levels would result in eutrophication and a reduction in levels of community richness / complexity. Further autecological studies are needed in order to quantify the capacities of species for reproduction, dispersal, colonisation and their physiological responses to a warming environment.

Thermal limits of Antarctic intertidal invertebrates

Antarctic shallow water temperatures are low but relatively stable, varying little around –1.8°C in winter to a few degrees higher in summer (Barnes et al 2006) and some Antarctic marine invertebrates have been shown to be highly stenothermal (Peck & Conway 2000, Peck 2005). This low and relatively constant environment contrasts sharply with conditions in the intertidal zone, at the Peninsula study sites, where temperatures can vary by ~40 °C over an annual cycle (Chapter 2, 4). Summer maxima can reach 17°C and winter minima – 25°C (Chapter 5). Despite the perception that Antarctic marine species are generally stenothermal and can only survive in temperature windows of at most 6°C to 12°C, with the lower limit being set by the freezing point of seawater (-1.8°C) (Peck & Conway 2002, Peck 2005), the species found in the intertidal environment in the current study were almost entirely marine in origin. and clearly have to deal with a much greater range in temperature. Although Peck (2005) defines the lower limit of survival fro marine taxa as being set by the freezing point of seawater, intertidal individuals are exposed to summer temperatures considerably lower than this and have also been shown to be present under winter conditions, which are even more extreme.

Further investigations are needed to gauge individual's physiological responses to these temperatures. Preliminary findings of animals collected under summer conditions, revealed that the limpet *Nacella concinna* was found to be able to survive temperatures of –6°C and complete freezing of all the osmotically active water within the tissues. Summer supercooling points of all taxa tested were all lower than this value. Although preliminary, these results challenge the view that Antarctic marine ectotherms have evolved to be stenothermal. Both the cooling rate and duration of exposure to minimum temperatures were found to influence survival chances in the current study and it may be that short term extreme environmental events are within at least some marine invertebrates physiological capacities. The cold tolerance of the high intertidal mite *R. gressitti* was even more extreme with a mean summer SCP of -23.1°C despite being active and feeding when collected. Unlike most terrestrial invertebrates it appears that it may have overcome the problem of ice nucleating agents in the gut (Worland and Lukesova 2000).

Likewise, the response of most intertidal animals to maximum summer heat extremes has not been studied, although it has been shown under controlled laboratory conditions that some behaviours become compromised. For example short-term acclimations of the limpet *N. concinna* showed that it cannot right itself if turned over when exposed to temperatures above 5°C (Peck 2005, Peck et al. 2004, 2006). However these studies focus on what is required to make a particular process fail and do not address cyclical exposure, or what might be needed in terms of recovery time and cost. Intertidal temperatures in summer can exceed this for periods of ~2-3 hours, however no mass mortality was observed under field conditions. As with lower thermal limits it is highly likely that the rate of change in temperature and the duration of exposure affects survivability. With the peninsula region of Antarctica being one of the fastest warming areas on Earth (King et al. 2003, Meredith & King 2006), it may well be that summer maximum temperatures more strongly influence the long-term viability and durability of intertidal assemblages rather than the conditions experienced during winter months.

Latitudinal richness and diversity patterns

The latitudinal gradient of decreasing richness from tropics to the poles is generally accepted as ecology's oldest recognised pattern (Willig et al. 2003). Although it is rare for studies to address comparable community level assessments as here, the more general overview of Clarke & Johnston (2002) provides the benchmark for patterns of diversity into the Antarctic. They emphasise that a simple latitudinal decrease is not an appropriate description, not least as it is clear that some groups reach their maximum diversity in the Antarctic. The finding of highest diversity at the southern end of this transect (Chapter 6) runs counter to many perceptions of diversity patterns within the Antarctic. The high diversity at Rothera does provide a completely untested link with some recent terrestrial studies (Maslen & Convey 2006) that have also reported surprisingly high diversity at far south sites on the Antarctic Peninsula, in this case suggesting evidence for long-term regional refuges from glacial wipeout.

The current study found anomalously low diversity on South Georgia shores as did Barnes & Arnold (2001) for littoral and sublittoral encrusting assemblages. South Georgia is geographically isolated, and planktonic larvae are not abundant in the Southern Ocean (Bowden 2006). Long distance larval dispersal may not be so important in generating intertidal communities there, but colonisation by species rafting on both anthropogenic and natural debris may play a role. South Georgia is an old and fairly big island so is a reasonable 'target' for colonists. Perhaps the main colonists are those which survived the last period of glaciation- either by migrating to deeper water or surviving in refugia, although during the last period of glaciation the South Georgia icecap extended far offshore suggesting that this may be unlikely .

Implications of increasing anthropogenic activity-

Alien invertebrates, fungi, microbes and vascular plants occur on most of the sub-Antarctic islands resulting in some profound impacts on indigenous biota (Frenot et al. 2005). The current vectors for introduction are largely associated with the movement of cargo and people related to commercial activities (e.g. fishing), national scientific programmes and tourist operations. Currently there is virtually no knowledge of the extent of southern polar intertidal communities or the latitudinal ranges of individual species. In addition to this, a warming environment and the five-fold increase in tourism over the past fifteen years has seriously increased the potential for the introduction and establishment of non-native species with the consequent increase in the chance of detrimental effects on existing communities. The potential risk is highlighted in the recent discovery of a diverse fouling community encrusting the hull of a barge intended for deployment on the sub Antarctic island of Macquarie. The community comprised a total of 20 species, one species, the amphipod *Monocorophium acherusicum* was estimated to have over 136,000 individuals including ovigerous females (Lewis et al. 2006). Other potential vectors for the introduction of invasive species include rafting on marine flotsam, both natural e.g. kelp (Smith 2002) and anthropogenic e.g. plastic bottles rope and line, glass bottles, metal, aerosol can and wood (Barnes 2002, Convey et al. 2002, Barnes & Fraser 2003).

Summary and directions for further research

This project perhaps raises more questions than it answers. The findings represent a paradigm shift in the perception of the Antarctic intertidal zone, from the view that there are virtually no intertidal fauna and certainly no true community to the fact that true communities do exist and in places, southern polar shores can be not just as rich, diverse and abundant as the adjacent terrestrial and shallow sublittoral, but also as southern cool temperate communities. Even more surprisingly large components of these communities can persist throughout the winter. Answering fundamental questions such as what processes structure the community composition, for example, what are the levels and timing of recruitment, colonisation, timing and extent of reproductive activity, and how do these compare with shallow sublittoral habitats. How do animals survive winter conditions, and conversely how do they respond to summer maxima which in a warming world may be the limiting factor to their survival.

