Nearshore Antarctic reef assemblages: influence of sedimentation and benthic irradiance

by

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Declaration

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Dedication

This thesis is dedicated to my mother Vera, and my late father, David, who provided so much inspiration and encouragement to follow my dreams of becoming a marine biologist. For the countless childhood opportunities they provided for exploring the intertidal rock pools and subtidal rocky reefs of Victoria's Bass Strait coast, and for teaching me the value of nature and the importance of caring for our natural environment.

Thank you both from the bottom of my heart.

Thesis Abstract

Sediment runoff accelerated by human activities is known to be a major threat to nearshore marine communities worldwide, however impacts of sedimentation in Antarctica are largely unknown. Each summer at Australia's Casey Station, meltwater entrains sediment from crushed rock roadways causing visible surface plumes in Brown Bay. Observations during previous studies indicated a paucity of reef species in Brown Bay compared to other bays in the Windmill Islands. Differences were attributed to two possible factors: 1) elevated sedimentation rates resulting from human activities, and 2) lower benthic irradiance caused by thicker snow cover overlying sea ice. This thesis examines the potential impacts of sedimentation and benthic irradiance on shallow rocky reef assemblages in Antarctica using both manipulative in situ *and aquarium experiments.*

Digital video transects quantitatively confirmed that reefs in Brown Bay supported a significantly lower cover of biota, fewer total species and individuals, and fewer sponge species compared to nearby 'control' bays. Recruitment to artificial substrata in Brown Bay and 'control' bays was numerically dominated by spirorbid polychaetes and encrusting bryozoan species after 13 and 37 months. Recruitment varied significantly between bays, although overall fewer species and fewer bryozoan species recruited at Brown Bay. More taxa recruited when sedimentation was experimentally inhibited in Brown Bay (using Plexiglas shields), indicating sediment loads were hindering recruitment. Aquarium experiments showed a 0.5 mm thick sediment layer prevented zoospore settlement and early post-settlement growth of the brown alga, Himantothallus grandifolius, and smothering of attached zoospores by a thin layer of sediment caused reduced germ tube growth. Translocated individuals of red alga, Palmaria decipiens, in Brown Bay and 'control bays' had thalli lengths 80 - 99% shorter after 12 and 36 months compared to lengths at initial deployment. Reduced thallus growth was apparent even when sedimentation was artificially reduced, indicating that factors other than sedimentation influence the growth of adult P.decipiens. A clear effect of irradiance levels on thallus growth of this species in the absence of sedimentation was subsequently identified in aquarium experiments, and results correlated with the field observations.

Anthropogenically increased sedimentation rates in Antarctica were shown to influence recruitment success of sessile reef taxa (flora and fauna), while benthic irradiance was identified as a strong determinant of macroalgal distribution. Sound environmental management of runoff accelerated by human activities in Antarctica is considered critical for reducing impacts on marine environments, particularly in light of climate change predictions for polar environments.

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The research described in this thesis would not have been possible without the assistance of a large number of dedicated .people from a variety of backgrounds and organisations.

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- Craig Johnson (*School of Zoology, University of Tasmania*) for academic advice, critical review of experimental and statistical design, and ongoing encouragement to finish this thesis.

I would also like to thank my colleagues of thirteen years, the men and women of the Australian Antarctic Division Headquarters in Kingston, Tasmania, and the expeditioners on Australia's National Antarctic Research Expeditions (ANARE) between 1994 and 2006. Without their professional and technical assistance, and sheer dedication to their goals, no research would be possible in the challenging environment of Antarctica. The camaraderie and skill of those men and women have taught me more than they could imagine.

A big thank you to my dive supervisors and dive team members for enabling me to conduct my field research in utmost safety, despite the gruelling schedule of cold and difficult, long and tiring months each 'summer' at Casey. Thank you for indulging my weird and not so wonderful experimental ideas and for keeping us all sane with the daily banter of old jokes and tired humour. A very special mention should go to my ever reliable dive buddies, Letitia Lamb (in association with Diver Bill) and Cath Samson, who tirelessly unrolled

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Chapter 1
General Introduction and Description of Bay Environments

General introduction

Antarctic benthos has been collected, studied and identified for more than 100 years through samples obtained by explorers and scientists alike. Yet, while many of the early descriptions were of taxa sampled remotely from deep water off ships, the nearshore shallow habitats have until relatively recently been the subject of few investigations. With the advent of SCUBA in the 1950s, marine ecological research conducted *in situ* in the shallow waters along the Antarctic coast began to reveal diverse and unique ecological assemblages.

Difficult coastal access, extreme environmental conditions and a highly seasonal presence of researchers in Antarctica have limited marine nearshore research to locations adjacent to national research stations, particularly in areas of McMurdo Sound (e.g. Dayton *et al.* 1970, 1990) and the Antarctic Peninsula (e.g. Barnes 1995a, 1995b, Barnes & Brockington 2003, Barnes *et al.* 2006, Smale 2008). Vast areas of the Antarctic coast are beyond daily access from established research stations and consequently are under-researched. Clarke (1996b) identified large sections of the Antarctic continental shelf that are either unsampled or unrepresented in the literature, including a 150° longitudinal sector along most of East Antarctica that has been the subject of only a few published papers addressing the nearshore benthos (e.g. Gruzov 1977, Kirkwood & Burton 1988). As a consequence, and in comparison with temperate, tropical and even Arctic research, the scientific investigation of nearshore Antarctic marine ecology is still in its infancy.

Ice scour and vertical zonation

Antarctic benthic environments are a contrast between stable water quality (consistently low temperatures with generally high salinity and dissolved oxygen, Knox 1994), highly variable seasonal fluctuations in light intensity (Kirst & Wiencke 1995, and

Wiencke 1996), and strong and often variable physical disturbance, particularly by ice (Gutt 2001). Ice is recognised as a major factor influencing the distribution of Antarctic benthos (Gutt & Starmans 2001, Brown *et al.* 2004). Ice mediated disturbance has both predictable components (e.g. scouring of shallow substrata by ice foot movement relative to local tidal range) and more random components (e.g. scouring by icebergs driven by wind and water currents). Regardless of predictability, ice scour has the potential to cause *"local eradication of benthic fauna with a frequency that is related to depth"* (Clarke 1996b), and therefore is a strong determinant of benthic zonation in Antarctic nearshore waters.

Zonation of marine flora and fauna within the upper sub-littoral has been described for the more commonly studied regions of Antarctica, such as McMurdo Sound (Dayton 1970, 1990), and the Antarctic Peninsula (Clarke 1996a, 1996b, 1996c, Barnes *et al.* 2006, Smale 2008). Marine macroalgae are a common feature of many Antarctic shores and species have evolved strategies to anticipate the annual loss of sea ice and to opportunistically dominate hard substrata in shallow waters (Wiencke & Clayton 2002).

Fauna within the zone of maximum sea ice abrasion (~0 - 4 m depth) tend to be motile foragers (molluscs and echinoderms) or cryptically attached filter feeders (bryozoans and polychaetes) located in cracks and under ledges where they are protected from ice scour (Gruzov 1977, Dayton 1990). Below the scour zone however, the benthos is dominated by sessile filter-feeding invertebrates (such as sponges, tube worms, and ascidians) and roaming motile echinoderms and molluscs (Dayton 1990, Knox 1994); perennial macroalgae are scarce even below the ice scour zone (Cummings *et al.* 2006).

Multiscale spatial patterns in benthic community structure

A feature commonly ascribed to marine benthos, including Antarctic benthos, is high variability across a range of spatial scales, with high patchiness in abundances and biomass (Arntz *et al.* 1994). Once thought to exhibit a latitudinal gradient of increasing marine benthic biodiversity from poles to equator (Thorson 1950), at least in the Southern Hemisphere, the pattern of benthic biodiversity is now believed to vary in more complicated ways (Gray 2001). The general consensus is that the Antarctic benthos is

more diverse than the Arctic, having had significantly more time (>20 million years c.f. 2 -
3 million years) to develop *in situ* (Dayton 1990, Clarke 1996b). In addition, the rate of
endemism at the species level is reportedly between 57 and 95% within major Antarctic
faunal groups (Knox 1994). Small-scale variability (metres) in benthic distribution patterns
is also prominent in the Antarctic and believed to reflect inherently high habitat
heterogeneity, and spatial variability in ice abrasion, recruitment and predation (Clarke
1996b).

Generalised zonation patterns are useful when describing generalised environments
but as with marine environments elsewhere, the Antarctic consists of a range of habitats and
geographical features that determine local ecological patterns. Indeed, variation in extent
and duration of sea ice cover, in association with variable thicknesses of overlying snow
layers, is recognised as one of the greatest determinants of nearshore benthic community
structure (Knox 1994). The interaction of coastline shape, terrestrial topography, marine
bathymetry, exposure to ocean swell and currents, and the vagaries of local weather (such
as wind direction and fetch) determines the local characteristics of sea ice. Sea ice and
overlying snow layers filter >99% of incident radiation creating significantly reduced light
levels available for benthic primary productivity (McMinn *et al.* 1999). Consequently,
nearshore areas that have persistent sea ice cover for most of the year are less likely to
support extensive macroalgae and associated benthic grazers.

Effects of sediment on benthic community structure

The Antarctic, unlike the Arctic, is largely devoid of major rivers and the marine
environment has historically been exposed to relatively little meltwater flow (Dayton
1990). As a consequence, natural sedimentation rates in nearshore Antarctic waters are
generally low (Isla *et al.* 2001) and therefore assumed to be an insignificant determinant of
nearshore ecology. The one exception is close to glaciers where the rate of sedimentation
can be high "leading to eradication of all but those species tolerant of such high inorganic
loads" (Clarke 1996a).

At lower latitudes, elevated sedimentation rates associated with land clearing, agriculture, urbanisation and storm events have been shown to cause a reduction in the diversity and abundance of sessile species, in particular the loss of algal species and the increased dominance of opportunistic suspension feeders (Saiz Salinas & Urdangarin 1994). Excessive sedimentation may affect the choice of settlement site by larvae (Hunt & Scheibling 1997), cause smothering of slow growing, encrusting species (Moore 1977), and/or clog feeding apparatus (Ellis *et al.* 2002). The taxa most at risk from altered sediment regimes are the sessile filter-feeders and attached algae that are least able to avoid smothering and choking effects (Moore 1977, Ellis *et al.* 2002). New recruits are generally less adaptable than adults and persistent exposure to elevated sedimentation rates over time can cause changes in recruitment and a shift in community structure (Hinchey 2006, Balata *et al.* 2007).

Anthropogenic sedimentation in Antarctica

In Antarctica, despite naturally low sedimentation rates, benthic environments near to human activities may be exposed to elevated sediment regimes. Human activities along Antarctic coastal margins are small in scale and intensity compared to those on most other land masses; for example, Australia's Casey Station has a small direct foot print (<0.5 km^2), with land disturbance generally restricted to the establishment of buildings and cargo storage, and the maintenance of vehicular roadways between them. However, the presence of heated, artificial structures within the polar landscape has the potential to alter the local pattern of snow deposition thereby creating areas with reduced snow cover that expose rock and soil to erosional processes. Snow clearing around buildings and along roadways using heavy machinery also disturbs the surface geology and removes the natural insulating layer of snow that restricts wind and water erosion of soils and rock. In addition, the requirement for functional roadways throughout the summer period often necessitates the addition of crushed local rock to stabilise the road surfaces. Thus, unnaturally high levels of rock dust and soils within human-influenced landscapes are available for transportation by wind and water.

For a period of ~six weeks from mid-December, the daily maximum temperatures at Casey Station are often above freezing, and meltwater flows off the station roads and down the catchment gradients into the marine environment, entraining dust and soils along the way. At peak flow, surface sediment plumes are visible at the interface of the meltwater and seawater. In the vicinity of Casey Station within a ten year period from 1996, no sediment plumes have been observed entering the marine environment at any location other than in the bay whose catchment includes the station.

The impact of elevated sedimentation rates on Antarctic benthos is unknown. Apart from an opportunistic study of the effects of a sediment slump event on the benthos near McMurdo Station, where 84% mortality of soft coral was attributed to sudden resuspension and subsequent resettlement of sediment (Slattery & Bockus 1997), there has been no research specifically addressing the susceptibility of Antarctic species or assemblages to elevated sedimentation levels. The importance of research into sediment-mediated impacts on nearshore marine habitats is elevated by predictions of climate change, where increased temperatures are expected to result in increased snow melt and reduction of glaciers, ice shelves and sea ice (Anisimov *et al.* 2007). This could potentially lead to increased terrestrial sediment loads entering the Antarctic marine environment.

Research focus and thesis structure

The focus for research in this thesis was to identify potential sediment-mediated disturbance to the nearshore epibenthos on hard substrata in the Windmill Islands region near Casey Station, East Antarctica. The research was prompted by the author's personal observations of surface sediment plumes on local marine waters during summer meltwater runoff within the Casey Station catchment, and an apparent absence of some of the more common subtidal benthic taxa on hard substrata at the site of sediment plume formation.

The thesis structure follows a logical development of firstly assessing the natural spatial variability in epibenthic communities on hard substrata in the Windmill Islands region, and then investigating whether specific aspects of the nearshore ecology could be

affected by altered sedimentation rates. The major research questions that form the basis of

each of the four research chapters are outlined below.

Chapter Two: *Marine macrobenthic assemblages on nearshore hard substrata in the*
                     Windmill Islands, East Antarctica

Nearshore benthic assemblages on hard substrata have not previously been surveyed

in the Windmill Islands, and have only been reported for a single location along almost

3000 km of the East Antarctic coast (Gruzov 1977). Assemblages within five shallow, low

energy environments in the Windmill Islands were assessed using digital video surveys to

identify basic ecological characteristics and the scales that accounted for greatest spatial

variability in assemblage structure. The characteristics of the benthic assemblages were

compared as a means of assessing whether the bay exposed to human-induced sediment

plumes was significantly different from those bays outside the influence of human

activities.

Chapter Three: *Effects of sedimentation on the recruitment of sessile marine species on*
                    shallow Antarctic reefs

The importance of recruitment to the formation and maintenance of benthic marine

communities is well known (Connell & Keough 1985). Recruitment of sessile epibenthos

to artificial hard substrata was used as an indication of natural recruitment trends at four

bays within the Windmill Islands. Temporal variability in the diversity of taxa and rates of

recruitment were quantified for each bay.   Additionally, the potential impact of

sedimentation on recruitment was explored using manipulative *in situ* experiments designed

to reduce natural sedimentation rates.

Chapter Four: *Effects of sedimentation and irradiation on spore settlement and early*
                    post-settlement gametophyte growth of Himantothallus grandifolius
                    (Desmarestiales, Phaeophyceae) in Antarctica

Settlement and early post-settlement growth of macroalgal spores was investigated in

aquarium-based experiments at Casey Station.   Induction of spore release from wild

Himantothallus grandifolius (Phaeophyceae) was undertaken in the laboratory followed by

a series of factorial experiments where spores were exposed to combinations of five levels

of irradiation and five levels of sediment load, to assess the potential influence of light and

sedimentation, and their possible interaction, on recruitment of macroalgae to hard substrata.

Chapter Five: ***Effects of sedimentation and irradiance levels on growth of an endemic Antarctic red alga, Palmaria decipiens (Reinsch) Ricker***

The natural distribution of macroalgae is determined by a variety of factors, not least of which is the benthic light environment. Algal assemblages are noticeably absent from some bays in the Windmill Islands yet abundant in others. Experimental translocation of naturally established macroalgae *Palmaria decipiens* (Rhodophyceae) into bays where they are not naturally found was undertaken to assess whether 'adult' individuals could survive and grow at these bays. Field manipulation of sedimentation levels was undertaken to assess whether sediments are excluding macroalgae from growing in bays where they are normally absent, whether the light environment affects their growth or whether there is a synergistic effect of both the sediment and light regimes. *P.decipiens* was also exposed to a variety of irradiance levels during aquarium experiments to assess the influence of light on thallus growth in the absence of sedimentation.

Readers should note that each research chapter has been developed as a self contained paper for publication. Consequently, repetition of some aspects of each chapter, particularly those associated with the descriptions of study locations, is unavoidable. Significant collaboration with colleagues will be acknowledged with co-authorship of publications; however, I have been responsible for all the experimental designs, sample collection and processing (with the exception of sediment trap data described later in this chapter), data analysis and writing that are included within this thesis.

Description of environments at each of the bays used as research locations

Casey Station (66.28°S, 110.53°E) is one of three permanent Australian research stations on the Antarctic continent, and is located on the coast adjacent to the Windmill Islands (*Fig.1.1*). Surveys of epibenthic assemblages (*Chapter 2*) were conducted in five shallow, semi-enclosed bays (<15 m deep) within 2 - 3.5 km of Casey Station, and subsequent *in situ* manipulative experiments (*Chapters 3 and 5*) were undertaken in a subset of those bays.

The first bay (Brown Bay) was chosen due to observations of a surface sediment plume, thought to result from station activities, during the summer months. The other bays (McGrady Cove, Newcomb Corner, O'Brien Bay 1, and O'Brien Bay 2) were chosen as 'control' bays within 2 - 3.5 km of the station, but ostensibly outside the influence of station activities. A description of the natural environment of each bay provides an indication of natural variability in parameters that could otherwise influence research outcomes.

Geographical features

Brown Bay, McGrady Cove and Newcomb Corner are small embayments within the larger Newcomb Bay (*Fig.1.1*). Brown Bay is 500 m north-east of Casey Station and is free of sea ice for ~4 - 6 wks per year. The bay receives most of the meltwater generated within the station catchment area via melt streams that enter the bay from Thala Valley on the western shore. Brown Bay's southern shore consist of low (3 - 4 m) ice cliffs, while the northern and western shores are weathered outcrops of bedrock, boulders and cobble, that continue into the water.

McGrady Cove is located in the eastern corner of Newcomb Bay ~2 km north-east of Casey Station (*Fig.1.1*). The bay is ice free for ~4 wks each year, and receives meltwater streams flowing from the ice plateau below the Løken Moraines. The southern and eastern shore consists of ice cliffs up to 8 m high, while the western shore is a weathered bedrock ridge with boulders and cobble.
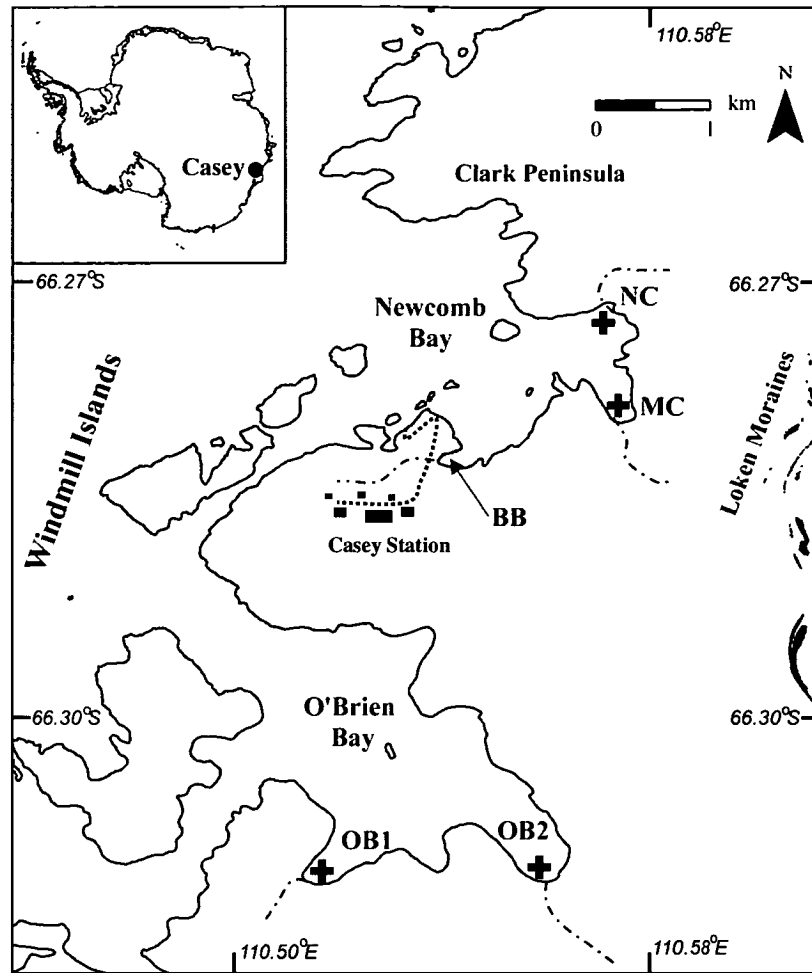
Figure 1.1   Map of the Windmill Islands coastline near Casey Station, East Antarctica illustrating the relative position of bays used as research locations and places mentioned in the text. BB=Brown Bay, MC=McGrady Cove, NC=Newcomb Corner, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2. Approximate path of major melt stream entering each bay is depicted by dashed lines; the Casey road is depicted as dotted line.