I must go down to the seas again for the call of the running tide

Is a wild call and a clear call that may not be denied;

And all I ask is a windy day with the white clouds flying,

And the flung spray and the blown spume and the seagulls crying.

Sea Fever – John Masefield

1909

References

References

Aarset AV (1982) Freezing tolerance in intertidal invertebrates - a review. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 73: 571-580

Abbott RT (1968) Seashells of North America. Golden Press, New York

Abele LG (1974) Species-diversity of decapod crustaceans in marine habitats. Ecology 55: 156-161

Acker S (1972) Mangrove Ecology. Oceans 5: 34-43

Anisimov O, Fitzharris B, Hagen JO, Jefferies R, Marchant HJ, Nelson F, Prowse TD, Vaughan DG (2001) Polar regions (Arctic and Antarctic). In: McCarthy JJ (ed) Inter-governmental Panel on Climate Change (IPCC). Climate change 2001: impacts, adaptation, and vulnerability. Contribution of Working Group II. Cambridge University Press, Cambridge

Ansart A, Vernon P (2003) Cold hardiness in molluscs. Acta Oecologica-International Journal of Ecology 24: 95-102

Ansart A, Vernon P (2004) Cold hardiness abilities vary with the size of the land snail Cornu aspersum. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 139: 205-211

Antezana T (1999) Plankton of southern Chilean fjords: trends and linkages. Scientia Marina 63: 69-80

Aristotle (343 BC) Historia Animalium. eBooks@Adelaide The University of Adelaide

Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos Oceanography and Marine Biology, pp 241-304

Arntz WE, Gutt J, Klages M (1997) Antarctic marine biodiversity: an overview. In: Battaglia B, Valencia J, Walton D (eds) Antarctic Communities: Species, Structure and Survival. Cambridge University Press, Cambridge, pp 3-14

Astorga A, Fernandez M, Boschi EE, Lagos N (2003) Two oceans, two taxa and one mode of development: latitudinal diversity patterns of South American crabs and test for possible causal processes. Ecology Letters 6: 420-427

Audouin VJ, Milne-Edwards H (1832) Introduction Recherches pour Servir a I'Histoire Naturelle au Littoral de la France Tome 1. Cruchard, Paris, pp 302

Baardseth E (1970) A square scanning, two stage sampling method of estimating seaweed quantities. Report of the Norway Institute of Seaweed Research 33: 1-14

Bale JS (1993) Classes of insect cold-hardiness. Functional Ecology 7: 751-753

Ballantine WJ (1961) A biologically defined exposure scale for the comparative description of rocky shores. Field Studies Council

Barnes DKA (1999) The influence of ice on polar nearshore benthos. Journal of the Marine Biological Association of the United Kingdom 79: 401-407

Barnes DKA (2002) Biodiversity - invasions by marine life on plastic debris. Nature 416: 808-809

Barnes DKA (2005) Changing chain: past, present and future of the Scotia Arc's and Antarctica's shallow benthic communities. Scientia Marina 69: 65-89

Barnes DKA, Arnold R (2001) Competition, sub lethal mortality and diversity on Southern Ocean coastal rock communities. Polar Biology 24: 447-454

Barnes DKA, Arnold RJ (1999) Possible latitudinal dines in Antarctic intertidal and subtidal zone communities encrusting ephemeral hard substrata. Journal of Biogeography 26: 207-213

Barnes DKA, Brockington S (2003) Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica. Marine Ecology-Progress Series 249: 145-155

Barnes DKA, De Grave S (2000) Biogeography of Southern polar bryozoans. Vie Et Milieu-Life and Environment 50: 261-273

Barnes DKA, De Grave S (2001) Ecological biogeography of southern polar encrusting faunas. Journal of Biogeography 28: 359-365

Barnes DKA, Fraser KPP (2003) Rafting by five phyla on man-made flotsam in the Southern Ocean. Marine Ecology-Progress Series 262: 289-291

Barnes DKA, Fuentes V, Clarke A, Schloss IR, Wallace MI (2006a) Spatial and temporal variation in shallow seawater temperatures around Antarctica. Deep-Sea Research Part Ii-Topical Studies in Oceanography 53: 853-865

Barnes DKA, Hodgson DA, Convey P, Allen CS, Clarke A (2006b) Incursion and excursion of Antarctic biota: past, present and future. Global Ecology and Biogeography 15: 121-142

Barnes DKA, Kuklinski P (2004) Variability of competition at scales of 10(1), 10(3), 10(5), and 10(6) M: encrusting arctic community patterns. Marine Biology 145: 361-372

Barnes DKA, Lehane C (2001) Competition, mortality and diversity in South Atlantic coastal boulder communities. Polar Biology 24: 200-208

Barnes DKA, Linse K, Waller C, Morely S, Enderlein P, Fraser KPP, Brown M (2006c) Shallow benthic fauna communities of South Georgia Island. Polar Biology 29: 223-228

Barnes DKA, Rothery P, Clarke A (1996) Colonisation and development in encrusting communities from the Antarctic intertidal and sublittoral. Journal of Experimental Marine Biology and Ecology 196: 251-265

Beckley LE, Branch GM (1992) A quantitative scuba-diving survey of the sublittoral macrobenthos at sub-Antarctic Marion Island. Polar Biology 11: 553-563

BenedettiCecchi L, Cinelli F (1997) Spatial distribution of algae and invertebrates in the rocky intertidal zone of the Strait of Magellan: are patterns general? Polar Biology 18: 337-343

Benedetti-Cecchi L, Maggi E, Bertocci I, Vaselli S, Micheli F, Osio GC, Cinelli F (2003) Variation in rocky shore assemblages in the northwestern Mediterranean: contrasts between islands and the mainland. Journal of Experimental Marine Biology and Ecology 293: 193-215

Bergstrom DM, Chown SL (1999) Life at the front: history, ecology and change on southern ocean islands. Trends in Ecology & Evolution 14: 472-477

Bigg EK (1953) The supercooling of water. Proceedings of the Physical Society of London Section B 66: 688-694

Blackburn TM, Gaston KJ (2003) Why macroecology? In: Blackburn TM, Gaston KJ (eds) Macroecology Concepts and Consequences. Blackwell Science, Oxford, pp 1-14

Blankley WO, Grindley JR (1985) The intertidal and shalow subtidal food web at Marion Island. In: Seigfried W, Condy P, Laws R (eds) Antarctic Nutrient Cycles and Food Webs. Springer- Verlag, Berlin Heidelberg

Block W (1984) A comparative-study of invertebrate supercooling at Signy Island, maritime Antarctic. British Antarctic Survey Bulletin: 67-76

Block W (1990) Cold tolerance of insects and other arthropods. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 326: 613-&

Block W, Convey P (1995) The biology,life-cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. Journal of Zoology 236: 431-449

Block W, Duman JG (1989) Presence of thermal hysteresis producing antifreeze proteins in the Antarctic mite, *Alaskozetes antarcticus*. Journal of Experimental Zoology 250: 229-231

Boschi EE (2000) Biodiversity of marine decapod brachyurans of the Americas. Journal of Crustacean Biology 20: 337-342

Boschi EE, Gavio MA (2005) On the distribution of decapod crustaceans from the Magellan biogeographic province and the Antarctic region. Scientia Marina 69: 195-200

Bowden DA (2005) Quantitative characterization of shallow marine benthic assemblages at Ryder Bay, Adelaide Island, Antarctica. Marine Biology 146: 1235-1249

Bowden DA (2006) Benthic assemblage development and larval ecology of marine invertebrates at Adelaide Island, Antarctica. PhD, Milton Keynes

Branch M, Branch GM (1981) The Living Shores of South Africa. C. Struik, Cape Town

Brethes JC, Ferreyra G, de la Vega S (1994) Distribution, growth and reproduction of the limpet *Nacella* (*Patinigera*) *concinna* (Strebel 1908) in relation to potential food availability, in Esperanza Bay (Antarctic Peninsula). Polar Biology 14: 161-170

Brey T, Klages M, Dahm C, Gorny M, Gutt J, Hain S, Stiller M, Arntz WE, Wagele JW, Zimmermann A (1994) Antarctic benthic diversity. Nature 368: 297

British Antarctic Survey (2004) Antarctica, 1:10 000 000 scale map. BAS (Misc) 11. British Antarctic Survey, Cambridge

Broughton DA, McAdam JH (2005) A checklist of the native vascular flora of the Falkland Islands (Islas Malvinas): New information on the species present, their ecology, status and distribution. Journal of the Torrey Botanical Society 132: 115-148

Brown KM, Fraser KPP, Barnes DKA, Peck LS (2004) Links between the structure of an Antarctic shallow-water community and ice-scour frequency. Oecologia 141: 121-129

Burn AJ (1984) Life cycle strategies in two Antarctic collembola. Oecologia 64: 223-229

Bustamante RH, Branch GM (1996) Large scale patterns and tropic structure of southern African rocky shores: the roles of geographic variation and wave exposure. Journal of Biogeography 23: 339-351

Cannon RJC, Block W (1988) Cold tolerance of microarthropods. Biological Reviews 63: 23-77

Cannon RJC, Schenker R (1985) Cold tolerance of a cryptostigmatid mite at Signy Island, maritime Antarctic. British Antarctic Survey Bulletin: 1-5

Carr MH, Neigel JE, Estes JA, Andelman S, Warner RR, Largier JL (2003) Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. Ecological Applications 13: S90-S107

Caswell H (1978) General formula for sensitivity of population-growth rate to changes in life-history parameters. Theoretical Population Biology 14: 215-230

Chao A (1984) Non-parametric estimation of the number ofclasses in a population. Scandanavian Journal of Statistics 11: 265-270

Chase JM (2000) Are there real differences among aquatic and terrestrial food webs? Trends in Ecology & Evolution 15: 408-412

Chown SL (1996) Kelp degradation by *Paractora trichosterna* (Thomson) (Diptera: Helcomyzidae) at sub-Antarctic South Georgia. Polar Biology 16: 171-178

Chown SL, Convey P (in press b) Biogeography. In: Bergstrom DM, Convey P, Huiskes AHL (eds) Trends in Antarctic Terrestrial and Limnetic Ecosystems. Kluwer, Dordrecht

Chown SL, Convey P (in press a) Spatial and temporal variability across lifes heirachies in the terrrestrial Antarctic. Philosophical Transactions of the Royal Society

Chown SL, Gremmen NJM, Gaston KJ (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. American Naturalist 152: 562-575

Clarke A (1991) Cold adaptation. Journal of Zoology 225: 691-699

Clarke A (1992) Is there a latitudinal diversity cline in the sea. Trends in Ecology & Evolution 7: 286-287

Clarke A (2003) Evolution, adaptation and diversity: global ecology in an Antarctic context. In: Huiskes A, Gieskes W, Rozema J, Schorno R, Van DerVies S, Wolff W (eds) Antarctic Biology in a Global Context, Proceedings, pp 3-17

Clarke A, Barnes DKA, Hodgson DA (2005) How isolated is Antarctica? Trends in Ecology & Evolution 20: 1-3

Clarke A, Crame JA (2003) The importance of historical processes in global patterns of diversity. In: Blackburn TM, Gaston KJ (eds) Macroecology: concepts and consequences. 43rd Annual Symposium of the British Ecological Society, Birmingham, 2002. Blackwell Science, Oxford, pp 130-151

Clarke A, Harris CM (2003) Polar marine ecosystems: major threats and future change. Environmental Conservation 30: 1-25

Clarke A, Holmes LJ, White MG (1988) The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands 1969-82. British Antarctic Survey Bulletin 80: 65-86

Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. Oceanography and marine biology 41: 47-114

Clarke A, Leakey RJG (1996) The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem. Limnology and Oceanography 41: 1281-1294

Clarke KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Connell JH (1961) Effects on competition, predationby *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31: 61-104

Connell JH (1972) Community interactions on marine intertidal rocky shores. Annual Review of Ecology and Systematics 3: 169-192

Connell JH (1979) Intermediate-disturbance hypothesis. Science 204: 1345-1345

Convey P (2001a) Antarctic ecosystems. In: Levin S (ed) Encyclopaedia of Biodiversity vol 1. Academic Press, San Diego, pp 171-184

Convey P (In press) Antarctic Ecosystems Encyclopaedia of Biodiversity. Elselvier

Convey P (1996a) The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. Biological Reviews of the Cambridge Philosophical Society 71: 191-225

Convey P (2003) Maritime Antarctic climate change:signals from terrestrial biology. In: Domack E, Burnett A, Leventer A, Convey P, Kirby M, Bindschadler R (eds) Antarctic Peninsula Climate Variability:`Historiacl and Palaeoenvironmental Perspectives. American Geophysical Union, Washington DC, pp 145-158

Convey P (1996b) Overwintering strategies of terrestrial invertebrates in Antarctica - The significance of flexibility in extremely seasonal environments. European Journal of Entomology 93: 489-505

Convey P (2001b) Terrestrial ecosystem response to climate changes in the Antarctic. In: Walther GR, C.A. B, P.J. E (eds) "Fingerprints" of climate change - adapted behaviour and shifting species ranges. Klewer, New York, pp 17-42