Newcomb Corner is located 2.2 km north-east of Casey Station, directly to the north of McGrady Cove (*Fig. 1.1*). The bay is ice free for ~12 wks each year, and receives meltwater streams flowing from the Clark Peninsula to the north and from the plateau below the Løken Moraines to the east. The eastern and northern shore consists of ice cliffs 5 - 20 m high.

O'Brien Bay is ~2 km south of Casey Station, and is similar in shape and size to Newcomb Bay (*Fig. 1.1*). O'Brien Bay 1 is a small embayment on the southern side of

O'Brien Bay ~3.5 km from Casey Station. This bay is ice free for <4 wks each year, and
receives meltwater via a valley on the south-western shore. The northern and western shore
is exposed bedrock, with weathered boulders and cobble, while the southern shore consists
of 5 - 8 m ice cliffs.

O'Brien Bay 2 is in the south-eastern corner of O'Brien Bay, is also free of sea ice
for <4 wks each year, and receives meltwater streams via the ice cliffs on the southern and
eastern shore. The western shore is an exposed bed rock ridge with weathered boulders and
cobble, while the southern and eastern shore consists of 10 - 20 m ice cliffs.

Physical characteristics

Physical characteristics for each bay were calculated from digitised maps and aerial
photographs using Geographical Information System (GIS) software (ArcGIS 9). The
average period that each bay was free of sea ice was documented by the author during
seven summer field seasons in the Windmill Islands between 1997 and 2006.

The four control bays have broadly similar physical characteristics as Brown Bay
(*Table 1.1*). However, Brown Bay is the smallest in area (0.04 km^2), shore length
(0.675 km) and catchment area (1.1 km^2), but has the highest percentage of ice free
shoreline (50%) and highest percentage of ice free catchment (75%).

Four of the bays (Brown, McGrady, O'Brien 1, and O'Brien 2) have similar shape
(parallel sided, open bays) and aspect (northerly facing). Newcomb Corner is slightly
different to the other bays in that it is not as enclosed, is open to the west and south, and has
an ice free period of ~12 wks.

Table 1.1   Physical characteristics of the Windmill Island research locations.

Locations (bays)	Brown	McGrady	Newcomb	O'Brien 1	O'Brien 2
bay area (km^2)	0.04	0.15	0.38	0.22	0.58
total shore length (km)	0.675	1.257	1.475	1.418	2.344
% of shore ice-free	50	34	0	46	33
aspect	55°, ENE	338°, NNW	250°, WSW	45°, NE	315°, NW
catchment area (km^2)	1.1	2.8	3.3	1.6	8.1
% of catchment ice-free	75	5	15	15	5
sea ice absent (weeks)	<6	<4	~12	<4	<4

Sea ice and snow thickness

Sea ice and overlying snow thicknesses were measured at each bay during diving operations in November 2002 and November 2003. At each bay, ice thickness was measured at five separate ice drill holes and snow thickness was measured at twelve random locations, all within 50 m of the survey/ experimental areas. Sea ice thickness was similar at each of the bays (*Table 1.2*) and is consistent with maximum annual sea ice formation for the region. Snow cover overlying the sea ice varied between bays, with Brown Bay having the deepest snow cover (>1 m), and the other bays having a relatively thin cover of snow (<0.3 m).

*Table 1.2   Sea ice and snow thicknesses, standardised benthic light levels, and seabed characteristics at each bay. * benthic light levels are based on a 'standardised' incident level of 2400 μmol photons.m^{-2}.sec^{-1} and light attenuation factors specifically calculated from measured incident and benthic light levels for each bay (see text for further details).*

Bays	Brown	McGrady	Newcomb	O'Brien 1	O'Brien 2
sea ice thickness (m)	1.32±0.01	1.35±0.01	1.27±0.02	1.32±0.01	1.31±0.01
snow on sea ice (m)	1.01±0.04	0.29±0.01	0.15±0.01	0.24±0.01	0.25±0.01
benthic light levels* (μmol photons.m^{-2}.sec^{-1})	0.03±0.01	1.79±0.01	30.60±0.18	1.32±0.01	0.93±0.01
mean slope of sea bed	10°	13°	25°	5°	17°
rugosity index	0.82	0.84	0.77	0.84	0.92

Benthic light environment

Levels of photosynthetically active radiation (PAR, 400 - 700 nm) at 300 mm above the snow surface, underwater 30 mm below the bottom of the sea ice and 300 mm above the sea bed at 6 m water depth were simultaneously recorded in each bay at solar noon on cloudless days in mid-December 2003, providing an estimate of optimal (best case) benthic irradiance under sea ice conditions. These measurements (μmol photons.m^{-2}.sec^{-1}) were made using a series of underwater quantum sensors (*Li-Cor LI-192SA*) connected to a multi-channel, data logger (*Li-Cor LI-1400*). These sensors measured continuous running averages of instantaneous readings over 15 sec intervals throughout the 2 hr deployment periods.

The PAR readings directly above the snow were compared with simultaneous PAR readings at 6 m depth to calculate an attenuation factor specifically related to the thickness

of snow and sea ice (and water clarity) at each bay. These attenuation factors were then applied to a 'standardised' incidence light level equivalent to levels measured on a bright, sunny day in mid-summer (2400 μmol photons.m^{-2}.sec^{-1}), to provide a comparable value for benthic irradiance at 6 m depth for each bay (*Table 1.2*).

Benthic irradiance was lowest at Brown Bay and highest at Newcomb Corner, although at the time of measuring irradiance, the ice edge was within 30 m of the Newcomb Bay site and light levels are considered higher than would normally be expected beneath 1.3 m of sea ice and 0.15 m of snow.

Sea bed slope and rugosity

The slope of the sea bed in each bay (*Table 1.2*) was measured using an underwater inclinometer constructed from a 1 m length of aluminium tubing. Slopes were measured by divers at seven random locations along the 6 m depth contour in each bay.

The rugosity, or small-scale underwater topography, was measured using the contour to linear distance ('chain and tape') method developed by Talbot & Goldman (1972). This method calculates a ratio of the length of chain moulded to the sea bed to the linear distance between its start and end (McCormick 1994). In the Windmill Islands, a chain length of 8 m was used. The rugosity ratio approaches 1 as the topography of the sea bed declines (i.e. gets flatter), and is closer to 0 with increased topography. Rugosity was measured by divers at five random locations along the 6 m contour in each bay (*Table 1.2*).

The sea bed at 6 m in Newcomb Corner is steeper (25°) and has greater topography (lower rugosity index) than the other bays, indicating a more bouldery terrain that drops off into deeper water. In contrast, Brown Bay, McGrady Cove and O'Brien Bay 1 have relatively low sloping sea beds (<14°), and similar rugosity (~0.8); O'Brien Bay 2 has the highest rugosity index and intermediate sea bed slope.

Water quality

Water quality profiles were measured using a hand-held, multi parameter water quality probe (YSI 6-series 6600 sonde fitted with YSI temperature, conductivity, dissolved oxygen and pH sensors) attached to a YSI data logger. Sensors were calibrated in the

laboratory according to manufacturer specifications prior to undertaking measurements in the field. Profiles were conducted beneath three holes drilled through the sea ice at each bay, with three vertical profiles conducted in each hole. Water quality profiles were undertaken at all bays on 12 October 2002 (*Fig.1.2*).

Water temperature at the time of profiling was generally between -0.9 and -1.7°C through all depths at all bays. However, a sub-surface warm water layer was evident at Newcomb Corner at depths between 2 and 4 m, where the mean water temperatures were above 0°C, and are more than 1°C higher than at similar depths in other bays.
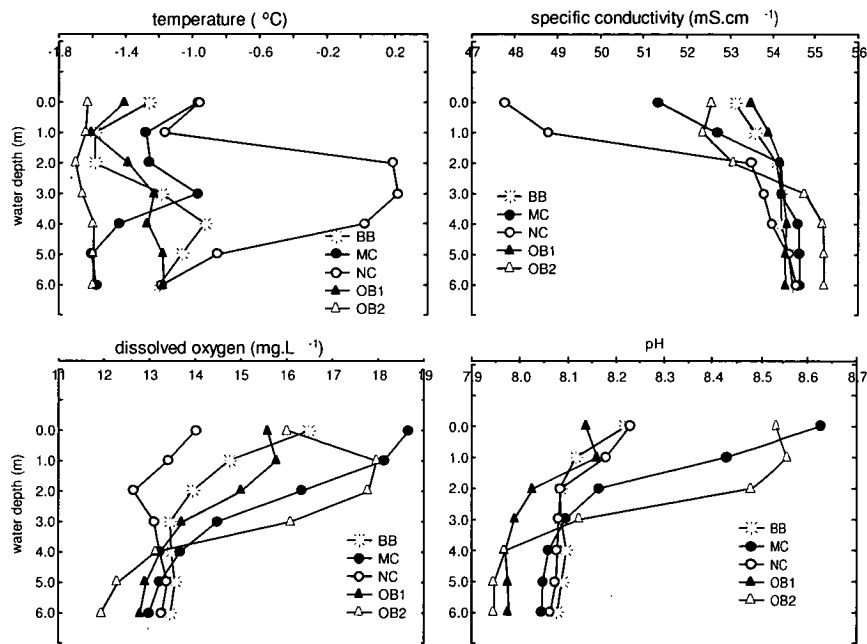
Figure 1.2   Water quality profiles in each bay - each data point is the mean of three readings from three profiles (n=9). For clarity, SE values have been excluded: $SE_{temperature}$ = 0.01 - 0.07; $SE_{conductivity}$ = 0.09 - 0.37; $SE_{dissolved\ oxygen}$ = 0.17 - 0.66; SE_{pH} = 0.02 - 0.07

Specific conductivity profiles were similar at each bay (*Fig.1.2*), with lower values apparent in surface waters likely due to freshwater melt from sea ice and terrestrial runoff. The surface water at Newcomb Corner had lower conductivity than surface waters at the other bays, suggesting a greater freshwater influence at the time of profiling.

Near-surface concentrations of dissolved oxygen were more variable between bays than concentrations in deeper water (*Fig.1.2*). Dissolved oxygen concentrations varied from 14 - 19 mg.L^{-1} in surface waters (0 m) and 12 - 13.5 mg.L^{-1} at 6 m depth.

At all bays, pH values were marginally higher in the upper 2 m of surface waters (pH 8.1 - 8.6) compared with readings below 3 m depth (pH 8.0 - 8.1) indicating the influence of freshwater in surface waters. At McGrady Cove and O'Brien Bay 2, pH values were slightly higher in the upper 3 m water depth than at the other bays which may be a result of glacial sediment input from nearby melt streams at those locations. All other results are within the expected range for polar marine waters.

Sediment flux

Sediment flux was calculated from weights of sediment collected in replicate sediment traps deployed at each bay. Sediment traps consisted of 140 mm lengths of 54 mm diameter polycarbonate tubes suspended from weighted float lines at a height of approximately 1 m above the sea bed. Sediment traps were deployed continuously through the period from February 2002 to February 2006 and were collected and replaced approximately every month through the summer periods and left unsampled through the winter (February to November). Sediment traps were not sampled during the 2004/05 Antarctic summer and hence the 2005/06 'winter period' included sediments collected between February 2004 and November 2005. Flux calculations were based on the sediment trap diameter (mm^2), length of deployment (days) and sediment weights (g) to give flux in g.m^{-2}.day^{-1}.

Three replicate sediment traps were deployed at each bay at each time but often only one or two traps were recovered, with the subsurface marker buoys of 'lost' traps believed to have been snagged by passing sea ice and dragged irretrievably into deeper water. Missing values for sediment flux are attributable to lost sediment traps or the inability to sample traps due to unsafe sea ice conditions. All sediment traps at Newcomb Corner were lost at all times other than December and January/February in the 2002/03 season, and consequently Newcomb Corner is not included in the analysis below.

Due to the unbalanced data, a two factor ANOVA design was used to test for differences between the bays (4 levels, random) and seasons (4 levels, fixed) using years as replicates (n=3). A significant interaction was evident ($F_{9,32}=3.42$, $P=0.0048$) with sediment flux at Brown Bay significantly higher than at other bays during January/February ($Fig. 1.3$).
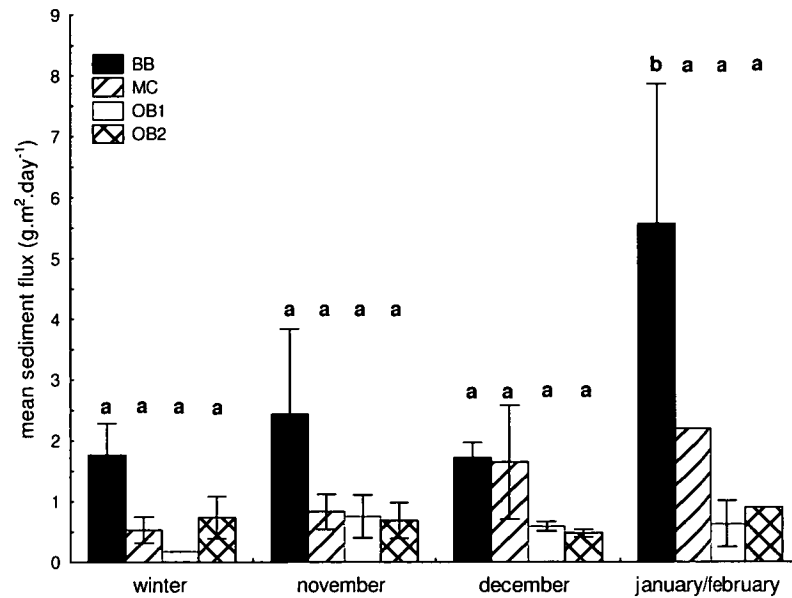
Figure 1.3   Mean sediment flux (±SE) across four time periods at the bays. Letters above bars refer to groupings determined by Tukey HSD test results, bars with similar letters are not significantly different. BB = Brown Bay, MC = McGrady Cove, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2. 'winter' = March to October

Summary

All five bays are considered to have broadly similar environments in terms of area (<0.6 km^2) and water flow (sheltered, low energy, low current). Four of the bays (Brown, McGrady, O'Brien 1, and O'Brien 2) have similar shape (parallel sided, open bays), aspect (northerly facing), sea bed slope ($<20°$), underwater relief (rugosity index >0.82), and similar sea ice cover (1.3 m thick for >10 months each year). Newcomb Corner differs from the other bays, being less enclosed, opening to the west and south, and has higher sea bed slope, rugosity and slightly thinner sea ice (1.27 m) through an average ice free period of ~12 wks.

Average snow depth on sea ice varies between bays (0.15 – 1.01 m) and benthic light environments at 6 m depth also vary (0.026 – 30.599 μmol photons.m^{-2}.sec^{-1}). Newcomb Corner has the thinnest snow cover and highest benthic light levels whereas Brown Bay has the thickest snow cover and lowest benthic light levels compared to all other bays. Sediment flux also varies between bays and between seasons, with Brown Bay consistently having the highest recorded sediment flux during each sampling period throughout the year. Water quality profiles measured at each bay exhibit similar characteristics with most variability between bays apparent in the upper water column (0 – 2 m depth).

The most apparent environmental differences between the bays are mean sediment flux and differing benthic light levels at 6 m depth. As will be seen in the following chapters, those parameters feature prominently as main factors in the designs used during manipulative experiments.

Chapter 2
Marine macrobenthic assemblages on nearshore hard substrata in the Windmill Islands, East Antarctica

Abstract:

Epibenthic assemblages on hard substrata in the upper sub-littoral of semi-enclosed bays in the Windmill Islands, East Antarctica were assessed using digital video transects and analysed using PointCount software. The overall aim was to identify natural variability to allow assessment of potential impacts of anthropogenic sediment runoff into Brown Bay from Australia's Casey Station. Forty-five different taxa within 11 phyla were counted on the 450 video quadrats analysed across all bays, dominated by sponges, cnidarians, polychaetes, bryozoans and echinoderms. Low diversity and evenness compared to published results was attributed to the low energy environments. The benthic assemblage at Brown Bay was different in several respects from assemblages at 'control bays', with some taxa absent from Brown Bay (e.g. Gellius sp., Potamilla antarctica, Sterechinus neumayeri, and encrusting bryozoa) and other taxa (i.e. Ophiura crassa and Homaxinella balfourensis) significantly more common at Brown Bay than at control bays. Results suggest that the benthos in Brown Bay were exposed to different environmental conditions than the 'control' bays, despite superficial similarities between all bays. Differences were attributed to two possible factors - potentially elevated sedimentation rates resulting from human activities, and lower benthic irradiance caused by thicker snow cover overlying sea ice.

Introduction:

The biodiversity of Antarctic marine environments is high relative to that of the Arctic (Dayton 1990, Arntz *et al.* 1994, Gray 2001), being rich in abundance and taxonomically diverse (Clarke 1996c). The rich diversity is believed to have evolved in the Southern Ocean during its long period of biogeographic isolation and as a result of the large areal expanse of habitats compared to the Arctic Ocean. These factors have also led to a high level of endemism (Dayton 1990, Clarke 1996, Gutt 2001).

Ice scour

Physical disturbance is recognised as a strong determinant of marine community structure, and some level of disturbance may act to promote high diversity (Connell 1978, Sousa 1979, Pain & Levin 1981, White & Pickett 1985). Nearshore marine benthic communities in polar environments are exposed to severe physical disturbances resulting from the annual formation and movement of ice (Dayton *et al.* 1969, Dayton 1990, Gutt 2001). Impacts of icebergs and growlers on benthic environments have been studied in detail (Gutt *et al.* 1996, Gutt 2001, Gutt & Starmans 2001, Smale *et al.* 2007), and, depending on water depth, direct disturbance by ice can range from being locally negligible to the single most important impact (Gutt 2001). The development of an 'ice foot' at the connection point of sea ice to the shore, and its subsequent vertical movement due to tides can also cause a physical scour of the shallow nearshore benthos to a depth determined by the thickness of sea ice and the tidal range (Barnes 1995a). The effect of the ice foot is more predictable and spatially specific than the random scour of icebergs. The third type of ice disturbance is due to the formation of anchor ice near the sea bed that often incorporates benthos, and whose buoyant force eventually overcomes the attachment strength of the benthos, resulting in the ice (and benthos) floating to the surface. Dayton *et al.* (1969) concluded that anchor ice is a significant factor structuring the benthos in McMurdo Sound to a depth of 33 m; however anchor ice does not form in all sub-littoral environments in Antarctica (Gutt 2001).

For the past 40 years, the benthos on hard substrata in nearshore Antarctic waters has been studied *in situ* by divers (e.g. Neushal 1966, Dayton *et al.* 1970). As a result, broad sub-littoral zonation patterns have been described from a variety of locations around the continent (Gruzov 1977, Kirkwood & Burton 1988, Dayton *et al.* 1986, Dayton 1990, Beckley & Branch 1992, Gambi *et al.* 1994, Barnes 1995a, 1995b, Barnes & Brockington 2003, Barnes *et al.* 2006). The established view, at least from the earliest studies, is that the upper sub-littoral (from 0 to 15 m or so) is largely devoid of permanent macroscopic benthic communities as a result of annual ice scour. This idea purports that, in general, during the ice-free season (high summer) this zone is dominated by macroalgae, mats of

benthic diatoms, and transient grazers such as urchins, echinoderms and molluscs, but generally there are few sessile species (Gruzov 1977, Dayton 1990). However, more recent studies (Gambi *et al.* 1994, Barnes 1995b, Barnes *et al.* 2006, Smale 2008) have recognised that there are variants to this pattern. For example, in areas of low ice impact, rich communities of sessile organisms can develop on shallow sub-littoral substrata, (Barnes *et al.* 2006), and in areas protected from ice disturbance, sessile forms dominate at shallow depths (Smale 2008). Certainly it is clear that factors other than ice abrasion can be important determinants of benthic structure. Barnes (1995b) lists the length of period of sea ice cover, as well as substratum type and wave or current action as important factors influencing development of benthic assemblages, while Gambi *et al.* (1994) conclude that the amount of light reaching the benthos (for algal dominated assemblages) and species-specific interactions are also important.