Convey P, Barnes DKA, Morton A (2002) Debris accumulation on oceanic island shores of the Scotia Arc, Antarctica. Polar Biology 25: 612-617

Convey P, Block W, Peat HJ (2003) Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? Global Change Biology 9: 1718-1730

Convey P, Greenslade P, Pugh PJA (2000) The terrestrial micro-arthropod fauna of the South Sandwich Islands. Journal of Natural History 34: 597-609

Convey P, McInnes S (2005) Exceptional tardigrade- dominated ecosystems in Ellsworth Land, Antarctica. Ecology 83: 519-527

Convey P, Pugh PJA, Jackson C, Murray AWA, Ruhland CT, Xiong FS, Day TA (2002) Response of Antarctic terrestrial microarthropods to long-term climate manipulations. Ecology 83: 3130-3140

Convey P, Smith RIL (1997) The terrestrial arthropod fauna and its habitats in northern Marguerite Bay and Alexander Island, maritime Antarctic. Antarctic Science 9: 12-26

Cook AJ, Fox AJ, Vaughan DG, Ferrigno JG (2005) Retreating glacier fronts on the Antarctic Peninsula over the past half-century. Science 308: 541-544

Crame JA (2000) Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. Paleobiology 26: 188-214

Crisp DJ, Davenport, J. & Gabbott, P.A. (1977) Freezing tolerance in *Balanus balanoides*. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 57: 359-361

Danks HV (1999) Life cycles in polar arthropods - flexible or programmed? European Journal of Entomology 96: 83-102

Davenport J (1997) Comparisons of the biology of the intertidal subantarctic limpets *Nacella concinna* and *Kerguelenella lateralis*. Journal of Molluscan Studies 63: 39-48

Davenport J, Barnett PRO, McAllen RJ (1997) Environmental tolerances of three species of the harpacticoid copepod genus *Tigriopus*. Journal of the Marine Biological Association of the United Kingdom 77: 3-16

Davenport J, Davenport JL (2005) Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. Marine Ecology-Progress Series 292: 41-50

Davenport J, MacAllister H (1996) Environmental conditions and physiological tolerances of intertidal fauna in relation to shore zonation at Husvik, South Georgia. Journal of the Marine Biological Association of the United Kingdom 76: 985-1002

Davidson IC, Crook AC, Barnes DKA (2004) Quantifying spatial patterns of intertidal biodiversity: Is movement important? Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 25: 15-34

Day TA, Ruhland CT, Grobe CW, 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

Dayton PK (1971) Competition, disturbance, and community organization - provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-&

Dayton PK (1990) Polar benthos. In: Smith W (ed) Polar oceanography. Academic Press, London, pp 631-685

Dayton PK, Robillia.Ga, Devries AL (1969) Anchor ice formation in Mcmurdo Sound Antarctica and its biological effects. Science 163: 273-&

de Villiers AF (1976) Littoral ecology of Marion and prince Edward Islands (Southern Ocean). South African Journal of Antarctic Research, Supplement 1: 1-40

Dell RK (1972) Antarctic benthos. Advances in marine biology 10: 1-216

Denny MW (1988) Biology and the Mechanics of the Wave-swept Environment. Princeton University Press, Princeton, New Jersey

Devries AL (1971) Glycoproteins as biological antifreeze agents in antarctic fishes. Science 172: 1152-&

Devries AL (1984) Role of glycopeptides and peptides in inhibition of crystallization of water in polar fishes. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 304: 575-588

Devries AL, Komatsu SK, Feeney RE (1969) Purification and characterization of a freezing-point-depressant glycoprotein from Antarctic fish. Abstracts of Papers of the American Chemical Society: B308-&

Duman JG, De Vries AL (1972) Freezing behavior of aqueous-solutions of glycoproteins from blood of an Antarctic fish. Cryobiology 9: 469-472

Duman JG, Horwarth KL, Tomchaney A, Patterson JL (1982) Antifreeze agents of terrestrial arthropods. Comparative Biochemistry and Physiology a-Physiology 73: 545-555

Edwards RRC (1978) Ecology of a coastal lagoon complex in Mexico. Estuarine and Coastal Marine Science 6: 75-92

Elton C (1927) Animal Ecology. Sidgwick & Jackson, London

EPICA cm (2004) Eight glacial cycles from an Antarctic ice core. Nature 429: 623-628

Ernsting G, Block W, Macalister H, Todd C (1995) The invasion of the carnivorous carabid beetle *Trechisibus-Antarcticus* on South Georgia (Sub-Antarctic) and Its effect on the endemic herbivorous beetle *Hydromedion-Spasutum*. Oecologia 103: 34-42

Fowbert JA, Smith RIL (1994) Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. Arctic and Alpine Research 26: 290-296

Fraser KPP, Clarke A, Peck LS (2002) Feast and famine in Antarctica: seasonal physiology in the limpet *Nacella concinna*. Marine Ecology-Progress Series 242: 169-177

Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom DM (2005) Biological invasions in the Antarctic: extent, impacts and implications. Biological Reviews 80: 45-72

Gaines SD (1999) Can Rapoport's rule be rescued? Modelling the causes of the latitudinal gradient in species richness. Ecology

Galeron J, Herman RL, Arnaud PM, Arntz WE, Hain S, Klages M (1992) Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica. Polar Biology 16: 3-18

Gambi MC, Lorenti M, Russo GF, Scipione MB (1994) Benthic associations of the shallow hard bottoms off Terra-Nova Bay, Ross Sea - zonation, biomass and population-structure. Antarctic Science 6: 449-462

Gaston KJ, Spicer JI (1998) Biodiversity an introduction. Blackwell Science, Oxford

Gende SM, Edwards RT, Willson MF, Wipfli MS (2002) Pacific salmon in aquatic and terrestrial ecosystems. Bioscience 52: 917-928

Gerighausen U, Brautigam K, Mustafa O, Peter HU (2003) Expansion of vascular plants on an Antarctic island a consequence of climate change? Antarctic Biology in a Global Context, Proceedings, pp 79-83

Gloersen P, Campbell WJ, Cavalieri DJ, Comiso JC, Parkinson CL, Zwally HJ (1993) Satellite Passive Microwave Observations and Analysis of Arctic and Antarctic Sea-Ice, 1978-1987 Annals of Glaciology, Vol 17, pp 149-154

Gotelli NJ, Entsminger GL (2004) EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim/index.htm.