Benthic research in Antarctica

Most quantitative research on nearshore hard substrata in the Antarctic has been undertaken at McMurdo Sound (e.g. Dayton *et al.* 1986, Dayton 1990) and along the Antarctic Peninsula (e.g. Barnes 1995a, 1995b, Barnes & Brockington 2003, Bowden 2005a, Barnes *et al.* 2006). These locations represent opposite ends of the spectrum for Antarctic environments in terms of latitude (78° *vs.* 60 - 65°S), and therefore local climate and ice conditions (i.e. deep Antarctic *vs.* maritime Antarctic). In contrast, few benthic studies (e.g. Gruzov 1977 and Kirkwood & Burton 1988) have been conducted along the east Antarctic coast between 0 - 160°E longitude (at latitudes 66 - 70°S); areas that might be considered representative of almost half of Antarctic nearshore environments. In addition, many earlier studies have investigated benthic assemblages along exposed coasts where the increased potential for ice scour from icebergs and smaller ice pieces, together with high energy water movement, are likely to lead to higher rates of physical disturbance. Benthic assemblages of low energy environments in areas largely protected from direct impacts of drifting icebergs are less well known.

Benthic survey techniques

In situ photographic methods (fixed photographs and video) have been used for many years to assess sub-littoral marine communities (Ninio *et al.* 2003), and are now used more commonly than *in situ* count methods such as grid quadrats and belt transects (Kingsford & Battershill 1998). The main advantage of photographic surveys over *in situ* counts is the ability to sample over larger areas, or with greater replication, in a given time period. This feature is critically important when diving assessments are conducted in extreme environments such as under sea ice in polar waters where additional safety precautions necessarily reduce dive times more than usual, and climatic conditions often necessitate short periods in the field. Additional advantages of photographic/video surveys include: camera-based data capture removes biases due to multiple observers (Benedetti-Cecchi *et al.* 1996, Ninio *et al.* 2003); creates a permanent archival record of the survey that can provide additional information at a later date and/or allow direct comparison with images collected in the future; and images can be reformatted and processed using image analysis software (Kingsford & Battershill 1998). Disadvantages of photographic-based assessment of benthic assemblages include the requirement for specialised equipment and therefore the possibility of technical problems, biases due to under estimates of cryptic, small or rare species (Foster *et al.* 1991), and the potential for problems with resolution limiting taxonomic identification.

Digital video assessments of nearshore epibenthos have additional advantages over methods based on 35 mm and digital stills photography. Firstly, a video transect can be analysed as a single unit (Ninio *et al.* 2003), or alternatively a random selection from the multiple overlapping frames within a video transect can be analysed as individual quadrats (Porter *et al.* 2002). Secondly, there is less likelihood of bias due to unintentional (or intentional) positioning of quadrats that might occur when individual photo quadrat positions are selected by the camera operator. Consequently, video analysis results are more likely to be representative of the benthos although cryptic, small and rare taxa are still potentially underestimated. Aronson *et al.* (1994) discuss the relative merits of underwater survey methods and conclude that video transects followed by point-count analysis of

random frames is the most resource efficient method. However, it is acknowledged that

identification of some species cannot be reliably undertaken from photographic quadrats

(stills or video).

Human impact research at Casey Station

The impacts of human activities in Antarctica are now being recognised through

investigation of the effects of pollution and physical disturbance (Duquesne & Riddle 2002,

Stark *et al.* 2003). The presence of year-around research stations in Antarctica and their

associated infrastructure (roads and buildings) has the potential to cause localised impacts

to terrestrial, lacustrine and/or marine communities. Each summer at Australia's Casey

Station, a road (~1,000 m) is graded and stabilised with crushed local rock to allow heavy

machinery to transfer food and supplies from the wharf to storage areas. For a period of

~six weeks from mid-December, the mean daily maximum temperatures at Casey Station

are often above freezing, and meltwater flows off the station roads, down the catchment

gradients through a small valley and into Brown Bay. At peak flow, surface sediment

plumes are visible at the interface of the meltwater and seawater in the bay. Within a ten

year period from 1996, no sediment plumes have been observed entering the marine

environment in the Casey region at any site other than at Brown Bay. Initial qualitative

assessments of the benthos in Brown Bay suggest a depauperate community relative to

similar bays in the Casey region (author's unpublished data), leading to hypotheses that the

benthic community is potentially impacted by elevated sediment loads originating from

Casey Station.

The overall objective of this study was to document the epibenthic assemblages on

hard substrata in the upper sub-littoral of semi-enclosed bays in the Windmill Islands. The

aims were to (1) quantitatively survey the benthos using digital video techniques, assessing

variability in assemblage structure across a variety of spatial scales, and (2) compare the

benthic assemblages with similar bays outside the influence of Casey Station.

Materials and Methods:

Location description

The surveys were conducted in five shallow bays (<15 m deep) in the vicinity of Australia's Casey Station (66.28°S, 110.53°E) within the Windmill Islands of eastern Antarctica *(Fig.2.1)*. The first bay (Brown Bay) was selected on the basis of an observed surface sediment plume, thought to result from station activities, during the summer months. The other bays (McGrady Cove, Newcomb Corner, O'Brien Bay 1, and O'Brien Bay 2) were chosen as 'control' bays within 2 - 3.5 km of the station, but thought to be outside the influence of station activities.

Brown Bay, McGrady Cove and Newcomb Corner are small embayments within the larger Newcomb Bay *(Fig.2.1)*. Brown Bay is 500 m north-east of Casey Station and is free of sea ice for ~4 - 6 wks per year. The bay receives most of the meltwater generated within the station catchment area via melt streams that enter the bay from Thala Valley on the western shore. Brown Bay's southern shore consist of low (3 - 4 m) ice cliffs, while the northern and western shores are weathered outcrops of bedrock, boulders and cobble, that continue into the water.

McGrady Cove is located in the eastern corner of Newcomb Bay ~2 km north-east of Casey Station *(Fig.2.1)*. The bay is ice free for ~4 wks each year, and receives meltwater streams flowing from the ice plateau below the Løken Moraines. The southern and eastern shore consists of ice cliffs up to 8 m high, while the western shore is a weathered bedrock ridge with boulders and cobble. Newcomb Corner is located 2.2 km north-east of Casey Station, directly to the north of McGrady Cove *(Fig.2.1)*. The bay is ice free for ~8 wks each year, and receives meltwater streams flowing from the Clark Peninsula to the north and from the plateau below the Løken Moraines to the east. The eastern and northern shore consists of ice cliffs 5 - 20 m high.
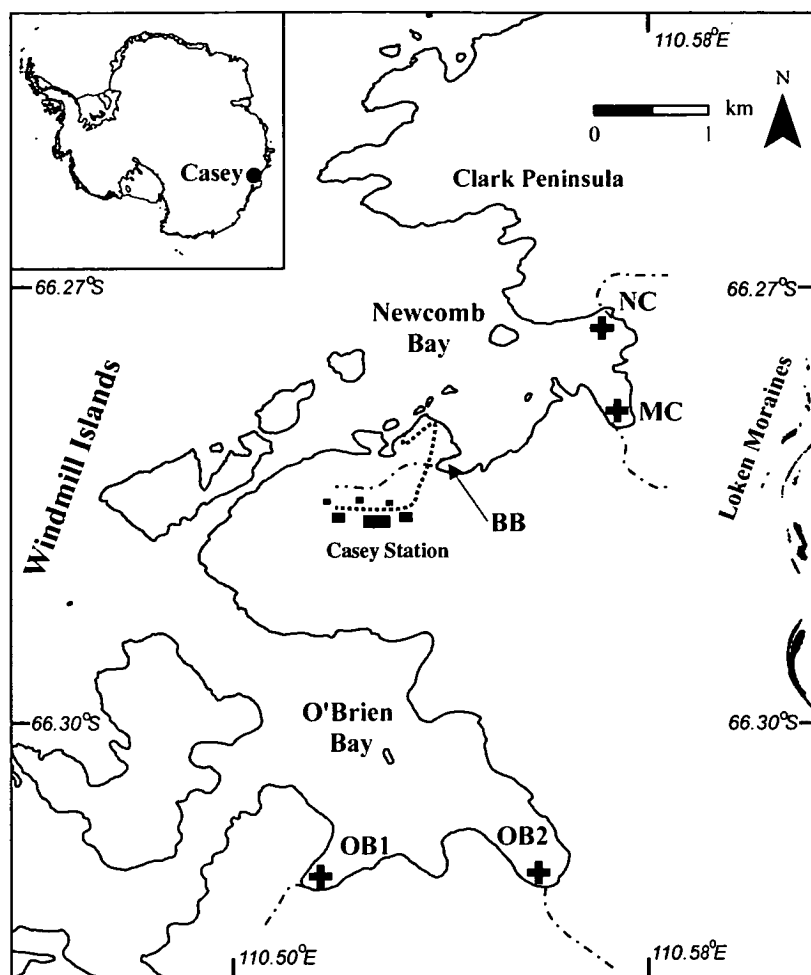
Figure 2.1   Map of the Windmill Islands coastline near Casey Station illustrating sampling bays, and places mentioned in the text. BB=Brown Bay, MC=McGrady Cove, NC=Newcomb Corner, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2. Approximate path of major melt stream entering each bay is depicted by dashed lines; the Casey road is depicted as dotted line.

O'Brien Bay is 2 km south of Casey Station, and is similar in shape and size to Newcomb Bay (*Fig.2.1*). O'Brien Bay 1 is a small embayment on the southern side of O'Brien Bay approximately 3.5 km from Casey Station. This bay is ice free for <4 wks each year, and receives meltwater via a valley on the south-western shore. The northern and western shore is exposed bedrock with weathered boulders and cobble, while the southern shore consists of 5 - 8 m ice cliffs. O'Brien Bay 2 is in the south-eastern corner of O'Brien Bay, is also free of sea ice for <4 wks each year, and receives meltwater streams

via the ice cliffs on the southern and eastern shore. The western shore is an exposed bed

rock ridge with weathered boulders and cobble, while the eastern shore consists of 10 -

20 m ice cliffs.

All five bays were considered to have broadly similar environments in terms of area

(<0.6 km^2), water flow (sheltered, low energy, low current), and sea ice cover (1.3 m thick

for >10 months each year). Four of the bays (Brown, McGrady, O'Brien 1, and O'Brien 2)

also have similar shape (parallel sided, open bays) and aspect (northerly facing). Newcomb

Corner is slightly different to the other bays in that it is not as enclosed and opens to the

west and south.

A survey depth of 6 m was chosen as it is the average depth at the head of Brown

Bay nearest the observed sediment plumes, and was standardised across all bays to avoid

depth-related effects. The 6 m depth contour was a similar distance offshore at each of the

bays.

Survey design

The survey was designed to assess the natural variability of hard substratum

epibenthos at low energy and ice-covered locations within the innermost reaches of bays

along the Windmill Islands coast. The survey had two aims:

(1)   to assess the natural variability of epibenthos on hard substrata at several scales

within protected bays of the Windmill Islands; and

(2)   to assess differences between the hard substratum epibenthos at Brown Bay

(potentially impacted by elevated sediments from Casey Station) and 'control' bays.

The design was hierarchical in nature encompassing a variety of spatial scales from

kilometres (bays), to tens of metres (sites), through to metres (quadrats within transects). In

each bay, two sites approximately 50 m apart were selected randomly prior to divers

entering the water. Since large areas of each bay had soft sediment environments the

survey was stratified to include only areas of hard substratum within the 6 m depth range.

Video transects were recorded by divers using a 3CCD digital video camera (SONY

TRV-900E) in an underwater housing (Light & Motion Stingray) fitted with two 20 W high

intensity discharge (HID) lights, and two parallel lasers for scale. A tape measure was laid along the 6 m contour as a guide for the videographer who recorded three 20 m video transects approximately parallel to the tape, with transects spaced ~3 – 5 m apart. A swim rate of ~5 m.min^{-1} was used to record the video while holding the camera vertical at a height of 0.4 m off the sea bed.

Surveys were conducted at all five bays within a ten day period during December 2002. All bays were covered by sea ice of 1.3 – 1.4 m thickness at the time of the survey, and the horizontal water visibility was in excess of 100 m.

Video analysis

Video transects were recorded at 30 frames per second directly onto mini-DV tapes using 'progressive scan' camera mode that maximises the clarity of individual frames. Each video transect was digitally split into individual, non-overlapping quadrats of 0.5 x 0.3 m. The length of video per transect varied depending on slight variations in swim speed and transect length but typically between 55 - 75 non-overlapping quadrats were obtained from each video transect. Video quadrats with >25% cover of hard substrata were selected from the total quadrats from each transect and, of these, 15 quadrats per transect were selected randomly for analysis.

Video analysis was conducted using PointCount software (Dustan *et al.* 1999) that automatically overlaid 50 random points onto images. Analysis of the image was conducted by selecting the taxa (or substratum type) directly under each point from a menu of taxa. Taxa were identified to the lowest taxonomic group possible, with more than 60% of taxa identified to species level. Rarer and lesser known species were designated to higher taxonomic groupings and allocated operational taxonomic codes such as '*spirorbid polychaetes*', '*sponge 1*', '*gastropod 2*', etc. When identifying taxa, a reference collection was maintained to provide consistent identification across all bays. Video analysis and identification of taxa was undertaken by the same person. Count data of each taxon from the 50 random points per quadrat was used to estimate percentage cover.

Statistical analysis

Initial exploration of percentage cover data from quadrats was based on Bray-Curtis similarity measures (fourth root transformed data) using the PRIMER *v6.1.6* statistical package (Plymouth Marine Laboratory, UK). Similarities among assemblage measures were viewed graphically using non-metric multidimensional scaling (nMDS) ordination. Taxa contributing most to differences between bays were identified using similarity of percentages (SIMPER), with significance levels adjusted using the Bonferonni procedure. The significance of variance in community structure among bays and at different scales was estimated using permutation-based non-parametric multivariate analysis of variance (PERMANOVA; Anderson 2001).

Analysis of Variance (ANOVA) was undertaken using GMAV (Underwood and Chapman, 1998) on the mean number of species, mean number of individuals, Shannon-Wiener diversity (H' base e), Margalef richness and Pielou's evenness (J') indices that were calculated using DIVERSE (in PRIMER). Homogeneity of variances was analysed using Cochran's test (Snedecor & Cochran 1989), and in all cases was found to be heterogeneous. Transformation of data could not attain homogeneity and untransformed data were used in ANOVA calculations but with a more conservative significance level of 0.01 (Underwood 1997). When significant, differences between main effects and/or interactions were analysed using the Tukey HSD (honestly significant difference) test, which is itself highly conservative.

To better interpret overall patterns of natural variability, individual ANOVA were undertaken on the percentage cover of the most common taxa. Variance components for each ANOVA were calculated from mean squares to provide estimates of the proportion of total variance explained by experimental factors (Underwood 1997).

A priori comparisons of means (Sokal & Rohlf 1995) were undertaken to assess biodiversity indices and major taxa grouping differences between Brown Bay and the control bays.

Results:

Species area curves for each bay (*Fig.2.2*) illustrate that 15 quadrats selected randomly from each transect capture the majority of the total taxa within each bay (60 - 80% at all bays other than Brown Bay). To sample an equivalent proportion of taxa at Brown Bay, a replication level of >35 quadrats per transect would be required, amounting to a 230% increase in effort. Increased replication above 15 quadrats per transect was considered to be of limited advantage within the constraints of the study.
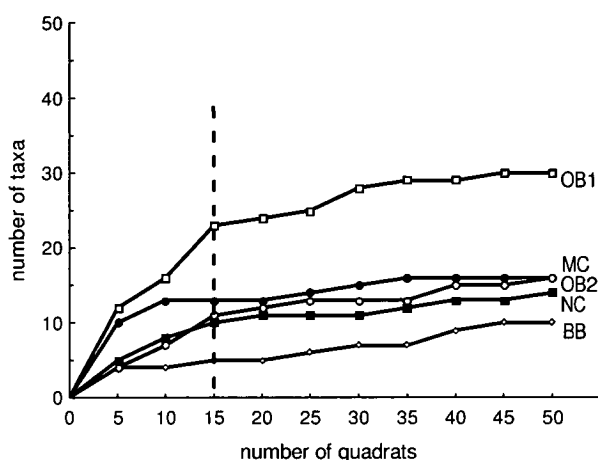
Figure 2.2   Species – area curves for each bay illustrating that replication of n=15 quadrats is satisfactory to capture the majority of taxa.

The benthic community

Forty-five different taxa within 11 phyla were counted on the 450 video quadrats analysed across all bays (*Table 2.1*). The distribution of individual taxa varied between the bays, with eight taxa (17.7% of total) common to all bays, five taxa (11%) observed at four bays, 4 taxa (9%) at three bays, five taxa (11%) at two bays and 23 taxa (51% of total) observed at only one bay.

The most commonly encountered taxa were benthic diatoms, red encrusting algae and spirorbid polychaetes. The most speciose phylum was Porifera with 13 sponge species identified. All 13 were observed at O'Brien Bay 1, while only 2 - 4 species occurred at each of the other bays. Most sponges accounted for <1% cover per quadrat, although

between 1 and 5% of quadrats at McGrady Cove and Newcomb Corner were covered with *Gellius* sp., and between 1 and 5% of quadrats at Brown Bay were covered with *Homaxinella balfourensis*.

The large Antarctic anemone, *Isotaelia antarctica*, and hydroids were found in each bay (*Table 2.1*) but generally accounted for <1% cover. The large nemertean, *Parbolasia corrugatus*, was only observed in quadrats from O'Brien Bay 1.

Four polychaete taxa were counted across the bays, with the large solitary tubeworm, *Potamilla antarctica*, and the small spirorbids found at four and five bays, respectively (*Table 2.1*). The spirorbids accounted for >1% of cover at each bay and up to 5 - 10% at O'Brien Bay 2 and 10 - 20% at Newcomb Corner. Of the five mollusc taxa observed across the bays, only the Antarctic scallop, *Adamussium colbecki*, and the common Antarctic clam, *Laternula elliptica*, were counted at all bays but most commonly observed at Brown Bay and O'Brien Bay 2 (both with 1 - 5% cover).

Pycnogonids (sea spiders) were only observed in quadrats at O'Brien Bay 2. Encrusting bryozoans (most commonly *Inversiula nutrix*) were observed at McGrady Cove (1 - 5% cover), Newcomb Corner (5 - 10%) and the two O'Brien Bay locations (<1% at O'Brien Bay 1 and 5 - 10% at O'Brien Bay 2) but not at Brown Bay.

Echinoderms were observed in all bays (nine taxa in total) but almost always with low cover (*Table 2.1*). None of the four asteroid species were counted at Brown Bay, and only *Perknaster antarcticus* and *Starfish1* were counted at more than one bay. The regular urchin, *Sterechinus neumayeri*, was observed at three bays but accounted for >1% of cover only at O'Brien Bay 1. The holothurian, *Psolus charcoti*, was also only counted at O'Brien Bay 1 (<1%). The large ophiuroid species, *Ophiosparte gigas*, was counted at all bays but accounted for <1% cover at each, while the small ophiuroid, *Ophiura crassa*, was found at all bays and accounted for 1 - 5% cover at Brown Bay and <1% cover at the other bays. Species associated with soft substrata, *Abatus nimrodi* and *Abatus ingens*, were observed in sediments at the base of hard substrata in O'Brien Bay (<1%).