Green RH, Singh SM, Hicks B, McCuaig JM (1983) An Arctic intertidal population of *Macoma balthica* (Mollusca, Pelecypoda) - genotypic and phenotypic components of population-structure. Canadian Journal of Fisheries and Aquatic Sciences 40: 1360-1371

Gressitt JL (1970) Subantarctic entomology, particularly of South Georgia and Heard Island. Pacific Insect Monographs 23

Gruzov EN (1977) Seasonal alterations in coastal communities in the Davis Sea. In: G.A. L (ed) Adaptations within Antarctic Ecosystems: Proceeding of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institute, Washington, pp 263-278

Gurjanov EF (1968) Influence of water movements upon species composition and distribution of marine fauna and flora throughout Arctic and North Pacific intertidal zones. Sarsia 34: 83-84

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biology 24: 553-564

Gutt J, Starmans A, Dieckmann G (1996) Impact of iceberg scouring on polar benthic habitats. Marine Ecology-Progress Series 137: 311-316

Håkanson L (1981) A Manual of Lake Morphometry. Springer- Verlag, Berlin

Hansen TN, Baust JG (1988) Differential scanning calorimetric analysis of antifreeze protein activity in the common mealworm, *Tenebrio molitor*. Biochimica Et Biophysica Acta 957: 217-221

Hansom JD (1983) Ice-formed intertidal boulder pavements in the Sub-Antarctic. Journal of Sedimentary Petrology 53: 135-145

Hargens AR, Shabica SV (1973) Protection against lethal freezing temperatures by mucus in an Antarctic impet. Cryobiology 10: 331-337

Harper JL, Hawksworth DL (1995) Preface. In: Hawksworth DL (ed) Biodiversity: measurement and estimation. Chapman & Hall, London, pp 5-12

Hedgpeth JW (1969b) Introduction to Antarctic zoo-geography. Antarctic map folio series 11: 109

Hedgpeth JW (1969a) Preliminary observations of life between tidemarks at Palmer Station, 64 degrees 45,S 64 degrees 05,W. Antarctic Journal of the United States 4: 106-&

Hodgson D, Vyverman W, Tyler PA (1997) Diatoms of meromictic lakes adjacent to the Gordon River, and of the Gordon River estuary in south-west Tasmania. Bibliotheca Diatomology 35: 1-172

Hodgson DA, Johnston NM, Caulkett AP, Jones VJ (1998) Palaeolimnology of Antarctic fur seal *Arctocephalus gazella* populations and implications for Antarctic management. Biological Conservation 83: 145-154

Holdgate MW, Baker PE (1979) The South Sandwich Islands: I. General description. British Antarctic Survey Scientific Reports 91: 76pp

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ

Hull S, Winter LJ, Scott GW (2001) Habitat heterogeneity, body size and colour polymorphism in Idotea granulosa (Isopoda) on the northeast coast of England. Journal of the Marine Biological Association, UK 81: 949-954

Huston M (1979) General hypothesis of species-diversity. American Naturalist 113: 81-101

Huston MA (1996) Biological diversity. Cambridge University Press, Cambridge

Huston MA (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393-401

Jazdzewski K, De Broyer C, Pudlarz M, Zielinski D (2001) Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. Polar Biology 24: 910-917

Jazdzewski K, Jurasz W, Kittel W, Presler E, Presler P, Sicinski J (1986) Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King-George-Island, South-Shetland-Islands. Polar Biology 6: 5-16

Kareiva P, Anderson M (1989) Spatial aspects of species interactions: the wedding of models and experiments. In: A Hastings (ed) Community Ecology. Springer, New York, pp 35-50

King D (2005) Climate change: the science and the policy. Journal of Applied Ecology 42: 779-783

Kirkwood JM, Burton HR (1988) Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctica. Marine Biology 97: 445-457

Kuklinski P, Barnes DKA, Taylor PD (2006) Latitudinal patterns of diversity and abundance in North Atlantic intertidal boulder-fields. Marine Biology 149: 1577-1583

Lae R (1994) Changes in fish and crustacean communities of a tropical lagoon, Lake Togo, submitted to alternate phases of opening and closing belt. Aquatic Living Resources 7: 165-179

Lawrence JM, McClintock JB (1987) Intertidal invertebrate and algal communities on the rocky shores of the Bay of Morbihan, Kerguelen (South Indian-Ocean). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 8: 207-220

Lawton JH (1999) Are there general laws in ecology? Oikos 84: 177-192

Le Hir M, Hily C (2005) Macrofaunal diversity and habitat structure in intertidal boulder fields. Biodiversity and Conservation 14: 233-250

Lee RE, Costanzo JP (1998) Biological ice nucleation and ice distribution in cold-hardy ectothermic animals. Annual Review of Physiology 60: 55-72

Lee SY (1999) Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. Australian Journal of Ecology 24: 355-366

Lehtonen KK (1996) Ecophysiology of the benthic amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea: Seasonal variations in body composition, with bioenergetic considerations. Marine Ecology-Progress Series 143: 87-98

Linse K, Barnes DKA, Enderlein P (2006) Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. Deep-Sea Research Part Ii-Topical Studies in Oceanography 53: 921-931

Littlepage JL (1965) Oceanographic investigations in McMurdo Sound, Antarctica. In: Llano G (ed) Biology of the Antarctic Seas II. Antarctic research series. American Geophysical Union, Washington DC, pp 1-37

Long SP, Mason CF (1984) Saltmarsh Ecology

Longhurst AR (1998) The Southern Ocean Ecological Geography of the Sea. Academic Press, San Diego, pp 339-366

Longton RE (1988) Biology of Polar Bryophytes and Lichens. Cambridge University Press, Cambridge

Loomis SH (1995) Freezing tolerance of marine invertebrates Oceanography and Marine Biology - an Annual Review, Vol 33, pp 337-350

Lubchenco J (1980) Algal zonation in a New England rocky intertidal community, an experimental analysis. Ecology 61: 333-344

Luxton M (1967) Ecology of saltmarsh Acarina. Journal of Animal Ecology 36: 257-&

Lyons WB, Howard-Williams C, Hawes I (1997) Ecosystem Processes in Antarctic Ice-free Landscapes. Balkema, Rotterdam

Magurran AE (2004) Measuring Biological Diversity. Blackwell, Malden, MA

Maslen NR, Convey P (2006) Nematode diversity and distribution in the southern maritime Antarctic - clues to history? Soil Biology and Biochemistry 38: 3141-3151

May R (1999) Unanswered questions in ecology. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 354: 1951-1959

McAllen R, Block W (1997) Aspects of the cryobiology of the intertidal harpacticoid copepod *Tigriopus brevicornis* (O. F. Muller). Cryobiology 35: 309-317

McDowall RM (2005) Falkland Islands biogeography: converging trajectories in the South Atlantic Ocean. Journal of Biogeography 32: 49-62

McGuinness KA (1987) Disturbance and organisms on boulders .1. Patterns in the environment and the community. Oecologia 71: 409-419

McGuinness KA (1990) Physical variabilty, diversity gradients and the ecology of temerate and tropical reefs. Australian Journal of Ecology 15: 465-476

McGuinness KA, Underwood AJ (1986) Habitat structure and the nature of communities on intertidal boulders. Journal of Experimental Marine Biology and Ecology 104: 97-123

McKindsey CW, Bourget E (2001) Diversity of a northern rocky intertidal community: The influence of body size and succession. Ecology 82: 3462-3478

McQuaid CD, Branch GM (1985) Trophic structure of rocky intertidal communities - response to wave action and implications for energy-flow. Marine Ecology-Progress Series 22: 153-161

Menge BA (1976) Organization of New-England rocky intertidal community - role of predation, competition, and environmental heterogeneity. Ecological Monographs 46: 355-393

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250: 257-289

Menge BA, Lubchenco J, Ashkenas LR, Ramsey F (1986) Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama - direct and indirect consequences of food web complexity. Journal of Experimental Marine Biology and Ecology 100: 225-269

Menge BA, Sutherland JP (1987) Community regulation - variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. American Naturalist 130: 730-757

Miller LK (1982) Variations in Freezing Tolerance in Insects Overwintering in Interior Alaska. Cryo-Letters 3: 291-291

Moe RL, Delaca TE (1976) Occurrence of macroscopic algae along Antarctic Peninsula. Antarctic Journal of the United States 11: 20-24

Morin PJ (1999) Community Ecology. Blackwell Science, Malden, MA

Murphy DJ (1983) Freezing resistance in intertidal invertebrates. Annual Review of Physiology 45: 289-299

Nolan CP (1991) Environmental aspects of growth in the Antarctic molluscs *Nacella concinna* (Patellidae) and *Yoldia eightsi* (Nuculanidae) at Signy Island, South Orkney Islands, Hull

Norton TA (1991) Conflicting constraints on the form of intertidal algae. British Phycological Journal 26: 203-218

Ochyra R, Bednarek-Ochyra H, Smith RIL (2002) New and rare moss species from subantarctic South Georgia. Nova Hedwigia 74: 121-147

Paine RT (1966) Food web complexity and species diversity. American Naturalist 100: 65-75

Paine RT (1969) *Pisaster tegula* interaction - Prey patches, predator food preference, and intertidal community structure. Ecology 50: 950-&

Paine RT, Levin SA (1981) Inter-tidal landscapes - Disturbance and the dynamics of pattern. Ecological Monographs 51: 145-178

Pearsall J (1999) The New Oxford Dictionary of English. Oxford University Press, Oxford, pp 2152

Peck LS (2002) Ecophysiology of Antarctic marine ectotherms: limits to life. Polar Biology 25: 31-40

Peck LS (2005) Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change. Antarctic Science 17: 497-507

Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. Biological Reviews 81: 75-109

Peck LS, Conway LZ (2000) The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves Evolutionary Biology of the Bivalvia, pp 441-450

Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in Antarctic marine species. Functional Ecology 18: 625-630

Picken G (1985) Benthic research in Antarctica: Past, present and future. In: Gray J, Christiansen M (eds) Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. John Wiley & Sons Ltd

Picken GB (1980) Distribution, growth, and reproduction of the Antarctic impet *Nacella* (Patinigera) *concinna* (Strebel, 1908). Journal of Experimental Marine Biology and Ecology 42: 71-85

Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands - flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences of the United States of America 92: 4382-4386

Portner HO, Berdal B, Blust R, Brix O, Colosimo A, De Wachter B, Giuliani A, Johansen T, Fischer T, Knust R, Lannig G, Naevdal G, Nedenes A, Nyhammer G, Sartoris FJ, Serendero I, Sirabella P, Thorkildsen S, Zakhartsev M (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (Gadus morhua) and common eelpout (Zoarces viviparus). Continental Shelf Research 21: 1975-1997

Price PW (1984) Insect Ecology. Wiley Interscience, New York

Pruett L, Cimino J (2000) Global Maritime Boundaries Database (GMBD). Veridian - MRJ Technology Solutions, Fairfax, Virginia, pp http://earthtrends.wri.org/text/coastal-marine/variable-61.html

Pugh PJA (1994) Supercooling points and water-content in Acari. Acta Oecologica-International Journal of Ecology 15: 71-77

Pugh PJA (2004) Biogeography of spiders (Araneae : Arachnida) on the islands of the Southern Ocean. Journal of Natural History 38: 1461-1487

Pugh PJA, Davenport J (1997) Colonisation vs. disturbance: The effects of sustained ice-scouring on intertidal communities. Journal of Experimental Marine Biology and Ecology 210: 1-21

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405: 212-219

Raffaelli D, Hawkins S (1997) Preface Intertidal Ecology. Chapman & Hall, London, pp vii-x

Rapoport EH (1982) Areography. Geographic strategies of species. Pergamon Press, Oxford

Ricciardi A, Bourget E (1999) Global patterns of macroinvertebrate biomass in marine intertidal communities. Marine Ecology-Progress Series 185: 21-35

Rios C, Mutschke E (1999) Community structure of intertidal boulder-cobble fields in the Straits of Magellan, Chile. Scientia Marina 63: 193-201

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Rothery P, Block W (1992) Characterising supercooling point distributions. Cryo-letters 13: 193-198

Roy K, Jablonski D, Valentine JW, Rosenberg G (1998) Marine latitudinal diversity gradients: Tests of causal hypotheses. Proceedings of the National Academy of Sciences of the United States of America 95: 3699-3702

Ruuskanen A, Back S, Reitalu T (1999) A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. Marine Biology 134: 139-145

Salt RW (1961) Principles of insect cold-hardiness. Annual Review of Entomology 6: 55-&

Sanders HL (1968) Marine benthic diversity - a comparative study. American Naturalist 102: 243-&

Schenker R (1986) Biological andecological notes on *Neohyadesia signyi* (Acari;Astigmata). British Antarctic Survey Bulletin: 85-91

Scott GW, Hull SL, Hornby SE, Hardy FG, Owens NJP (2001) Phenotypic variation in *Fucus spiralis* (Phaeophyceae): morphology, chemical phenotype and their relationship to the environment. European Journal of Phycology 36: 43-50

Sejr MK, Jensen KT, Rysgaard S (2000) Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biology 23: 792-801

Shabica SV (1971) General ecology of Antarctic limpet *Patinigera polaris*. Antarctic Journal of the United States 6: 160-&

Shabica SV (1972) Tidal zone ecology at Palmer Station. Antarctic Journal of the United States 7: 184-185

Shabica SV (1976) The natural history of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot). Ph.D.