Table 2.1 *Taxonomic list and distribution of flora and fauna across the five bays.*

BB=Brown Bay, MC=McGrady Cove, NC=Newcomb Corner, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2, where o *<1% cover,* ● *= 1 - 4.9% cover,* ●● *= 5 - 9.9% cover,* ●●● *= 10 - 19.9% cover,* ●●●● *= 20 - 29.9% cover,* ●●●●● *>30% cover*

Phylum	Class	Taxon	BB	MC	NC	OB1	OB2
Porifera	Demospongiae	Gellius sp.		●	●	o	o
		Homaxinella balfourensis	●	o	o	o	o
		Inflatella belli				o	
		Isodictya spp.	o	o		o	o
		Latrunculia apicalis				o	
		Lissodendoryx c.f. styloderma				o	
		Mycale acerata		o		o	
		Polymastia invaginata				o	
		Sphaerotylus antarcticus				o	
		sponge1	o			o	
		sponge2				o	
		sponge3				o	
		sponge4				o	
Cnidaria	Anthozoa	Isotaelia antarctica	o	o	●	o	o
		gorgonian1			o	o	
Cnidaria	Hydrozoa	hydroids	o	o	o	●	o
Nemertea	Anopla	Parbolasia corrugatus				o	
Annelida	Polychaeta	Potamilla antarctica		o	o	●	o
		Flabelligera mundata				o	
		spirorbids	●	●	●●●	●	●●
		Polychaete1		o		o	●
Mollusca	Bivalvia	Adamussium colbecki		●			o
		Laternula elliptica	●	o	o	o	●
Mollusca	Gastropoda	Neobuccinum eatoni				o	
		gastropod1			o		
		gastropod2					o
Chelicerata	Pycnogona	sea spiders					o
Bryozoa	Gymnolaemata	encrusting bryozoan		●	●●	o	●●
Echinodermata	Asteroidea	Diplasterias brucei				o	
		Lysasterias perrieri					o
		Perknaster antarcticus			o	o	
		Starfish1		o		o	o
Echinodermata	Echinoidea	Abatus nimrodi / A. ingens				o	
		Sterechinus neumayeri		o	o	●	
Echinodermata	Holothuroidea	Psolus charcoti				●	
Echinodermata	Ophiuroidea	Ophiosparte gigas	o	o	o	o	o
		Ophiura crassa	●		o	o	o
Chordata	Ascidiacea	Sidnyum radiatum			o	o	o
		ascidian1				o	
		ascidian2				o	
Protista	Diatomophyceae	benthic diatoms	o	●●	●●●	●●●●●	●●
Rhodophyta	Gigartinaceae	Iridaea cordata	o				
Rhodophyta	Florideophyceae	Palmaria decipiens			●		
		red encrusting algae	o	●●	●●●●	●	●
Phaeophyta	Phaeophyceae	Desmarestia menziesii			o		
		Total number of taxa	**12**	**17**	**19**	**37**	**20**

Three ascidian species were counted at O'Brien Bay 1 but only *Sidnyum radiatum* was observed (with <1% cover) in quadrats from other bays as well (Newcomb Corner and O'Brien Bay 2).

Flora occurred at each bay (*Table 2.1*) with the most obvious group being the multispecies benthic diatom mat that overlaid hard and soft substrata alike. Diatoms accounted for the greatest cover of all taxa at most sites (the exception being cover due to encrusting algae at Newcomb Corner), and accounted for 5 - 10% cover at McGrady Cove and O'Brien Bay 2, and 10 - 20% and >50% cover at Newcomb Corner and O'Brien Bay 1, respectively. At Brown Bay, diatoms accounted for <1% cover.

Two erect Rhodophyte species, *Iridaea cordata* and *Palmaria decipiens*, were observed at a single bay each. *I.cordata* accounted for <1% cover at Brown Bay, and *P.decipiens* accounted for 1 - 5% cover at Newcomb Corner. Red encrusting algae were found in all bays, comprising <1% cover at Brown Bay, 1 - 5% cover at O'Brien Bays 1 and 2, 5 - 10% cover at McGrady Cove and 20 - 30% cover at Newcomb Corner. The only Phaeophyte observed in the survey quadrats was *Desmarestia menziesii* which accounted for <1% cover at Newcomb Corner.

Hard substratum

Between 46 and 100% of the total number of video quadrats captured at each bay had >25% cover of hard substratum (*Fig.2.3a*). Significant differences among bays were apparent from ANOVA analysis ($F_{4,25}=8.81$, $P=0.0001$), with significantly more quadrats with >25% hard substratum at Newcomb Corner (100% of quadrats) compared to other bays, and significantly more quadrats with >25% hard substratum at O'Brien Bay 2 (76.9%) compared to Brown Bay (46.4%). Brown Bay, McGrady Cove (59.1%) and O'Brien Bay 1 (60.5%) had similar numbers of quadrats with >25% hard substratum cover.

(a):   **(b):**
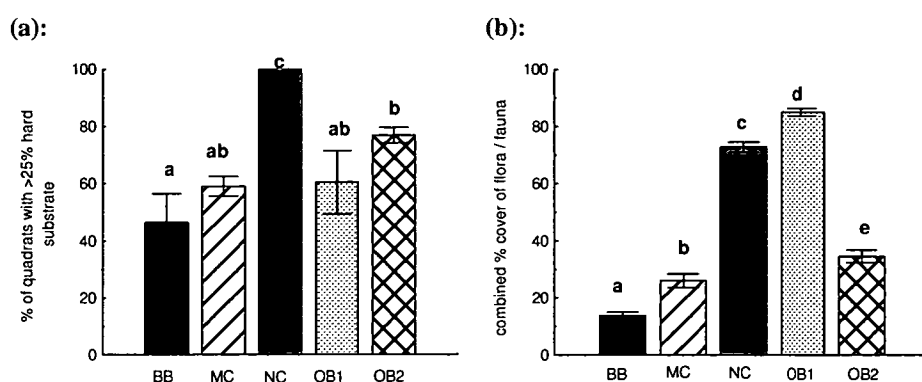
Figure 2.3 *(a) Percentage (±SE) of quadrats at each bay with >25% hard substratum cover, and (b) mean combined percentage cover on hard substrata (±SE) of flora and fauna per quadrat at each bay (n=15). Letters above bars refer to groupings determined by Tukey HSD test results, bars with similar letters are not significantly different. BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2*

Total biota cover

The mean total cover of flora and fauna as estimated from the video quadrats *(Fig.2.3b)* differed significantly among bays $(F_{4,420}=289.26, P<0.0001)$, with each bay having significantly different cover to all other bays. The lowest flora/fauna cover was at Brown Bay (13.9%) followed by McGrady Cove (26.1%), O'Brien Bay 2 (34.6%), Newcomb Corner (72.8%), while the highest cover was found at O'Brien Bay 1 (85%).

Multivariate analysis of percentage cover of the 45 taxa observed in the video quadrats (square root transformation, PERMANOVA) also revealed significant differences in community composition between bays $(F_{4,420}=65.6575, P=0.0001)$. Pairwise comparisons of bays indicate that all bays are different from each other, with the greatest dissimilarity between Brown Bay and each of the other bays *(Table 2.2)*. Brown Bay is most similar to O'Brien Bay 2, whereas Newcomb Corner and O'Brien Bay 2 are the most similar of all bay pairs.

Table 2.2   Multiple pairwise analysis results (Bray-Curtis dissimilarities on square-root transformed data, 9999 permutations, PERMANOVA). Note that alpha has not been corrected for multiple comparisons. BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2

Comparison pair	t-value	P value	Average dissimilarity
BB vs MC	6.0237	<0.0001	89.60
BB vs NC	11.2576	<0.0001	90.18
BB vs OB1	10.6947	<0.0001	93.08
BB vs OB2	7.8395	<0.0001	82.77
MC vs NC	5.5552	<0.0001	66.48
MC vs OB1	7.1164	<0.0001	78.24
MC vs OB2	4.4013	<0.0001	71.12
NC vs OB1	12.1236	<0.0001	64.55
NC vs OB2	7.6018	<0.0001	55.76
OB1 vs OB2	9.8513	<0.0001	70.33

A clear separation of bays is apparent in the two-dimensional nMDS ordination based on square-root percentage cover data (*Fig.2.4*). Brown Bay and O'Brien Bay 1 are distinctly separate from each other and the other bays, whereas McGrady Cove, Newcomb Corner and O'Brien Bay 2 are closer together (in nMDS space) suggesting assemblages at Brown Bay and O'Brien Bay 1 deviate most from those at the other bays.
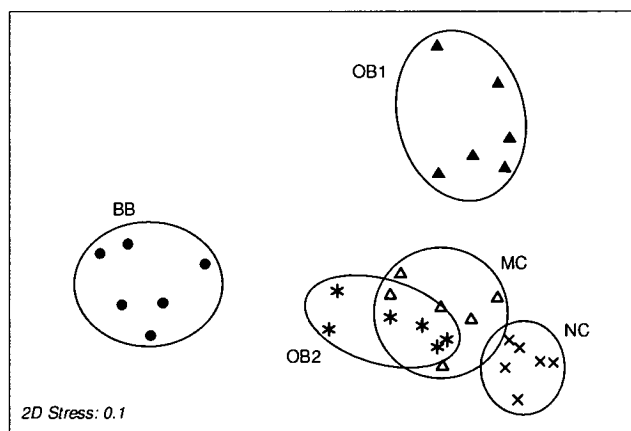
Figure 2.4   Patterns in community structure depicted as nMDS plot based on square-root transformed percentage cover data of all taxa for transects at each of five bays (n=6 independent transects at each bay). BB=Brown Bay, MC=McGrady Cove, NC=Newcomb Corner, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2

Biodiversity indices

Biodiversity measures calculated from PRIMER (i.e. DIVERSE) were used as the basis for initial comparisons between video transects at each bay (*Fig.2.5a-e*).

Mean number of species per transect (*Fig.2.5a*) differed significantly between bays (*Table 2.3*). Brown Bay transects had fewer species (mean of 7.8) than transects in all other bays except Newcomb Corner, whereas O'Brien Bay 1 transects had more species (19.7) than all other bays. McGrady Cove, Newcomb Corner and O'Brien Bay 2 had a similar mean number of species per transect (12.2, 9.8 and 11.5, respectively).

Table 2.3   Results of ANOVA for Mean Number of Species per Transect (ie. quadrats pooled across transects), P<0.05

Source	SS	df	MS	F	P	Error
Bay	485.47	4	121.37	50.57	0.0003	Site (Bay)
Site (Bay)	12.00	5	2.40	0.73	0.6061	Residual
Residual	65.33	20	3.27			
Total	562.80	29				

The mean number of individuals of each species per transect (*Fig.2.5b*) also differed significantly among bays (*Table 2.4*). Brown Bay transects had fewer individuals (mean of 7.3) and O'Brien Bay 1 transects supported more individuals (42.5) than all other bays, whereas McGrady Cove and O'Brien Bay 2 had similar numbers of individuals per transect (14.7 and 17.3, respectively). Newcomb Corner transects had the second highest density of individuals at a scale of transects of all bays (36.4).

Table 2.4   Results of ANOVA for Mean Number of Individuals per Transect (ie. quadrats pooled across transects), P<0.05

Source	SS	df	MS	F	P	Error
Bay	5443.46	4	1360.86	35.84	0.0007	Site (Bay)
Site (Bay)	189.87	5	37.97	4.49	0.0066	Residual
Residual	169.07	20	8.45			
Total	5808.40	29				

Margalef richness per transect (*Fig.2.5c*) exhibited significant differences between bays (*Table 2.5*), with the lowest values in transects at Newcomb Corner (2.5), similar and

intermediate richness at Brown Bay, McGrady Cove and O'Brien Bay 2 (3.6, 4.3 and 3.8,

respectively) and the highest richness in transects from O'Brien Bay 1 (5.0).

Table 2.5   Results of ANOVA for Margalef Richness per Transect (ie. quadrats pooled across transects), P<0.05

Source	SS	df	MS	F	P	Error
Bay	20.73	4	5.18	16.01	0.0047	Site (Bay)
Site (Bay)	1.62	5	0.32	0.60	0.7024	Residual
Residual	10.84	20	0.54			
Total	33.18	29				

O'Brien Bay 1 also had the lowest level (0.36) of Pielou's evenness (J') per transect

(*Fig.2.5d*), which differed significantly from evenness in the other bays (*Table 2.6*). All

other bays exhibited similar evenness (0.72 – 0.82).

Table 2.6   Results of ANOVA for Pielou's Evenness per Transect (ie. quadrats pooled across transects), P<0.05

Source	SS	df	MS	F	P	Error
Bay	0.78	4	0.19	26.97	0.0014	Site (Bay)
Site (Bay)	0.04	5	0.01	1.67	0.1884	Residual
Residual	0.09	20	0.01			
Total	0.90	29				

Shannon-Wiener diversity (*H'*, base e) values (*Fig.2.5e*) were heterogeneous and

could not be adequately transformed, resulting in the use of the more conservative

significance level of 0.01. Consequently, H' did not differ significantly between bays

(*Table 2.7*).

Table 2.7   Results of ANOVA for Shannon-Wiener Diversity per Transect (ie. quadrats pooled across transects), untransformed, P<0.01

Source	SS	df	MS	F	P	Error
Bay	2.33	4	0.58	6.55	0.0318	Site (Bay)
Site (Bay)	0.45	5	0.09	3.01	0.0347	Residual
Residual	0.59	20	0.03			
Total	3.37	29				

(a)

(b)

(c)

(d)

(e)
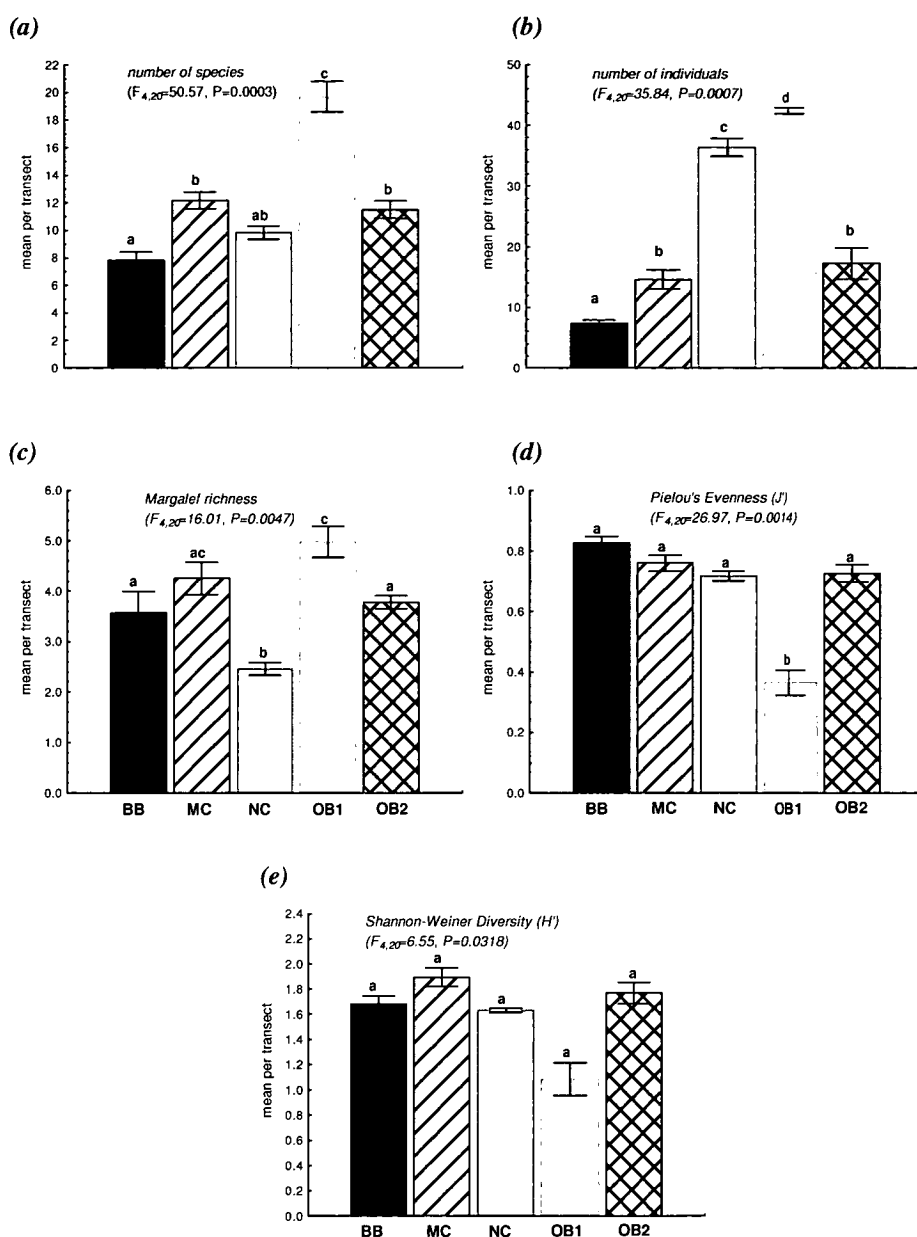
Figure 2.5a-e   Biodiversity measures for video transects from each bay (±SE, n=6) - (a) number of species, (b) number of individuals, (c) Margalef richness, (d) Pielou's evenness, and (e) Shannon Wiener diversity. Letters above bars refer to groupings determined by Tukey HSD test results; within each plot, bars with similar letters are not significantly different. BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2.

Percentage cover

Sixteen taxa were counted in quadrats at three or more bays and were selected for individual analysis using ANOVA (*Fig.2.6*). Variances were heterogeneous for all taxa but data could not be satisfactorily transformed to achieve homoscedasticity; hence, a more conservative significance level of 0.01 was used.

The sponge, *Gellius* sp., was absent from Brown Bay (*Fig.2.6a*) yet accounted for approximately 1.5% cover at McGrady Cove and Newcomb Corner and 0.5% cover at O'Brien Bay 1 and O'Brien Bay 2. In contrast, the percentage cover of the sponge, *Isodictya* spp., was not significantly different between any bays, and *Homaxinella balfourensis*, with 4.8% cover in Brown Bay, had significantly higher cover there than at any of the other bays.

Polychaete 1 had significantly higher cover at O'Brien Bay 2 (3.2%) compared to all other bays (*Fig.2.6a*). The large tubeworm, *Potamilla antarctica*, was absent from Brown Bay, and had significantly higher cover at O'Brien Bay 1 (1.5%) compared to the other bays. Spirorbid polychaetes were observed with similar cover at Brown Bay, McGrady Cove and O'Brien Bay 1 (~2% cover), with significantly higher cover at O'Brien Bay 2 (8.8%), and highest cover at Newcomb Corner (13.5%).

The percentage cover of the large anemone, *Isotaelia antarctica*, was highly variable at each bay at the scale of transects (*Fig.2.6a*), but was not significantly different between the bays. Hydroids had significantly less cover at Newcomb Corner compared to O'Brien Bay 1 but cover was not significantly different from either bays at Brown Bay, McGrady Cove and O'Brien Bay 2.
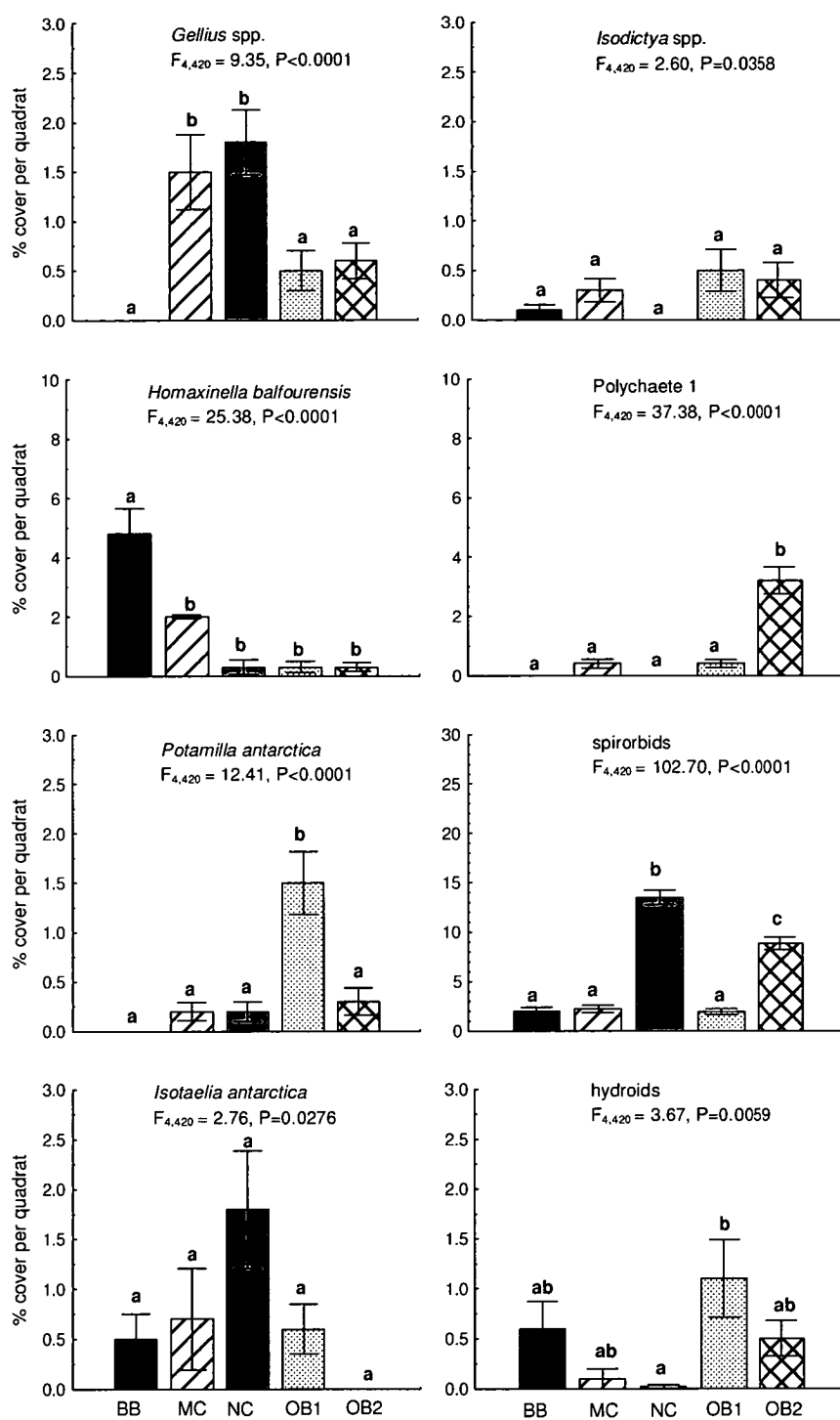
Figure 2.6a   Mean percentage cover of eight common taxa by bay (±SE, n=90). Letters above bars refer to groupings determined by Tukey HSD test results; within each plot, bars with similar letters are not significantly different. BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2

The circum-Antarctic urchin, *Sterechinus neumayeri*, was absent from Brown Bay and O'Brien Bay 2 (*Fig.2.6b*), yet accounted for significantly more cover at O'Brien Bay 1 than all other bays (1.1%).

The bivalve, *Laternula elliptica*, had significantly more cover (*Fig.2.6b*) at Brown Bay and O'Brien Bay 2 (2.5 and 2.1%, respectively), compared to McGrady Cove (0.8%), Newcomb Corner (0.1%) and O'Brien Bay 1 (0.6%). The large ophiuroid, *Ophiosparte gigas*, accounted for approximately the same cover at all bays (<0.4%). The small ophiuroid, *Ophiura crassa*, had significantly higher cover at Brown Bay (1.8%) than at all other bays (<0.2%).

Encrusting bryozoa were absent from Brown Bay (*Fig.2.6b*), had the highest cover at Newcomb Corner (7.4%) and O'Brien Bay 2 (6.2%), and significantly more cover at McGrady Cove (3.0%) than at O'Brien Bay 1 (0.7%) and Brown Bay. The colonial ascidian, *Sidnyum radiatum*, had similar cover at all bays (<0.3%).

Cover of red encrusting algae was significantly higher at Newcomb Corner (24.7%) compared to all other bays (*Fig.2.6b*), and lower at Brown Bay (0.7%) compared to McGrady Cove (6.4%) and Newcomb Corner. Benthic diatom cover was also variable between bays with greatest cover at O'Brien Bay 1 (65.5%), and significantly higher cover at Newcomb Corner (17.4%) than at McGrady Cove (7.9%) and O'Brien Bay 2 (8.8%). Brown Bay had the least diatom cover of all bays surveyed (0.6%).
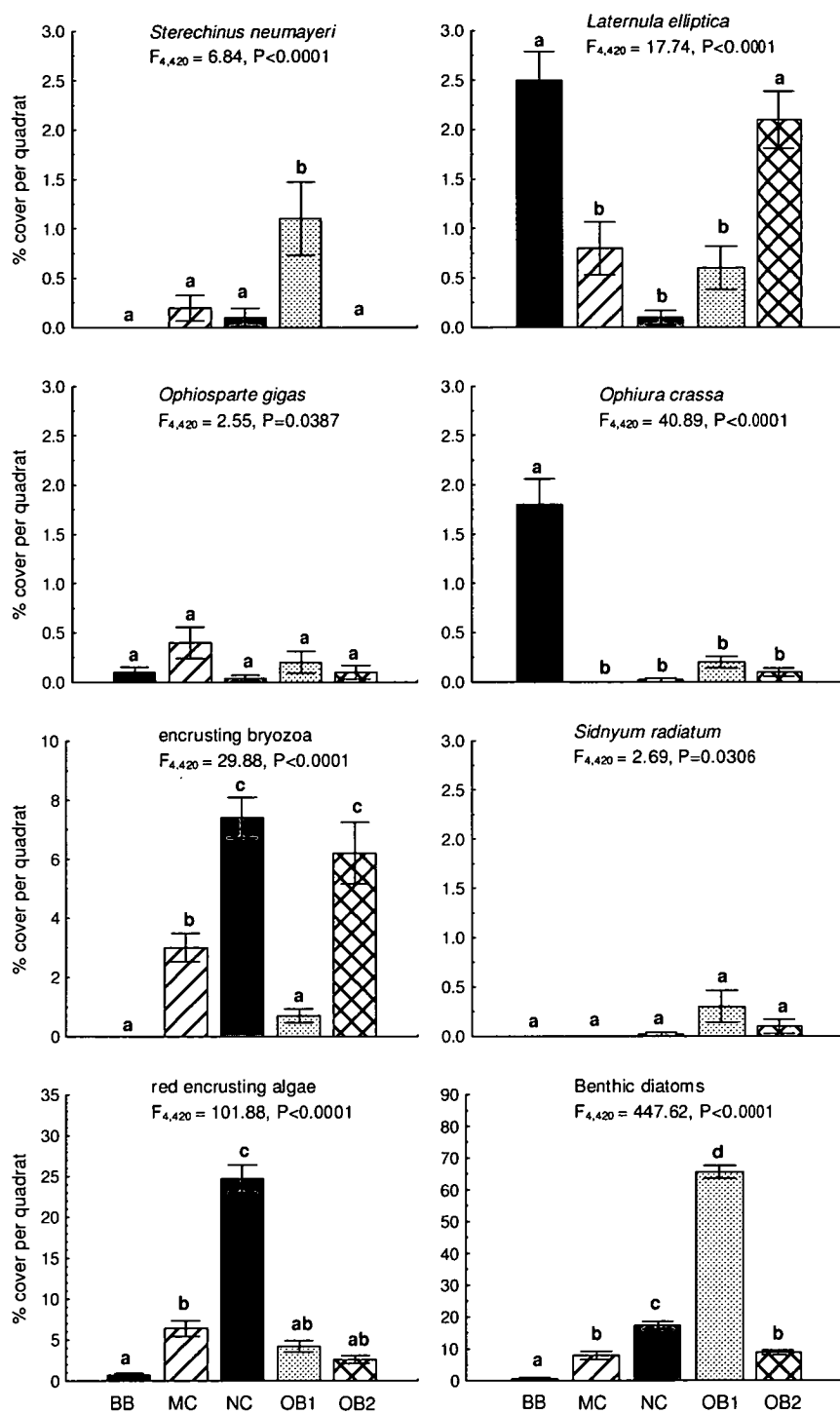
Figure 2.6b   Mean percentage cover of eight common taxa by bay (±SE, n=90). Letters above bars refer to groupings determined by Tukey HSD test results within each plot, bars with similar letters are not significantly different. BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2

Dissimilarity between bays

Interpretation of differences in the assemblages on hard substrata among bays using dissimilarity percentages (SIMPER) revealed that Brown Bay was the most dissimilar to each other bay (average dissimilarity <78.24%, *Table 2.8*), and the most similar bays were Newcomb Corner and O'Brien Bay 2 (average dissimilarity = 50.45%). The five main taxa responsible for observed differences between most bays were diatoms, encrusting algae, *Laternula elliptica*, spirorbid polychaetes, and encrusting bryozoa, although dissimilarity/ SD (Diss./SD) ratios were typically low (<1.4) indicating low confidence in significance of some of the dissimilarities. Notably, for Brown Bay comparisons diatoms provided the highest Diss./SD ratios for dissimilarity with each control bay.

Table 2.8   Contribution of specific taxa to analysis of dissimilarities (SIMPER) between bay pairs – five highest contributors only. Av.Diss. = average dissimilarity, Diss./SD =ratio of dissimilarity and SD, BB = Brown Bay, MC = McGrady Cove, NC = Newcomb Corner, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2

comparison (Av.Diss.)	taxa	% contribution	Diss./SD	comparison (Av.Diss.)	taxa	% contribution	Diss./SD
BB vs. MC (85.79%)	diatoms	13.39	1.11	MC vs. OB1 (73.39%)	diatoms	21.26	1.19
	encrust algae	12.37	1.01		encrust alg	9.94	1.05
	Laternula	12.02	0.96		spirorbids	7.96	1.04
	Homaxinella	10.61	0.82		encrust bry	7.50	0.97
	spirorbids	10.81	0.94		*Laternula*	5.54	0.63
BB vs. NC (87.81%)	encrust algae	17.25	2.19	MC vs. OB2 (62.63%)	spirorbids	14.84	1.08
	diatoms	16.55	2.55		diatoms	14.11	1.01
	encrust bry	12.83	2.13		encrust alg	11.54	0.99
	spirorbids	12.72	1.62		encrust bry	10.92	1.07
	Laternula	8.13	1.24		large polych	10.37	1.05
BB vs. OB1 (90.91%)	diatoms	29.62	2.40	NC vs. OB1 (62.14%)	encrust alg	15.01	1.50
	Laternula	9.23	1.12		spirorbids	13.30	1.54
	Homaxinella	7.78	0.86		encrust bry	12.78	1.79
	spirorbids	7.51	0.96		diatoms	9.60	1.32
	encrust algae	6.46	0.80		*Palmaria*	7.92	0.92
BB vs. OB2 (78.24%)	diatoms	18.35	1.84	NC vs. OB2 (50.45%)	encrust alg	20.17	1.54
	spirorbids	15.25	1.33		encrust bry	12.01	1.16
	encrust bry	10.52	1.12		*Palmaria*	11.67	1.01
	Homaxinella	10.14	0.85		large polych	9.37	1.09
	Laternula	10.04	0.96		*Laternula*	9.10	0.95
MC vs. NC (57.35%)	encrust algae	15.41	1.16	OB1 vs. OB2 (66.79%)	diatoms	15.98	1.23
	spirorbids	15.26	1.30		spirorbids	12.95	1.39
	diatoms	13.59	1.11		encrust bry	9.06	1.12
	encrust bry	12.09	1.17		*Laternula*	8.32	0.93
	Palmaria	10.08	0.92		encrust alg	7.63	0.91

A priori comparisons between Brown Bay and control bays

A priori comparisons of substrata cover between Brown Bay and the control bays were undertaken for a variety of biodiversity indices, major taxon groupings and select species (*Table 2.9*). Brown Bay had significantly fewer (*P<0.01*) species and individuals than the control bays. The cover of major taxon groups at Brown Bay was not significantly different to that in control bays, reflecting in part the high variability among transects at all bays.

The sponge, *Homaxinella balfourensis*, and ophiuroid, *Ophiura crassa*, are both significantly more common (*P<0.05*) at Brown Bay than in the control bays.

Table 2.9   *A priori* **comparison results between Brown Bay and the control bays.**
$(n=90, F_{0.05\,[1,445]} =3.86, F_{0.01\,[1,445]} =6.68)$

	MS	SS	Fs	significance
# species	121.37	2148.40	17.70	**P<0.01**
# individuals	1360.41	30088.50	22.12	**P<0.01**
Margalef richness	5.18	6.37	1.23	P>0.05
Shannon-Wiener Diversity	0.58	0.55	0.94	P>0.05
all Porifera	189.34	529.75	2.80	P>0.05
all Asteroida	0.70	0.55	0.94	P>0.05
all Echinoida	24.32	10.53	0.43	P>0.05
all Bryozoa	979.52	1345.25	1.37	P>0.05
all Ophiuroida	46.74	178.61	3.82	P>0.05
diatoms	61191.26	42392.90	0.69	P>0.05
spirorbid polychaetes	2506.29	1546.79	0.62	P>0.05
Homaxinella balfourensis	377.639	1505.36	3.99	**P<0.05**
Ophiura crassa	51.769	206.25	3.98	**P<0.05**
Laternula elliptica	92.68	187.79	2.03	P>0.05

Variance contribution at different spatial scales

Variance components were compared across bay, site and transect spatial scales to indicate the contribution of the different scales to the total variation in percentage cover of the various taxa and taxon groupings (*Table 2.10*). Most of the variance associated with the biodiversity indices is explained by the residual (or error) term, suggesting that differences between quadrats within transects is higher than differences between transects and between sites at each bay. The overall variance within the 'evenness' index is equally determined by variation at the scale of quadrats and bays. Most of the variance within the sponge,

macroalgae and bryozoa taxa groups, and the individual taxa of *Laternula elliptica*, *Homaxinella balfourensis* and *Ophiura crassa*, also occurs at the scale of quadrats. Variation in cover of encrusting algae, diatoms, spirorbids and total flora/fauna is attributed largely to differences among bays, as is the variance of 'silt on rock' and 'bare hard substrata'.

Table 2.10   *Variance components calculated from ANOVA results - contribution of each spatial scale (bay $\sim 10^4$ m, site $\sim 10^2$ m, transects $\sim 10^1$ m, quadrats (residual) $\sim 10^1$ m), as a percentage of total variance.*

source	total taxa	richness	evenness	Shannon	sponges	ophiuroids
Bay	26.8	12.2	51.0	29.6	5.6	7.9
Site (bay)	7.6	6.1	0.0	5.7	0.0	3.9
Transects (site(bay))	1.5	0.0	1.6	1.3	5.4	50.0
Residual	64.1	81.7	47.4	63.4	89.0	38.2

	encr. algae	macroalgae	diatoms	*Laternula*	*Homaxinella*	spirorbids
Bay	51.2	14.9	82.8	10.7	20.7	48.6
Site (bay)	0.0	18.2	0.3	7.1	1.1	6.5
Transects (site(bay))	10.1	1.9	1.4	9.6	0.0	7.9
Residual	38.7	65.0	15.5	72.6	78.2	37.0

	O.crassa	bryozoa	total flora/fauna	silt on rock	bare hard
Bay	26.9	12.9	74.6	56.3	53.1
Site (bay)	4.3	22.4	2.9	5.7	5.7
Transects (site(bay))	10.7	1.9	1.2	2.6	2.5
Residual	58.1	62.8	21.3	35.4	38.7

Discussion:

Marine macrofauna communities on hard substrata in the innermost reaches of bays in the Windmill Islands are dominated by sponges, cnidarians, polychaetes, bryozoans and echinoderms. These overall patterns are typical of the Antarctic nearshore benthos (Dayton *et al* 1970, Beckley & Branch 1992, Knox 1994, Clarke 1996c), although there are some clear distinctions between the characteristics of benthic assemblages in the Windmill Islands and other Antarctic locations.

Communities on hard substrata in the Windmill Islands

In the Windmill Islands, a total of 40 animal and five plant taxa were found in a combined survey area of 67.5 m². Diversity at small scales (~10 m) is highly variable between bays, ranging from 23 taxa per 2.25 m² (at O'Brien Bay 1) to 5 (at Brown Bay). These values, particularly those for Brown Bay, are low compared with results from other Antarctic studies. For example, Barnes & Brockington (2003) found >75 species in 2.75 m² at Adelaide Island off the Antarctic Peninsula.

Low diversity recorded in our surveys may be due to the focus on low energy environments in the innermost reaches of semi-enclosed bays. These bays have continuous sea ice cover for >10 months per year with correspondingly low light regimes and probably low mixing of water due to the absence of wind driven circulation. However, direct comparisons between studies are often difficult due to factors such as different survey methods (e.g. destructive *vs.* photographic) and different experimental designs (e.g. sampling depth profiles *vs.* a single depth).

The Windmill Island benthic assemblages exhibited low diversity (Shannon-Wiener 0.6 to 1.3 nats) and evenness (0.5 to 0.9) across all survey bays. Gambi *et al.* (1994) found similar patterns for sub-littoral hard substratum assemblages at comparable depths off Terra Nova Bay in the Ross Sea, and attributed them to relatively high densities of a few species. Similarly, benthic cover at the Windmill Islands is dominated by relatively few taxa such as spirorbids, encrusting bryozoa, diatoms and encrusting red algae. Indeed, diversity was lowest at O'Brien Bay 1 which also had the highest richness and lowest evenness indicating that the benthos is dominated by few taxa (e.g. diatoms). At Signy Island off the Antarctic Peninsula, Barnes (1995a,b) describes the shift in dominance from algal to animal groups (particularly bryozoa and sponges) with increasing depth below 3.5 m, but also concluded that *"benthos other than algae was scarce shallower than 12-15 m"*.

Epibenthic zonation in the Windmill Islands

Assemblages at 6 m depth at all Windmill Island bays are dominated by sessile filter-feeding invertebrates such as sponges, tube-dwelling polychaetes, bryozoans and hydroids. Motile invertebrates account for only 17 to 30% of total taxa we encountered in quadrats.

These results contrast to those from Ellis Fjord in the Vestfold Hills where the numerically dominant species on hard substrata at a comparable depth were mobile echinoderms (Kirkwood & Burton 1988). Similarly, Gruzov (1977) described the community of the upper sub-tidal zone (depth <10 m) in the Davis Sea as consisting of echinoderms, diatoms, annual macroalgae, mesograzers and a hydroid species. At Adelaide Island, Barnes & Brockington (2003) recognised a "high sub-littoral" zone (0 to 7 m depth) that was colonised by limpets, the bryozoan, *Inversiula nutrix*, and spirorbid polychaetes, but with very few other species. Results such as those have led to broad generalisations about the Antarctic upper sub-littoral zone as being largely devoid of attached filter feeders but being dominated by transient populations of mobile animals such as echinoderms, molluscs and crustaceans during ice-free periods (Dayton 1990). However, while a clear denuded zone is observed directly below the ice foot (0 – 4 m) in Windmill Island bays, the marine assemblages at 6 m depth within these shallow, semi-enclosed bays are more diverse than the generalisations suggest.

The 6 m depth contour is considered by many Antarctic researchers to be within the zone that is most physically disturbed by anchor ice formation and ice scour (Dayton *et al.* 1970, Gruzov 1977, Barnes & Brockington 2003). In the Windmill Islands there is no evidence of anchor ice formation and, at the survey bays, significant evidence of ice scour by the ice foot (see Barnes 1995a) is only apparent in water depths <4 m. It seems likely that the geographical shape and position of the semi-enclosed bays, the shallow bathymetry and low tidal range combine to provide significant protection from roving icebergs that are known to scour benthic habitats (see Peck *et al.* 1999, Gutt 2000). These factors, together with sea ice cover for >10 months per year, are likely to result in a low incidence of iceberg scour and potentially a higher cover and diversity of sessile invertebrates on hard substrata in shallow depths (e.g. 5 - 15 m). Note however, intermediate levels of ice disturbance may actually promote higher diversity by preventing dominant species monopolising space (Smale *et al.* 2007). It would appear that in the absence of significant ice scour, the depth-related zonation that Dayton *et al.* (1970) described for McMurdo benthos is skewed

towards the shallows. That is, Zone I ('bare zone' from 0 - 15 m at McMurdo) occurs from

0 - 4 m in the Windmill Island bays, and Zone II ('coelenterate-hydroid zone' from 15 -

33 m) extends from 4 m depth downward. Interestingly, similar observations were made

by Barnes *et al.* (2006) who recognised a rich and diverse community in shallow depths

within an *"unusually sheltered habitat"* in Moraine Fjord on South Georgia Island. They

concluded that the assemblage was a good example of how a Southern Ocean benthic

community can develop in the absence of disturbance from ice, waves and currents.