Sheaves MJ (1992) Patterns of distribution and abundance of fishes in different habitats of a mangrove-lined tropical estuary, as determined by fish trapping. Australian Journal of Marine and Freshwater Research 43: 1461-1479

Sinclair BJ, Marshall DJ, Singh S, Chown SL (2004) Cold tolerance of Littorinidae from southern Africa: intertidal snails are not constrained to freeze tolerance. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 174: 617-624

Sinclair BJ, Vernon P, Klok CJ, Chown SL (2003) Insects at low temperatures: an ecological perspective. Trends in Ecology & Evolution 18: 257-262

Smale D, Barnes DKA, Fraser KPP (in press) The influence of depth, site exposure and season on the intensity of iceberg scouring in nearshore Antarctic waters. Polar Biology DOI 10.1007/s00300-006-0236-0

Smith JMB, Simpson RD (1985) Biotic zonation on rocky shores of Heard Island. Polar Biology 4: 89-94

Smith RIL (1988b) Destruction of Antarctic terrestrial ecosystems by a rapidly increasing fur-seal population. Biological Conservation 45: 55-72

Smith RIL (1988a) Recording bryophyte microclimate in remote and severe environments. In: Glime JM (ed) Methods in Bryology. Hattori Botanical Laboratory, Nichinan, pp 275-284

Smith RIL (1990) Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In: Kerry K, Hempel G (eds) Antarctic Ecosystems, Ecological Change and Conservation. Springer-Verlag, Berlin

Smith RIL (1984) Terrestrial blant biology of the sub-Anatrctic and Anatrctic. In: Laws R (ed) Antarctic Ecology. Academic Press, London, pp 61-162

Smith SDA, Simpson RD (2002) Spatial variation in the community structure of intertidal habitats at Macquarie Island (sub-Antarctic). Antarctic Science 14: 374-384

Sokolova IM, Portner HO (2003) Metabolic plasticity and critical temperatures for aerobic scope in a eurythermal marine invertebrate (Littorina saxatilis, Gastropoda: Littorinidae) from different latitudes. The Journal of Experimental Biology 206: 195-207

Sømme L (1986) Ecology of *Cryptopygus sverdrupi* (Insecta, Collembola) from Dronning Maud Land, Antarctica. Polar Biology 6: 179-184

Sømme L (1995) Invertebrates in Hot and Cold Arid Environments. Springer-Verlag, Berlin

Sømme L, Block W (1982) Cold Hardiness of Collembola at Signy Island, Maritime Antarctic. Oikos 38: 168-176

Sømme L, Block W (1984) Ecophysiology of 2 intertidal mites at South Georgia. Oikos 42: 276-282

Sousa WP (1979) Disturbance in marine inter-tidal boulder fields - the non-equilibrium maintenance of species-diversity. Ecology 60: 1225-1239

Southward AJ (1958) The zonation of plants and animals on rocky sea shores. Biological Reviews of the Cambridge Philosophical Society 33: 137-177

Southward AJ (1965) Life on the seashore. Heinemann, London

Southwood TRE (1977) Habitat, Templet for ecological strategies - Presidential address to British Ecological Society, 5 January 1977. Journal of Animal Ecology 46: 337-365

Steele JH (1995) Can ecological concepts span the land and ocean domains? In: Powell TM, Steele JH (eds) Ecological Time Series. Chapman & Hall, New York, pp 5-19

Stehli FG (1968) Taxonomic diversity gradients in pole location: the recent model. In: Drake ET (ed) Evolution and Environment. Yale University Press, New Haven, pp 163-227

Stephenson TA, Stephenson A (1949) The universal features of zonation between tidemarks on rocky coasts. Journal of Ecology 38: 289-305

Stergiou KI, Browman HI (2005b) Bridging the gap between aquatic and terrestrial ecology - Introduction. Marine Ecology-Progress Series 304: 271-272

Stergiou KI, Browman HI (2005a) Imbalances in the reporting and teaching of ecology from limnetic, oceanic and terrestrial eco-domains. Marine Ecology-Progress Series 304: 292-297

Stern N (2006) The economics of climate change: The Stern Review. Cambridge University Press, Cambridge

Stevens GC (1989) THe latitudinal gradient in geographical range:how so many species exist in the tropics. American Naturalist 133: 240-256

Stockton WL (1973) Am intertidal assemblage at Palmer station. Antarctic Journal of the United States 8: 305-307

Storey KB, Storey JM (1996) Natural freezing survival in animals. Annual Review of Ecology and Systematics 27: 365-386

Stout WE, Shabica SV (1970) Marine ecological studies at Palmer-Station and vicinity. Antarctic Journal of the United States 5: 134-&

Strange IJ (1992) A Field Guide to the Wildlife of the Falkland Islands and South Georgia. Harper Collins, London

Szymelfenig M, Kwasniewski S, Weslawski JM (1995) Intertidal zone of Svalbard .2. Meiobenthos density and occurrence. Polar Biology 15: 137-141

Tavares M, De Melo GAS (2004) Discovery of the first known benthic invasive species in the Southern Ocean:the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. Antarctic Science 16: 129-131

Thatje S, Fuentes V (2003) First record of anomuran and brachyuran larvae (Crustacea:Decapoda) from Antarctic waters. Polar Biology 27: 195-201

Theede H, Schneppenheim R, Beress L (1976) Antifreeze Glycoproteins in Mytilus-Edulis. Marine Biology 36: 183-189

Tilman D (1989) Ecological experimentation: strengths and conceptual problems. In: E LG (ed) Long-term studies in ecology. Springer, New York, pp 136-157

Tomchaney AP, Morris JP, Kang SH, Duman JG (1982) Purification, Composition, and Physical-Properties of a Thermal Hysteresis Antifreeze Protein from Larvae of the Beetle, Tenebrio-Molitor. Biochemistry 21: 716-721

Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. International Journal of Climatology 25: 279-294

Underwood AJ (1980) The effects of grazing by gastropods and physical factors on the upper limits of distribution of inter-tidal macroalgae. Oecologia 46: 201-213

United Nations Environment Programme CA (1992) United Nations Convention on Biological Diversity. Environmental Law and Institutions Programme Activity Centre, N:pl.