Macroalgal distribution

At the time of the Windmill Island surveys (early summer, under sea ice) macroalgae

were minor components of the benthic assemblages, with the exception of encrusting red

algae at some bays. In contrast, other studies in Antarctica have identified the dominance

of encrusting red algae and/or macroalgae in assemblages at 5 - 8 m depth at Signy Island

(Barnes 1995b), Marion Island (Beckley & Branch 1992) and Terra Nova Bay (Gambi *et*

al. 1994). Persistent sea ice and snow cover is known to significantly reduce benthic light

levels and therefore influences the distribution of macroalgal assemblages (Wiencke 1996).

The Windmill Island survey bays all have long term sea ice and variable thickness of

snow cover over bay-wide scales ($>10^2$ m). These factors are likely to contribute to the low

cover of macroalgae we observed in the survey. Indeed, variance components analysis for

diatoms and encrusting algae attribute most variance to differences among bays (rather than

quadrats), in keeping with the spatial scale of variability in sea ice and snow cover.

Diatoms are listed as a common component of the benthos in the shallow sub-littoral

(Dayton *et al.* 1970, Gruzov 1977, Barnes 1995a, Barnes & Brockington 2003) and, in the

Windmill Islands they cover between 1 and 65% of quadrats.

High variation between bays is evident and is likely to be a response to, among other

things, varying light levels at a given depth. For example, the highest diatom cover was

recorded at O'Brien Bay 1 where the sea ice had only a thin cover of snow resulting in

greater light penetration (1.32 μmol photons.m^{-2}.sec^{-1}). Conversely, the lowest diatom

cover is at Brown Bay where snow cover on the sea ice was in excess of 1 m and the light

levels at 6 m depth were very low (0.03 μmol photons.m^{-2}.sec^{-1}).

The seasonality of algal dominated communities in Antarctica is well known

(Wiencke 1990) and so caution is necessary when comparing studies from different bays

and times of the year. However, most of the low energy bays surveyed in the Windmill

Islands do not have significant algal growth at any time of the year suggesting conditions in

these protected areas are largely unsuitable for algal growth.

Benthic assemblages at Brown Bay

Epibenthic assemblages on hard substrata in the Windmill Islands are highly variable

over a range of scales from metres to kilometres. For most taxa, the variation in cover

between quadrats within the same transect overshadows any variation between bays. High

variability at this scale makes differentiation between potentially impacted and non-

impacted locations difficult unless transects are used as a basis of replication. Despite this,

assemblages on hard substrata at Brown Bay are different in several respects from those at

control bays. Some taxa found at all control bays were absent from Brown Bay (e.g. *Gellius*

sp., *Potamilla antarctica*, *Sterechinus neumayeri*, and encrusting bryozoa), while the

benthic assemblage in Brown Bay is depauperate in terms of total sponge taxa.

In contrast, two taxa (*Ophiura crassa* and *Homaxinella balfourensis*) are

significantly more common at Brown Bay than at control bays. Sessile filter-feeding

invertebrates are known to be affected by increased sediment loads due to clogging of

feeding apparatus and smothering (Moore 1977, Ellis *et al.* 2002). The absence of many

sponge species, encrusting bryozoa and *P.antarctica* in Brown Bay could therefore be the

result of elevated sedimentation rates. The urchin, *S.neumayeri*, is less likely to be directly

affected by sedimentation although elevated sedimentation rates might be responsible for

the low diatom and encrusting algae cover found at Brown Bay, and therefore limit food

availability for the sea urchin. The reason for the higher cover of the ophiuroid, *O.crassa*,

and the sponge, *H.balfourensis*, at Brown Bay is less clear. However, these species might

simply be more tolerant of elevated sedimentation rates and therefore more able to

capitalise on the lower abundance of competitors (or predators) and increased availability of space.

These results suggest that the benthos in Brown Bay may be exposed to different environmental conditions than the other bays, despite the superficial similarities between all bays. There are two main factors that are obviously different at Brown Bay compared to the control bays. Firstly, there is a higher snow cover overlying the sea ice at Brown Bay; >1 m snow depth compared to <0.3 m at other bays. Secondly, there are potential anthropogenic impacts affecting Brown Bay that originate from Casey Station causing elevated sedimentation and pollutant loading. However, while our surveys provide correlative evidence of differences in hard substrata assemblages between Brown Bay and the control bays, the causality of environmental variables such as sedimentation and/or light levels can only be determined using manipulative experiments.

Conclusions:

Macroscopic communities on hard substrata at survey locations in the Windmill Islands are dominated by sessile filter-feeding taxa that elsewhere in Antarctica are associated with deeper sub-littoral zones, but they are highly variable between bays (10^4 m), and at scales of 10^{-1} and 10^1 m but remarkably consistent between sites within bays (10^2 m). The differences are attributed to the lower incidence of ice disturbance evident in the protected bays, and presumed to be a result of persistent sea ice cover throughout much of the year. Assemblages on hard substrata in the potentially impacted location of Brown Bay have characteristics that differentiate them from similar bays outside the influence of Casey Station and therefore suggest that anthropogenic impacts might be having an impact on local marine environments. Manipulative experiments are the logical next step to test this idea and potentially identify a cause for the observed differences between assemblages in Brown Bay and the control bays. These experiments form the basis of the remaining chapters in this thesis.

Chapter 3
Effects of sedimentation on the recruitment of sessile marine species on shallow Antarctic reefs

Abstract:

Increased sedimentation rates are known to affect the recruitment of sessile marine assemblages on hard substrata, and increased rates of terrestrial runoff are recognised as being among the biggest threats to coastal marine communities worldwide. Human activities at Casey Station, East Antarctica each summer are thought to be causing elevated sedimentation rates in a local bay; however, the implications of altered sedimentation rates on the recruitment of species on shallow Antarctic reefs is currently unknown. Artificial substrata (horizontal and vertical) were deployed in four sheltered bays (one potentially 'impacted' and three 'controls') for periods of 13 and 37 months. Spirorbid polychaetes and encrusting bryozoan species numerically dominated recruiting assemblages at all bays and significantly more individuals recruited to vertical surfaces. Rates of recruitment varied significantly between bays, with fewer overall species and fewer bryozoan species apparent in the potentially impacted bay after 13 months. However, the total number of taxa recruiting to artificial substrata increased in the potentially impacted bay when sedimentation rates were reduced using Plexiglas shields, indicating that the anthropogenically elevated sediment loads occurring adjacent to Casey Station were hindering recruitment to hard substrata. These findings have major implications for environmentally responsible management of human activities along the Antarctic coast.

Introduction:

Deposition of terrigenous sediments is well established as a key determinant of the structure and dynamics of nearshore marine communities and that increased rates of terrestrial runoff and sedimentation are among the biggest threats to coastal marine communities worldwide (Rogers 1990, Edgar & Barrett 2000, Airoldi 2003, Lohrer *et al.* 2004, Fabricius 2005, Maldonado *et al.* 2008). However, the majority of research investigating the potential impacts of increased sedimentation has been conducted along coastlines adjacent to significant marine ecosystems such as the Great Barrier Reef

(Williams 2001, Larcombe & Woolfe 1999, Fabricius 2005), and in regions of high human

population density such as the Mediterranean (Airoldi & Virgilio 1998, Saiz-Salinas &

Urkiaga-Alberdi 1999, Piazzi & Cinelli 2001, Terlizzi *et al.* 2005). Relatively little

research has focused on the impacts of terrigenous sediments in high latitude shallow

marine environments; the few exceptions include the work of Johansson (2002) in Sweden,

Carney *et al.* (1999) in Alaska, and Barnes & Kuklinski (2005) in arctic Spitsbergen. No

known studies, other than an assessment following a sediment slumping event at McMurdo

Sound (see Slattery & Bockus 1997), have looked at potential impacts of sedimentation on

marine invertebrates (or algae) on the Antarctic coast.

Impacts of sedimentation

Increased sedimentation on marine communities can cause a reduction in the

diversity and abundance of sessile species, in particular the loss of algal species and the

increased dominance of opportunistic suspension feeders (Saiz Salinas & Urdangarin

1994). Excessive sedimentation may affect the choice of settlement site by larvae (Hunt &

Scheibling 1997, Maldonado 2008), cause smothering of slow growing, encrusting species

(Moore 1977), and/or clog feeding apparatus (Ellis *et al.* 2002). In general, juvenile stages

tend to be more susceptible than adults (even among those species able to utilise sediments

for food) and are less likely to survive sudden increases in sediment loading (Hinchey *et al.*

2006). Because the influx of terrigenous sediment to the marine environment is typically

not uniform in time but occurs as pulses associated with climatic events such as storms

(Lohrer *et al.* 2006a,b), or the peak summer snow melt in polar regions, it may be the

magnitude of discrete sedimentation events rather than a particular annual mean

sedimentation rate that largely drives shifts in community structure.

Recruitment to benthic communities

Recruitment is a key process in structuring benthic marine communities (Connell &

Keough 1985), and it is the magnitude of variability in annual recruitment rather than long

term averages that is important in shaping community structure (Connolly & Roughgarden

1999). Natural variability in the timing of larval release, larval mortality, and the length of

time that larvae spend in the plankton (if at all) are critical in determining the supply of potential recruits to available substrata (Rodríguez *et al.* 1993). Post-settlement pressures (e.g. predation and competition; Dayton 1971, Connell & Keogh 1985, Hunt & Scheibling 1997), and physical disturbance (e.g. ice-scour and pulses of sedimentation; Peck *et al.* 1999), are also important in determining whether juvenile invertebrates and algal spores survive to become successful recruits.

Recovery of communities after disturbance is dependent on the size and severity of the disturbance, and local abiotic (e.g. current flow, light regime) and biotic factors (e.g. larval supply, competition, and predation).

Assessing recruitment to hard substrata in Antarctica

Recruitment of sessile invertebrates to artificial hard substrata is often used as a proxy to assess recruitment to natural substrata, and readily lends itself to experimental analysis of the effects of anthropogenic disturbance on recruitment (Glasby 1998, Connell 2000, Maughan 2001). Settlement panels, ranging in size from 2 to 20 cm^2, made of glass, acrylic, wood, ceramic or slate are most commonly used.

In Antarctica, only a few studies have used artificial settlement panels to determine recruitment patterns. At McMurdo Sound, Dayton (1989) reported settling panels *"collecting nothing but two serpulid polychaetes"* after three years and Pearse & Pearse (1991) similarly reported very few taxa (mainly bryozoans) recruiting to glass slides deployed for one year; while Webster *et al.* (2006) found a wide variety of eukaryote sessile taxa (i.e. cnidarian, bryozoan, annelids) recruiting to glass slides after a similar period of immersion. In a recent study, Bowden (2005b) investigated the seasonality of recruitment to acrylic panels at sites on the Antarctic Peninsula, and observed recruitment of 41 taxa from nine phyla during one year, with distinct seasonal recruitment peaks.

All of these studies indicated that recruitment to hard substrata in Antarctica occurs at slower rates than in lower latitudes, and is dominated by bryozoa and spirorbid polychaetes.

Sedimentation in Antarctica

The Antarctic coastal marine environment has strongly seasonal features with many areas completely covered by sea ice for more than nine months of the year, followed by a brief one to three month period of open water during summer when high productivity within the water column reduces water clarity. During the summer months, intense solar radiation over long day lengths and above-zero temperatures cause snow and ice to melt, and result in melt streams and/or broad scale movement of water through terrestrial catchments to the marine environment. The majority of meltwater flows across ice covered terrain and therefore contains little terrigenous sediment. In areas within or adjacent to weathered bedrock, flowing water entrains terrestrial sediments that are subsequently deposited into the marine (or lacustrine) environment; however, natural rates of sedimentation in Antarctic coastal waters are considered low (Isla *et al.* 2001).

Human activities associated with research stations in Antarctica require the development of infrastructure such as roads to allow movement of cargo to and from supply vessels during the brief summer period. Each year at Australia's Casey Station, a one kilometre road is graded and stabilised with crushed local rock to allow heavy machinery to transfer food and supplies from the wharf to storage areas. In addition, vehicle tracks for access around the station buildings are maintained throughout the summer. For a period of approximately six weeks from mid-December, the mean daily maximum temperatures at Casey Station are often above freezing, and meltwater flows off the station's roads, and down the catchment gradients into Brown Bay. At peak flow, surface sediment plumes are visible at the interface of the meltwater and seawater in the bay. Within a ten year period from 1996, no sediment plumes have been observed entering the marine environment in the Casey region at any site other than Brown Bay.

This study was designed to assess the potential impact of terrigenous sediments resulting from annual road development (and general station activities) at Casey Station on natural recruitment of marine sessile invertebrates to artificial hard substrata in Brown Bay. The aims of the research were twofold: (1) to estimate spatial and temporal variability in recruitment onto hard substrata across a variety of bays (including Brown Bay) in the Casey

region, and (2) to assess the potential impact on recruitment of elevated sedimentation rates in Brown Bay by experimentally manipulating the sediment loading on artificial substrata in Brown Bay and in three bays outside the influence of Casey Station.

Materials and Methods:

Location Description

The work was conducted in four shallow bays (<15 m deep) in the vicinity of Australia's Casey Station (66.28°S, 110.53°E) within the Windmill Islands of eastern Antarctica (*Fig.3.1*). Brown Bay was chosen due to observations of a surface sediment plume, thought to result from station activities, during the summer months. The other bays (McGrady Cove, O'Brien Bay 1, and O'Brien Bay 2) were chosen as 'control' bays in the close vicinity of the station (2 - 3.5 km) but essentially outside the influence of station activities.

Both Brown Bay and McGrady Cove are small embayments within the larger Newcomb Bay (*Fig.3.1*). Brown Bay is 500 m north-east of Casey Station and is free of sea ice for ~4 - 6 wks per year. The bay receives most of the meltwater generated within the station catchment area via melt streams that enter the bay from a small valley on its western shore. Brown Bay's southern shore consist of low (3 - 4 m) ice cliffs, while the northern and western shores are weathered outcrops of bedrock, boulders and cobble, that continue into the water. McGrady Cove is located in the south-east corner of Newcomb Bay ~2 km north-east of Casey Station. The bay is ice free for ~4 wks per year, and receives meltwater streams flowing from the ice plateau below the Løken Moraines (*Fig.3.1*). The southern and eastern shore consists of ice cliffs up to 8 m high, while the western shore is a weathered bedrock ridge with boulders and cobble.
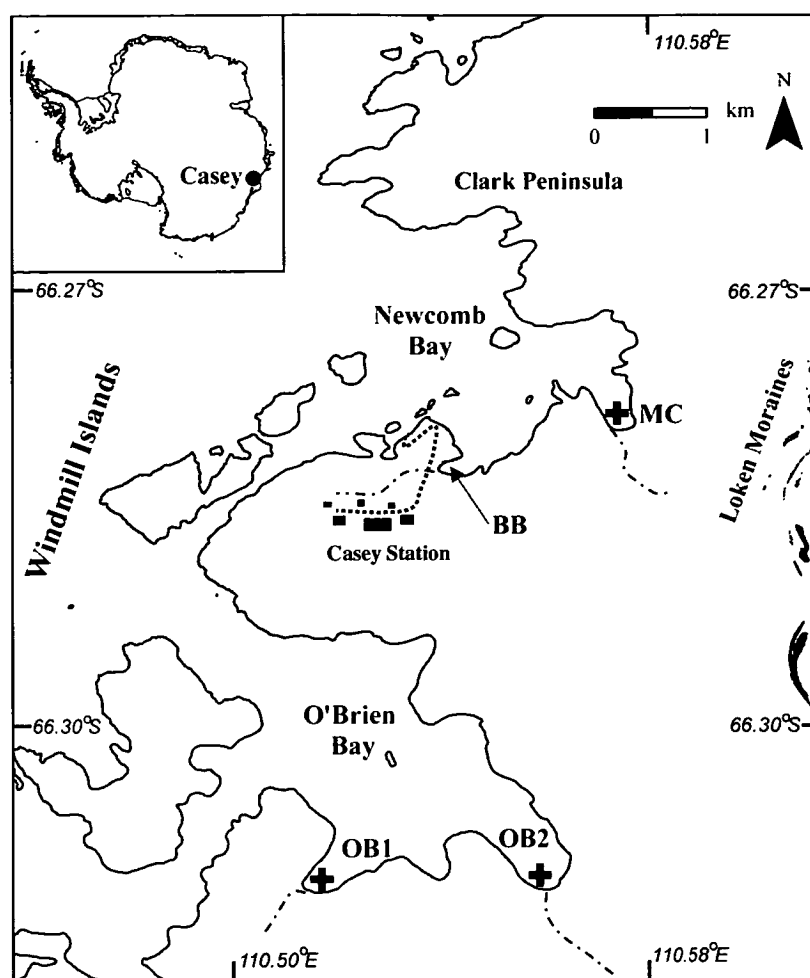
Figure 3.1   Map of the Windmill Islands coastline near Casey Station illustrating bays where settlement panels were deployed, and places mentioned in the text. BB=Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2. Approximate path of major melt stream entering each bay is depicted by dashed lines; the Casey road is depicted as dotted line.

O'Brien Bay is 2 km south of Casey Station, and is similar in shape and size to Newcomb Bay (*Fig.3.1*). O'Brien Bay 1 is a small embayment on the southern side of O'Brien Bay ~3.5 km from Casey Station. This bay is ice free for <4 wks per year, and receives meltwater via a valley on its south-western shore. The northern and western shore is exposed bedrock, with weathered boulders and cobble, while the southern shore consists of 5 - 8 m ice cliffs. O'Brien Bay 2 is in the south-eastern corner of O'Brien Bay, is free of sea ice for <4 wks per year, and receives meltwater streams via the ice cliffs on its southern

and eastern shores. The western shore is an exposed bed rock ridge with weathered boulders and cobble, while the eastern shore consists of 10 - 20 m ice cliffs.

All four bays were considered to have broadly similar environments in terms of area (less than 0.6 km^2), shape (parallel sided, open bays), aspect (northerly facing), water flow (sheltered, low energy, low current), and sea ice cover (1.3 m thick for >10 months each year). Snow cover overlying the sea ice varied between bays, with Brown Bay having the deepest snow cover (>1 m), and the other bays having a relatively thin cover of snow (<0.3 m).

Benthic environments within each bay consist of an irregular patchwork of isolated boulders (20 - 35% cover) within fine grained sediment basins (~90% <63 μm). Hard substrata are colonised to varying extent by encrusting invertebrate taxa such as sponges, bryozoans, polychaetes, and ascidians. Macroalgae were not observed at any of the bays where settlement panels were deployed. The bays chosen for placement of panels were approximately level areas supporting accumulated sediment adjacent to naturally colonised hard substrata. A water depth of 6 m was chosen as it represents the average depth at the head of Brown Bay nearest the observed sediment plumes, and was standardised across all bays to avoid depth-related effects.

Experimental Design

The experiment was designed to assess recruitment to artificial substrata in the four bays, across two recruitment periods of 13 and 37 months, respectively. Within this framework there were two related components:

(1) quantifying variability of recruitment to artificial hard substrata under naturally occurring sedimentation regimes (Experiment 1); and

(2) assessment of the impacts of sedimentation on recruitment to hard substrata by manipulating sedimentation rates within each locality (Experiment 2).

Experiment 1: Recruitment variability

A three-way factorial design was used to investigate the variability of recruitment to horizontally and vertically oriented artificial hard substrata at each of four bays, across two recruitment periods.

Settlement tiles (100 x 100 x 8 mm) were cut from dark grey, unglazed, porcelain floor tiles that had an irregular upper micro-topography on the front surface. Non-toxic aquarium silicon sealer was used to attach a plastic hanger to the top and bottom edge of each tile, and a unique number engraved on one of the hangars. Tiles were attached to over-turned, plastic 52 L fish bins (645 x 413 x 276 mm) that were weighted inside with rock-filled mesh bags. Four tiles were attached horizontally to the upper surface and another four vertically to the sides of the bins using plastic cable ties that allowed a 5 mm gap between the back of each tile and the fish bin surface. These 'experimental units' were lowered by divers into haphazardly selected locations on the sea bed. Two experimental units were deployed at each bay, approximately two metres apart. Tiles were collected underwater by divers cutting the attached cable ties and carefully placing each tile into individual, sealable containers that prevented front and back surfaces from being damaged during transit back to the laboratory.

The experimental units were deployed at each bay within a seven day period in November/December 2002. Randomly selected tiles (two from the horizontal and two from the vertical surfaces of each unit) were subsequently sampled in January/February 2004 after 13 months of immersion. The remaining tiles were collected in January/February 2006 after 37 months of immersion. Recruitment was compared between horizontally and vertically oriented tiles at the different bays, and across time periods.

Experiment 2: Effects of sedimentation on recruitment

The potential impacts of elevated sedimentation on recruitment to artificial hard substrata was investigated using a four-way factorial design, with two experimental units in each of three sediment treatments that were deployed at four bays for two recruitment periods. Due to the supposition that effects of sedimentation on recruitment would be most pronounced on upward facing surfaces, only horizontal tiles were included in Experiment 2.

Experimental units were constructed in an identical way to those used in Experiment 1 with four horizontal tiles (see above), except that in order to test for the effect of sedimentation, natural sedimentation was reduced by shielding settlement tiles. Three levels of sediment shielding were used: 'reduced sedimentation' (full Plexiglas shield installed over all tiles on the experimental unit), 'natural sedimentation' (no Plexiglas shield), and 'experimental control' (partial Plexiglas shield).

Full sediment shields were made from sheets of 3 mm thick clear UV acrylic (Plexiglas Sunactive GS) that permits transmission of >70% of UV wavelengths (315 – 380 nm) and thus does not confound the effect of sedimentation with markedly reduced UV levels. Shields were cut to fully overhang the experimental units by 200 mm on each side in order to reduce the natural fall of sediment reaching the tile surfaces. The shields were attached to stainless steel rods protruding from each corner of the experimental unit to a height of 200 mm above the surface of the tiles.

Partial Plexiglas shields (used for experimental controls) were attached to the stainless steel rods but approximately 80% of the overlying shield was cut away to allow sediment to reach all tiles on these experimental units. The aim was to mimic the presence of the shield without preventing sediment reaching the tiles, in case the presence of the shields alone affected recruitment, e.g. by altering water flow across the tiles). Experimental units within the 'natural sedimentation' treatment had no stainless steel rods or Plexiglas shield.

Divers deployed two experimental units of each of the three sediment treatments per bay, placing them in a haphazard arrangement (2 m apart) on the sea bed. Divers scraped the Plexiglas shields clean of sediment every 3 – 4 wks throughout each Antarctic summer and completely removed the shields at the end of each February when the snow melt (and therefore sedimentation) had ceased, reinstalling them early in the following November/ December prior to the start of the summer melt.

Sedimentation monitoring

To monitor local sedimentation rates throughout both experiments, two collection jars (30 mm diameter, 70 mm deep) were placed into holes cut into the upper surface of each experimental unit, in positions adjacent to tile attachment points. Jars were numbered and, during sampling, were capped underwater by divers, removed and replaced with a clean jar. Jars were sampled at ~4 wk frequency throughout the summer, and left in place throughout the eight month winter period (March to October). The exception was McGrady Cove where rotten ice conditions prevented sampling of sediment jars during January 2003 (second collection period). Collected jars were taken to Casey Station for analysis.

Laboratory analysis

The front and back surface of each settlement tile was rinsed with filtered seawater to remove motile fauna and unattached diatoms, and preserved in 4% seawater formalin. Motile fauna were retained and preserved but their analysis is not included here. A grid of 1 cm squares was overlaid onto the tile surface and all taxa on the tile were counted under a dissecting microscope, with the exception of taxa in the outer 1 cm margin of the tiles to avoid edge effects (Glasby 2000). Taxa were identified to the lowest taxonomic group possible, which varied from species-level for most bryozoans (using Hayward, 1995), to class for some groups (e.g. spirorbid polychaetes). When identifying taxa, a reference collection was maintained to provide consistent identification across all tiles; this reference collection has subsequently been archived with the Australian Antarctic Division. Only taxa on outward (or upward) faces of the settlement tiles were counted since those surfaces, unlike protected undersides, most closely represent the natural surfaces available for recruitment within the bays.

Sediment collected in the jars was vacuum filtered onto pre-weighed, glass fibre or cellulose acetate filter papers depending on sediment volumes, oven dried at 30°C for 24 hrs, and weighed to the nearest 0.1 mg. Distinction between sediment source (marine *vs.* terrestrial) was not possible due to the small amounts present.

Statistical analysis

Experiment 1: Recruitment variability

Initial exploration of raw abundance data from the tile surfaces was based on Bray-Curtis similarity measures (fourth root transformed data) using the PRIMER v.6.1.6 statistical package (Plymouth Marine Laboratory, UK). *A priori* non-parametric multivariate analysis of variance was undertaken using Bray-Curtis similarity measures over 9999 permutations (PERMANOVA; Anderson, 2001) to identify overall differences in recruitment associated with the main effects of orientation, sampling period (time) and location (bay). Similarities in community structure were viewed graphically using non-metric multidimensional scaling (nMDS). Taxa contributing most to differences between times, and/or bays were identified using similarity of percentages (SIMPER).

Analysis of Variance (ANOVA) was undertaken using GMAV (Underwood and Chapman, 1998) on the mean number of species (S) and mean number of individuals (N). Homogeneity of variances were analysed using Cochran's C-test, and data were transformed prior to analysis if heteroscedastic (Snedecor & Cochran, 1989). When significant, multiple pairwise comparisons were undertaken using the Tukey HSD (honestly significantly different) test.

Shannon-Wiener diversity (H', base e) and Pielou's evenness (J') indices were calculated using DIVERSE (PRIMER) for each experimental unit (two per bay) and analysed using ANOVA and Tukey HSD.

Due to an enforced unbalanced design, whereby vertical tiles were unable to be deployed in O'Brien Bay 2, full analysis of the main effects and interactions was undertaken on a balanced subset of the tile data (n=48, with tiles from O'Brien Bay 2 excluded). A four factor nested ANOVA design was used to test for differences between recruitment with main effects of orientation (horizontal vs. vertical; 2 levels, fixed), deployment time (13 months vs. 37 months; 2 levels, fixed), bay (Brown Bay, McGrady Cove, O'Brien Bay 1; 3 levels, random), and experimental unit (2 levels, random, nested within bay) with two replicate tiles per unit. Note that where the effect of experimental unit

is highly non-significant (P>0.25) *post hoc* pooling of tiles across experimental units within each treatment was undertaken (Underwood 1997).

A priori comparisons of means (Sokal & Rohlf, 1995) were undertaken to assess differences between recruitment (assessed as the number of species, number of individuals, Shannon-Wiener Diversity, Pielou's Evenness) at Brown Bay *versus* the control bays.

Experiment 2: Effects of sedimentation on recruitment

Initial exploration of multivariate community data was undertaken *a priori* using PERMANOVA (based on Bray Curtis similarities calculated from 4th root-transformed data with 9999 permutations). Univariate treatment effects were investigated using a four factor nested ANOVA design to test for differences in mean number of species and mean number of individuals recruiting to tiles with main effects of deployment time (2 levels, fixed), bay (4 levels, random), sediment treatment (3 levels, fixed), and experimental unit (2 levels, random, nested within bay and treatment) with two replicate tiles per unit. *Post hoc* pooling was undertaken when effect of experimental unit was highly non-significant (P>0.25).

A priori comparisons of means (Sokal & Rohlf, 1995) were undertaken to assess differences between recruitment (expressed as number of species and number of individuals) at Brown Bay *versus* the control bays.

Sedimentation rates

Daily sedimentation rates ($g.m^{-2}.day^{-1}$) were calculated for each sediment jar installed at the three bays (sediment jars were not installed at O'Brien Bay 2). The mean length of time within each sampling period is: 76 days (December 2002 – February 2003), 285 days (February – November 2003), 60 days (December 2003 – February 2004), and 727 days (February 2004 – January 2006).

'Natural' mean daily sedimentation rates were compared among times and bays using data from the experimental units in Experiment 1 only (i.e. non-shielded experimental units). A three factor ANOVA was used to examine main effects of time (4 levels, fixed), bay (three levels, random), and experimental unit (2 levels, random, nested within bay),

with two sediment jars per experimental unit in each time period. Differences in sedimentation rates among the different treatments were identified using a four factor ANOVA with main effects of time (4 levels, fixed), bay (3 levels, random, orthogonal), treatments (3 levels, fixed, orthogonal), and experimental unit (2 levels, random, nested within bay and treatment), with two sediment jars per experimental unit. *Post hoc* pooling of sediment jars across experimental units within each treatment was undertaken where the effect of experimental unit was highly non-significant (P>0.25).

Results:

All 144 settlement tiles were recovered across the two sampling events. Several experimental units were nudged by moving ice during the course of the experiments and had to be realigned by divers; however, their movement is not believed to have affected recruitment patterns and so they were included in the analysis.

Overall recruitment patterns

A total of 116,553 sessile individuals from 25 distinct taxa, within seven phyla (*Table 3.1*), were counted across all tiles. The most abundant taxa were spirorbid polychaetes which recruited to all but three tiles and accounted for 74% of total individuals (84,713 counts), while the most speciose invertebrate group was the bryozoa, with 15 species (3173 individual colonies) represented on the tiles. The most common spirorbid polychaetes were spiral and flattened to the tile surfaces; however, an erect form (possible a separate species) with the main length of tube growing away from the tile surface was seen on vertical tiles at some bays.

Table 3.1   List of sessile taxa recruiting to settlement tiles, and total number of individuals counted across all tiles in Experiments 1 and 2 (n=144)

Phylum	Class	taxon	total individuals
Porifera	Demospongiae	sponge mass	30
Annelida	Polychaeta	spirorbid	84,713
		spirorbid (erect)	74
		erect branching colony	228
Rhizopoda		spiral foraminifera	120
		spherical foraminifera	178
Cnidaria	Hydroida	erect stoloniferous hydroid	39
		black solitary polyp	196
Bryozoa	Gymnolaemata	*Aimulosia antarctica*	2
		Arachnopusia decipiens	91
		Beania challengeri	102
		Celleporella antarctica	119
		Ellisina antarctica	119
		Escharella watersi	2
		Escharoides praestita	7
		Escharoides tridens	1
		Fenestrulina crystallina	56
		Fenestrulina sp.	1
		Filaguria spatula	2
		Inversiula nutrix	1388
		Klugeflustra antarctica	2
		Micropora brevissima	429
		cup bryozoan	637
Chlorophyta		erect green shoot (possibly *Monostroma* sp.)	441
Rhodophyta	Florideophyceae	basal disc (some with shoots) (most likely *Palmaria* sp.)	26,873

Miscellaneous taxa included: two distinctive types of foraminifera; small, white hydroid polyps attached to a brown stolon and a black solitary polyp-like form (only at McGrady Cove). Two macroalgae taxa were identified on tiles deployed for 37 months. Overall, tiles deployed for 37 months had more individuals (92,494) and taxa (25) than those deployed for 13 months (23,571 and 20, respectively).

Experiment 1:Recruitment variability

Total Taxa

A total of 51,466 individuals from 23 taxa were counted on 32 horizontal tiles and 24 vertical tiles that were exposed to natural levels of sedimentation. The spirorbid polychaete accounted for almost 75% of total individuals (38,100 counts), and 13 species of bryozoa (1438 individual colonies) were counted. Tiles deployed for 37 months recruited more

individuals (41,786 across 20 taxa), than tiles deployed for 13 months (9,680 across 18 taxa, n=28). Horizontal tiles (n=36) recruited fewer individuals (20,484) from 19 species than vertical tiles (30,982 from 21 species, n=24).

Seven taxa (30% of total taxa observed) were found at all four bays (*Table 3.2*), while eight taxa (35%), one taxon (4%) and seven taxa (30%) were found at three, two and one bay, respectively.

Table 3.2   *Natural recruitment of taxa across all orientations, bays, and times (n=144). BB = Brown Bay, MC = McGrady Cove, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2, 13 = 13 month deployment, 37 = 37 month deployment. Open circles = total counts <10 individuals, solid circles = total counts of 10 or more individuals, no symbol indicates zero counts*

	Horizontal tiles								Vertical tiles					
bays	BB		MC		OB1		OB2		BB		MC		OB1	
deployment period	13	37	13	37	13	37	13	37	13	37	13	37	13	37
sponge			○				●	○			○		○	○
spiral foram	○	○	●	○	○	○	●	●			○	○	○	○
spherical foram	○	●	●	●			●	○	○	○	●	●		
hydrozoans			●											
black polyp									○		●			
spirorbid	●	●	●	●	●	●	●	●	●	●	●	●	●	●
erect spirorbid								○			●	●	○	●
branch tubeworm		●	●	○	●		●			●	●	●	●	●
Aimulosia antarctica											○	○		
Arachnopusia decipiens			●				○				●	●		○
Beania challengeri								○			●	●	●	
Celleporella antarctica	●	●	●	●	○		●	●	●	●	●	●	○	
Ellisina antarctica				○	○		○	●			○	●	●	●
Escharella watersi												○		
Escharoides praestita							○							
Escharoides tridens														
Fenestrulina crystallina			○		○		●	●			○	○	○	
Fenestrulina sp.														
Filaguria spatula								○						
Inversiula nutrix	●	●	●	●	○		●	●	●	●	●	●	●	●
Klugeflustra antarctica								○						
Micropora brevissima			●	○	●		●	○			●	●	●	●
cup bryozoan		●	●	●	●	○	●	●	○	●	●	●	●	●
Chlorophyte		●										●		
Rhodophyte		●		●		●		●		●		●		●
Total number of taxa	**5**	**9**	**13**	**9**	**9**	**4**	**13**	**15**	**6**	**8**	**16**	**16**	**12**	**11**

Of the nine taxa observed on Brown Bay tiles, seven were also found at all three of the other bays, and only one taxon (green alga) was exclusively found at Brown Bay. In addition, of the 16 taxa observed at three or fewer bays, 14 (or 87.5%) were never found at Brown Bay (i.e. were found only at control bays).

A posteriori comparison of multivariate recruitment data for tiles subjected to natural sedimentation indicated that the effect of experimental unit within bays was highly non-significant (PERMANOVA, $F_{3,24}=0.6398$, $P=0.8344$), and subsequent pairwise comparisons were undertaken after *post hoc* pooling of tiles across experimental units within each bay. Due to the low number of unique permutations for each pairwise comparison, Monte Carlo *P*-values were used instead of permutation *P*-values (Anderson, 2005).

A significant interaction between the main effects of orientation, time and bay was apparent (PERMANOVA, $F_{2,36}=2.5408$, $P=0.0100$) and subsequent *a posteriori* pairwise comparisons (PERMANOVA, 9999 permutations) indicated significant differences in recruitment across a variety of groupings (*Table 3.3*).

Recruitment to horizontal and vertical tiles was similar for Brown Bay (after 13 and 37 months) and for McGrady Cove (after 13 months), but was significantly different for the other groups. Highly significant differences between times were apparent for all bays and both tile orientations except for vertical tiles at O'Brien Bay 1 after 37 months. Recruitment to Brown Bay tiles (horizontal and vertical) after 13 and 37 months was significantly different to McGrady Cove and O'Brien Bay 1, and there were also significant differences between recruitment at McGrady Cove compared to O'Brien Bay 1.

Table 3.3   Results of a posteriori pairwise comparisons across orientation, times and bays

(PERMANOVA, 9999 permutations). Data was fourth root transformed using Bray – Curtis

dissimilarity measures, Monte Carlo P-values were used due to low number of unique values (35 in

*each case), BB = Brown Bay, MC = McGrady Cove, OB1 = O'Brien Bay 1, level of significance: ***

*P < 0.05, ** P < 0.01*

Orientation *(horizontal vs. vertical tiles*

Groups	13 months		37 months	
	t	*P*	*t*	*P*
BB	1.6778	0.0806	1.1936	0.2678
MC	1.6153	0.0837	2.1735	0.0264*
OB1	1.9496	0.0356*	3.2198	0.0026**

Time *(13 months vs. 37 months)*

Groups	Horizontal tiles		Vertical tiles	
	t	*P*	*t*	*P*
BB	3.6001	0.0017**	3.7221	0.0011**
MC	2.6931	0.0040**	2.3682	0.0084**
OB1	3.5881	0.0015**	1.6272	0.0865

Bays

Groups ·	Horizontal tiles - 13months		Vertical tiles -13 months	
	t	*P*	*t*	*P*
BB *vs.* **MC**	2.9269	0.0038**	2.7767	0.0042**
BB *vs.* **OB1**	3.3895	0.0023**	3.1993	0.0030**
MC *vs.* **OB1**	2.3001	0.0148*	1.7827	0.0521

Groups	Horizontal tiles - 37months		Vertical tiles -37 months	
	t	*P*	*t*	*P*
BB *vs.* **MC**	2.1497	0.0148*	2.9679	0.0050**
BB *vs.* **OB1**	4.0094	0.0008**	2.4721	0.0086**
MC *vs.* **OB1**	3.5158	0.0018**	1.8968	0.0418*

Patterns in the multivariate recruitment data are apparent in nMDS space (*Fig.3.2*):

horizontal and vertical tile groupings largely overlap (with the exception of O'Brien Bay 1);

there is almost complete separation of 13 month tiles from 37 month tiles at each bay, and

there is separation of 13 month Brown Bay tiles (vertical and horizontal) from 13 month

tiles at the other bays (*Fig.3.2c*). After 37 months the separation (in nMDS space) is less

apparent for Brown Bay tiles and tiles at the other bays (*Fig.3.2d*).

(a)   **(b)**

(c)   **(d)**
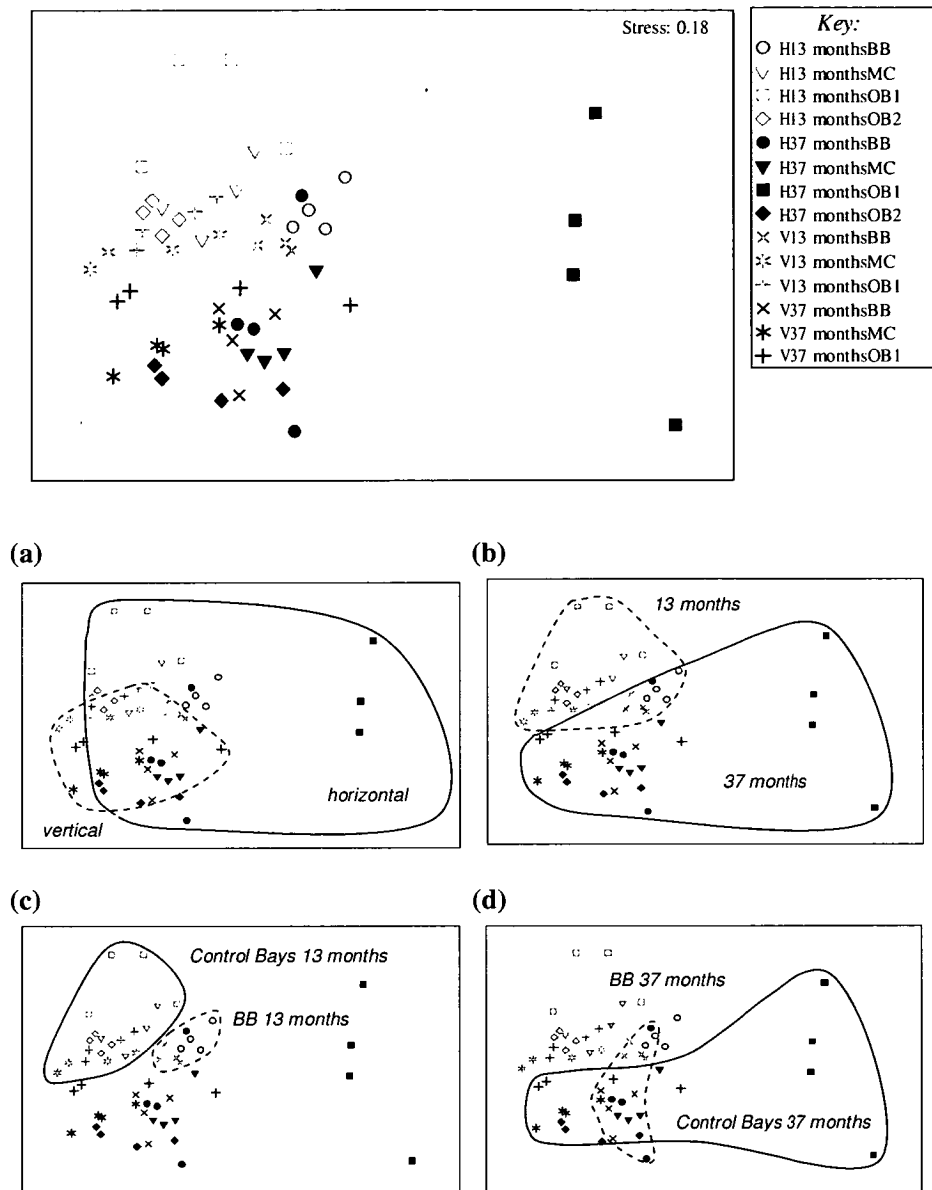
Figure 3.2   nMDS plot of all tiles illustrating significant differences between the main effects,
calculated from 4th root-transformed abundance data, (n=4) - (a) horizontal vs. vertical tiles, (b)
13month tiles vs. 37 month tiles, (c) BB vs. control bays at 13 months, (d) BB vs. control bays at 37
months. H= horizontal tiles, V= vertical tiles, open symbols represent tiles deployed for 13 months,
solid symbols represent tiles deployed for 37 months, BB=Brown Bay, MC=McGrady Cove,
OB1=O'Brien Bay 1, OB2=O'Brien Bay 2. Note that no vertical tiles were deployed at OB2.