Urban-Malinga B, Kotwicki L, Gheskiere TLA, Jankowska K, Opalinski K, Malinga M (2004) Composition and distribution of meiofauna, including nematode genera, in two contrasting Arctic beaches. Polar Biology 27: 447-457

Van der Putten N, Verbruggen C (2005) The onset of deglaciation of Cumberland Bay and Stromness Bay, South Georgia. Antarctic Science 17: 29-32

Vaughan DG, Doake CSM (1996) Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. Nature 379: 328-331

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Climatic Change 60: 243-274

Verrill AE (1882) Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No.7. American Journal of Science, (series 3) 24: 360-371

Vo□J (1988) Zoogeographie und Gemeinschaftsanalyse des Makrozoobethos des Weddellmeeres (Antarktis). Ber Polarforsch 45: 1-145

Waller CL, Barnes DKA, Convey P (2006) Ecological contrasts across an Antarctic land-sea interface. Austral Ecology 31: 656-666

Waller CL, Worland MR, Convey P, Barnes DKA (2006) Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. Polar Biology 29: 1077-1083

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416: 389-395

Walton DWH (1984) The terrestrial environment. In: Laws R (ed) Antarctic Ecology. Academic Press, London, pp 1-60

Webb JE, Hill MB (1958) The Ecology of Lagos Lagoon .4. On the Reactions of Branchiostoma-Nigeriense Webb to Its Environment. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 241: 355-391

Wentworth CR (1922) A scale of grade and class terms for clastic sediments. Journal of Geology 30: 377-392

Weslawski JM, Szymelfenig M, Zajaczkowski M, Keck A (1999) Influence of salinity and suspended matter on benthos of an Arctic tidal flat. Ices Journal of Marine Science 56: 194-202

Weslawski JM, Wiktor J, Zajaczkowski M, Swerpel S (1993) Intertidal Zone of Svalbard .1. Macroorganism Distribution and Biomass. Polar Biology 13: 73-79

Weslawski JM, Zajaczkowski M, Wiktor J, Szymelfenig M (1997) Intertidal zone of Svalbard .3. Littoral of a subarctic, oceanic island: Bjornoya. Polar Biology 18: 45-52

Whitaker RH (1975) Communities and Ecosystems. New York, MacMillan

White G (1789) The Natural History and Antiquities of Selborne, in the County of Southampton: with Engravings, and an Appendix. T. Bensley, for B. White and Son, London

White MG (1984) Marine benthos. In: Laws R (ed) Antarctic ecology. Academic press, London, pp 421-461

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology Evolution and Systematics 34: 273-309

Wise KAJ (1971) The collembola of Antarctica. Pacific Insects Monograph 25: 57-74

Worland MR, Block W (1986) Survival and Water-Loss in Some Antarctic Arthropods. Journal of Insect Physiology 32: 579-584

Worland MR, Convey P (2001) Rapid cold hardening in Antarctic microarthropods. Functional Ecology 15: 515-524

Worland MR, Leinaas HP, Chown SL (2006) Supercooling point frequency distributions in Collembola are affected by moulting. Functional Ecology 20: 323-329

Worland MR, Lukesova A (2000) The effect of feeding on specific soil algae on the cold-hardiness of two Antarctic micro-arthropods (Alaskozetes antarcticus and Cryptopygus antarcticus). Polar Biology 23: 766-774

Appendix 1

Appendix 1 – Full taxon list

Class/ group	Family/Genus- species	Subtidal	Intertidal	Terrestrial
Gastropoda	*Nacella concinna*	●	●	
	Margarella antarctica	●	●	
	Laevilitorina caliginosa	●	●	
	Onoba luvqueti	●	●	
	? *Guyvalvoria* sp.		●	
	Eubranchus sp.	●	●	
	Clione sp.	●	●	
Bivalvia	*Cyamiomactra laminifera*		●	
	Mysella charcoti	●	●	
	Adacnarca nitens	●		
	Yoldia eightsi	●		
Nudibrancha	*Eubranchus* sp	●	●	
	Unidentified 1		●	
	Unidentified 2		●	
Echinoidea	*Sterechinus neumayeri*	●	●	
Asteroidea	*Ophionotus victoriae*	●		
	Odontaster validus	●		
Anthozoa	Burrowing anemone		●	
Polyplacophora	chiton	●		
Malacostraca	*Prostebbingia gracilis*		●	
	Stenothoidae sp.	●	●	
	Prostebbingia brevicornis	●	●	
	Cheirimendon femoratus	●	●	
	Paramoera walkeri	●		
	Hippomedon kergueleni	●	●	
	Gondogeneia antarctica	●	●	
	Paraceradocus gibber	●		
	Cymodocella sp.	●	●	
	Unidentified amphipod		●	
	Notasellus sarsi		●	
	Munna antarctica	●	●	
Copepoda	*Tigriopus angulatus*		●	
Piscies	*Harpagifer antarcticus*	●	●	
	Artedidraconidae sp. (juvenile)		●	
	Pagothenia borchgevinski	●		
Polychaeta	*Barrukia cristata*	●	●	
	Terrebellidae	●	●	
	Capitella sp.	●		
	Aglaophamus trissophyllus	●		
	Protolaeospira stalagmia	●		
	Paralaeospira levinsi	●	●	
	Protolaeospira pedalis	●	●	
	Serpulidae	●	●	
	Unidentified		●	
Pycnogona	*Achelia communis*	●	●	
Anopla	*Antarctonemertes validum*	●	●	
	Parbolasia sp.	●	●	
	Parborlasia corrugata	●		
Hydrozoa	*Gonionemus* sp.	●	●	
	Tubularia sp.	●	●	
Calcarea	*Leucosolenia* sp.	●	●	
	Unidentified		●	
Ctenophore	Unidentified		●	
Gymnolaemata	*Celleporella antarctica*	●	●	
	Celleporella bougainvillei	●	●	
	Hippadanella inerma	●	●	
	Aimulosia antarctica	●	●	
	Arachnopusia inchoata	●	●	
	Micropora brevissima	●		
	Fenestrulina rugula	●	●	
	Smittina sp.	●		
	Klugerella antarctica	●		
	Ellisina antarctica	●	●	
	Beania erecta	●		
	Xylochotridens rangifer		●	
	Chaperiopsis quadrispinosa		●	
	Inversiula nutrix	●	●	
Stenolaemata	*Tubulipora* sp.	●	●	
	Idmidronea sp.		●	

	Discoporella sp.	●	●	
Arachnida	*Rhombognathus gressitti*		●	
	Alaskozetes antarcticus		●	●
	Halozetes belgicae			●
	Gamasellus racovitzai		●	●
	Stereotydeus villosus			●
	Rhagidia gerlachei			●
	Nanorchestes sp.			●
	Eupodes sp.			●
	Globoppia sp.			●
	Tydeids sp.			●
Hexapoda	*Cryptopygus antarcticus*		●	●
	Friesea grisea			●
Tardigrada				●
Nematoda			●	●