Univariate indices - total number of taxa (S), total number of individuals (N), Shannon-Wiener diversity (base e, H') and Pielou's Evenness (J') - varied between bays, tile orientation and deployment time (*Fig.3.3*).

During analysis of variance (ANOVA), the effect of experimental unit within bays was highly non-significant for the number of taxa ($F_{3,24}=0.36$, $P=0.7835$) and the number of individuals ($F_{3,24}=0.64$, $P=0.5969$), and subsequent ANOVA were undertaken after *post hoc* pooling of tiles across experimental units within each bay.

ANOVA identified significant first order interactions (orientation x bay) for the number of taxa (*Table 3.4*) and number of individuals (*Table 3.5*) recruiting to tiles. At Brown Bay there were no significant differences between numbers of taxa nor individuals recruited to horizontal compared to vertical tiles; whereas at McGrady Cove and O'Brien Bay 1, horizontal tiles recruited significantly fewer taxa and individuals than vertical tiles. Significant interactions (deployment time x bay) were also apparent for the number of taxa (*Table 3.4*) with significantly more taxa recruited to tiles at Brown Bay after 37 month deployment (compared to 13 month deployment at Brown Bay) and significantly fewer taxa on 37 month tiles (pooled across orientations) compared to 13 month tiles at McGrady Cove.

Table 3.4   Results of ANOVA for Number of Taxa (experimental units pooled across bay), P<0.05

Source	SS	df	MS	F	P	Error
Orientation	85.33	1	85.33	6.43	0.1266	Orient. x Bay
Time	0.75	1	0.75	0.02	0.9038	Time x Bay
Bay	92.54	2	46.27	22.21	0.0000	Residual
Orient. x Time	4.08	1	4.08	2.68	0.2430	Orient. x Time x Bay
Orient. x Bay	26.54	2	13.27	6.37	0.0043	Residual
Time x Bay	60.37	2	40.19	19.29	0.0000	Residual
Orient. x Time x Bay	3.04	2	1.25	0.73	0.4889	Residual
Residual	75.00	36	2.08			
Total	367.67	47				

Table 3.5   Results of ANOVA for Number of Individuals (experimental units pooled across bay), transformed Sqrt (X+1), P<0.05

Source	SS	df	MS	F	P	Error
Orientation	2720.17	1	2720.17	8.07	0.1048	Orient. x Bay
Time	2569.03	1	2569.03	10.22	0.0855	Time x Bay
Bay	1682.33	2	841.16	8.41	0.0010	Residual
Orient. x Time	350.89	1	350.89	2.16	0.2796	Orient. x Time x Bay
Orient. x Bay	674.10	2	337.05	3.37	0.0455	Residual
Time x Bay	502.69	2	251.34	2.51	0.0951	Residual
Orient. x Time x Bay	325.32	2	162.66	1.63	0.2107	Residual
Residual	3599.91	36	99.99			
Total	12424.43	47				

Diversity and evenness indices were calculated for each experimental unit rather than for each tile. ANOVA identified significant first order interactions (orientation x bay) for Shannon-Wiener diversity (H') (*Table 3.6*) and Pielou's evenness (J') (*Table 3.7*). At Brown Bay and McGrady Cove, H' and J' were not significantly different between tile orientations, whereas at O'Brien Bay 1, H' and J' for vertical tiles was less than that for horizontal tiles. In addition, H' and J' were significantly lower for horizontal tiles deployed at Brown Bay compared to horizontal tiles deployed at the other bays.

Table 3.6   Results of ANOVA for Shannon-Wiener Diversity (experimental units pooled across bay), untransformed, P<0.01

Source	SS	df	MS	F	P	Error
Orientation	0.15	1	0.25	1.35	0.3657	Orient. x Bay
Time	0.03	1	0.06	4.78	0.1604	Time x Bay
Bay	0.34	2	0.10	32.69	0.0000	Residual
Orient. x Time	0.00	1	0.02	2.39	0.2621	Orient. x Time x Bay
Orient. x Bay	0.32	2	0.19	62.75	0.0000	Residual
Time x Bay	0.30	2	0.01	3.84	0.0514	Residual
Orient. x Time x Bay	0.02	2	0.01	3.44	0.0660	Residual
Residual	0.17	12	0.00			
Total	1.33	23				

Table 3.7   Results of ANOVA for Pielou's Evenness (experimental units pooled across bay), untransformed, P<0.01

Source	SS	df	MS	F	P	Error
Orientation	0.25	1	0.25	1.35	0.3657	Orient. x Bay
Time	0.06	1	0.05	4.78	0.1604	Time x Bay
Bay	0.20	2	0.10	32.69	0.0000	Residual
Orient. x Time	0.02	1	0.02	2.39	0.2621	Orient. x Time x Bay
Orient. x Bay	0.38	2	0.19	62.75	0.0000	Residual
Time x Bay	0.02	2	0.01	3.84	0.0514	Residual
Orient. x Time x Bay	0.02	2	0.01	3.44	0.0660	Residual
Residual	0.04	12	0.00			
Total	0.98	23				

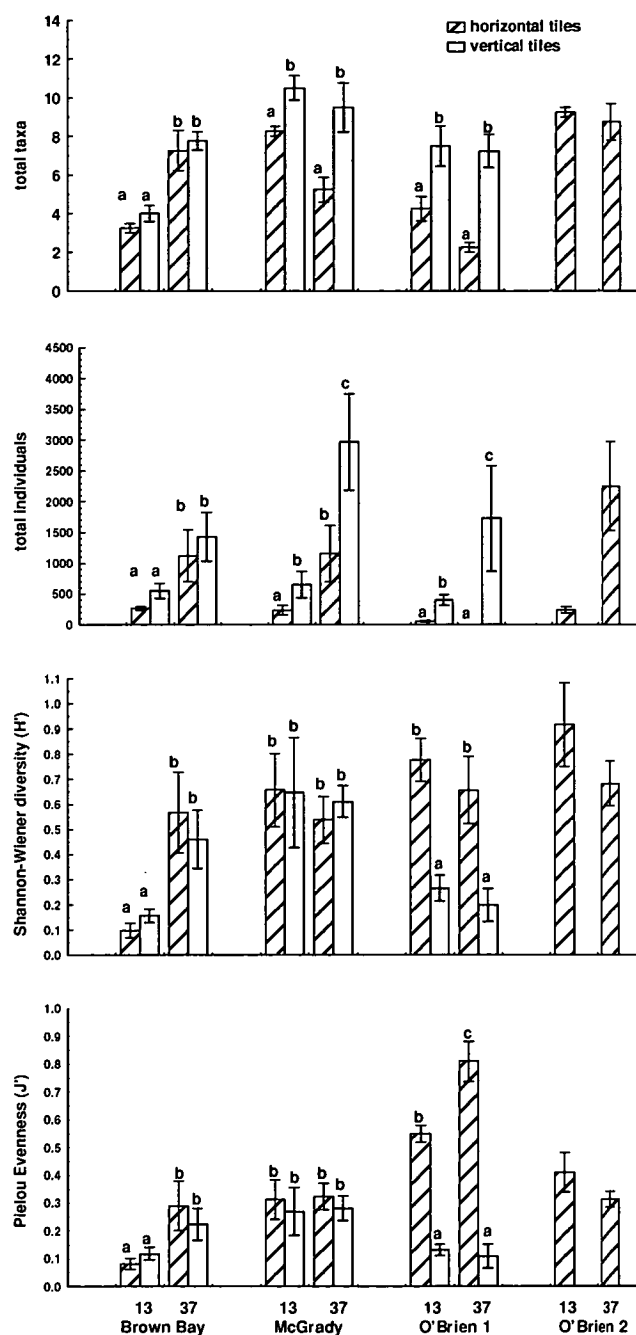*Figure 3.3   Mean number of taxa and individuals per tile (n=4) and mean diversity (H' base e) and evenness (J') per experimental unit (n=2) per bay for recruitment to tiles (±SE). '13' and '37' refer to tiles deployed for 13 months and 37 months, respectively. Within each bay, letters above bars refer to groupings designated by Tukey HSD results where bars with similar letters are not significantly different*

Significant interactions (deployment time x bay) were also apparent for Shannon-Wiener diversity (H') *(Table 3.6)* and Pielou's evenness (J') *(Table 3.7)*. At Brown Bay, H' and J' were significantly lower for tiles deployed for 13 months (pooled across orientations) compared to tiles deployed for 37 months, whereas at McGrady Cove and O'Brien Bay 1 there were no significant differences between the two deployment times.

A priori comparisons indicated that the mean number of taxa (5.56, n=16) and the mean number of individuals (422.2) recruiting to tiles in Brown Bay (pooled across both orientations and deployment times) was significantly less ($F_{1,32}$=*135.22*, *P<0.01*, $F_{1,32}$=*25,572.42*, *P<0.01*,respectively) than the combined mean number of taxa (11.75, n=32) and individuals (1114.2) recruiting to tiles in McGrady Cove and O'Brien Bay 1. No differences in Shannon-Wiener diversity and Pielou's evenness (pooled across orientations and deployment times) were apparent for total taxa between Brown Bay and the control bays.

Bryozoan taxa

Bryozoan species abundances varied between bays *(Table 3.2)* with the least number of species at Brown Bay (3 species) and the most at O'Brien Bay 2 (10 species).

The mean number of bryozoan species (2.25, n=16) and individuals (9.81) recruiting to tiles in Brown Bay (across both tile orientations and deployment periods) were significantly less ($F_{1,32}$=*8.75*, *P<0.01*, $F_{1,32}$=*2653.44*, *P<0.01*,respectively) than the combined mean number of species (3.78, n=32) and individuals (25.75) for McGrady Cove and O'Brien Bay 1 (*a priori* comparisons). Neither mean Shannon-Wiener diversity nor Pielou's evenness calculated for each experimental unit in Brown Bay differed significantly from the mean at the control bays.

Three species (20% of total number of bryozoan species) were found at all bays, five species (33%) at three bays, and five species (33%) at one bay only. All three bryozoan species found at Brown Bay were also found at all other bays. *Inversiula nutrix* was the most abundant bryozoan species counted at each time and tile orientation combination, with

Celleporella antarctica and the unidentified cup bryozoan also being common across the bays.

Significant interactions between orientation, times and bays were apparent for the number of bryozoan species and between orientation and bay for individuals recruited to tiles (Tables 3.8 and 3.9, respectively). After 13 months deployment, the number of bryozoan species and individuals that recruited to horizontal tiles was significantly fewer than those recruited to vertical tiles at both Brown Bay and McGrady Cove whereas at O'Brien Bay 1 the number of bryozoan species and individuals per tile was similar for horizontal and vertical tiles. After 37 months, horizontal tiles at Brown Bay had significantly more bryozoan species and individuals than vertical tiles whereas no differences were apparent between tile orientations at the other two bays.

Table 3.8   Results of ANOVA for Bryozoa Species (P<0.05)

Source	SS	df	MS	F	P	Error
Orientation	15.19	1	15.19	3.98	0.1841	Orient. x Bay
Time	2.52	1	2.52	0.26	0.6600	Time x Bay
Bay	37.04	2	18.52	15.60	0.0000	Residual
Orient. x Time	35.02	1	35.02	2.50	0.2548	Orient. x Time x Bay
Orient. x Bay	7.62	2	3.81	3.21	0.0521	Residual
Time x Bay	19.29	2	9.65	8.12	0.0012	Residual
Orient. x Time x Bay	28.04	2	14.02	11.81	0.0001	Residual
Residual	42.75	36	1.19			
Total	187.48	47				

Table 3.9   Results of ANOVA for Bryozoa Individuals (transformed sqrt(X+1), P<0.05)

Source	SS	df	MS	F	P	Error
Orientation	2720.17	1	2720.17	8.07	0.1048	Orient. x Bay
Time	2569.03	1	2569.03	10.22	0.0855	Time x Bay
Bay	1682.33	2	841.16	8.41	0.0010	Residual
Orient. x Time	350.89	1	350.89	2.16	0.2796	Orient. x Time x Bay
Orient. x Bay	674.10	2	337.05	3.37	0.0455	Residual
Time x Bay	502.69	2	251.34	2.51	0.0951	Residual
Orient. x Time x Bay	325.32	2	162.66	1.63	0.2107	Residual
Residual	3599.91	36	100.00			
Total	12424.45	47				

Macroalgal Recruits

Despite spirorbid polychaetes accounting for between 43% and 97% of total individuals, rhodophyte basal discs outnumbered spirorbids on horizontal tiles after 37 months at McGrady Cove, O'Brien Bay 1 and O'Brien Bay 2 (63% *cf.* 33%; 46% *cf.* 42%

and 53% *cf.* 43% of total individuals, respectively). At each bay, rhodophyte basal discs were only present on tiles that had been deployed for 37 months, and were more common (pooled across all bays) on horizontal tiles (mean: 417 per tile) compared to vertical tiles (mean: 285 per tile).

Taxonomic Groupings

SIMPER analysis identified the spirorbid polychaetes, rhodophyte basal discs, and two species of bryozoa (*Inversiula nutrix*, and the unidentified 'cup bryozoan') as the main taxa responsible for differences between times and bays. Mean numbers of recruits within major taxa groupings varied between tile orientations, deployment times and bay (*Fig.3.4*).

ANOVA indicated significant second order interactions (tile orientation x deployment time x bay) for polychaetes ($F_{2,36}=9.36$, $P=0.0005$), with numbers of polychaetes increasing over time on horizontal tiles at Brown Bay and O'Brien Bay 2 and on vertical tiles at all bays, while polychaete numbers decreased over time on horizontal tiles at O'Brien Bay 1.

Rhodophyte basal discs exhibited significant time x bay interactions ($F_{2,36}=10.79$, $P=0.0002$), with more basal discs apparent on tiles (both orientations) deployed for 37 months at Brown Bay and McGrady Cove than those deployed for 13 months. Basal disc counts were similarly low for tiles at O'Brien Bay 1 from both deployment periods. Higher counts of basal discs were also apparent on horizontal tiles at O'Brien Bay 2 after 37 months but this bay was excluded from the ANOVA due to the absence of vertical tiles at this bay and consequently significance was not assessed.

The number of bryozoa exhibited a significant second order interaction for the main effects of orientation, deployment time and bay ($F_{2,36}=4.73$, $P=0.0149$). Bryozoa became less abundant over time on horizontal tiles at O'Brien Bay 1 but remained similar at Brown Bay and McGrady Cove; abundance was not significantly different between deployment times for vertical tiles at any bay due to high variability. After a 37 month deployment, horizontal tiles (pooled across all bays) had fewer numbers of bryozoa than vertical tiles.

(a) Horizontal Tiles
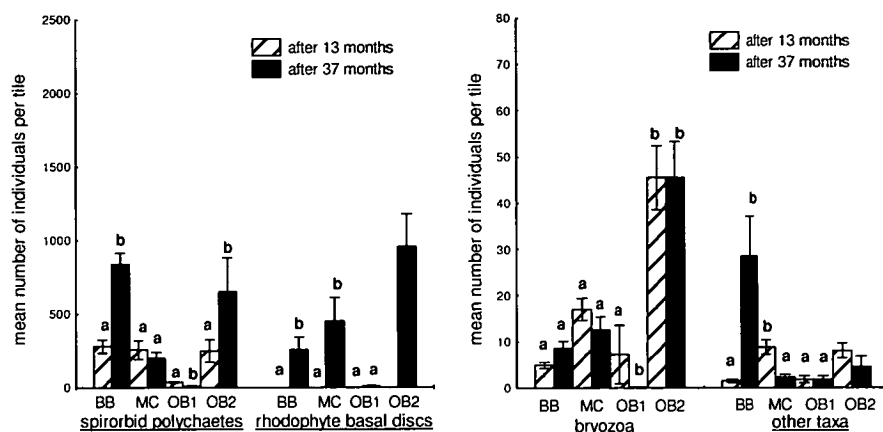
(b) Vertical Tiles
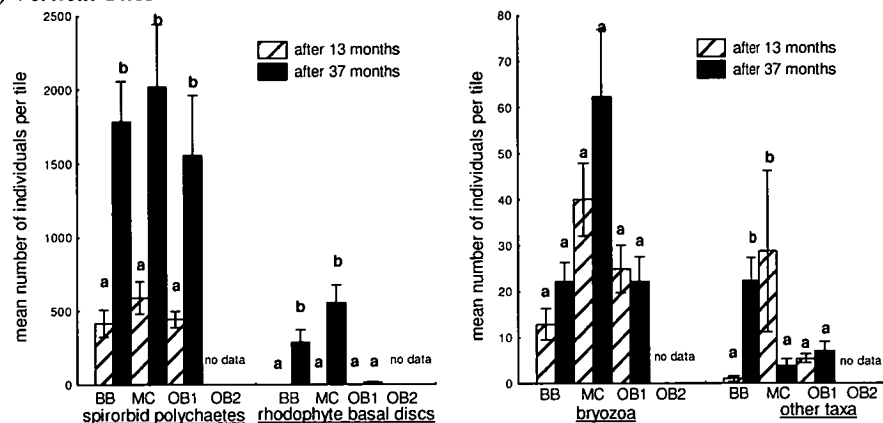
Figure 3.4   Mean abundance of major taxa groupings recruiting at each bay over time on (a) horizontal tiles, and (b) vertical tiles (n=4, ±SE). 'other taxa' include sponges, foraminifera, hydroids and green alga, BB=Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1, OB2=O'Brien Bay 2. For each bay, letters above bars refer to groupings designated by Tukey HSD results where bars with similar letters are not significantly different

Abundance of 'other taxa' exhibited a significant time x bay interaction ($F_{2,36}=35.27$, $P<0.0001$), with increases on vertical and horizontal tiles over time at Brown Bay and decreases over time at McGrady Cove; abundances were unchanged at O'Brien Bay 1.

Experiment 2: Effects of sedimentation on recruitment

Sedimentation monitoring

Overall, sedimentation rates exhibited a significant time x bay effect ($F_{2,36}=9.72$, $P=0.0411$), with the 'natural' rate of sedimentation entering Brown Bay being significantly higher (mean = 5.03 g.m^{-2}.day^{-1}, $n=48$) than at McGrady Cove (mean = 3.83 g.m^{-2}.day^{-1}) and sedimentation at both bays significantly higher than at O'Brien Bay 1 (mean = 1.72 g.m^{-2}.day^{-1}). Of the four sediment periods sampled (*Fig.3.5*), the period from Dec.02 – Feb.03 had significantly more sediment input at all three bays (mean = 4.5 g.m^{-2}.day^{-1}), and the period from Feb.03 – Nov.03 had the least (mean = 2.72 g.m^{-2}.day^{-1}). The first occasion when tiles were sampled was at the end of the 'third' sediment period (Feb.04), and therefore the average sediment loading across those first three periods (mean = 5.05 g.m^{-2}.day^{-1}) represents the average sediment loading of the 13 month tiles. Collection of the remaining tiles after 37 months (Jan.06) coincided with the end of the fourth sediment period (mean = 4.04 g.m^{-2}.day^{-1}). Note that because of logistical constraints to access to the bays in the summer of 2004/05, the second 'winter' period actually includes two winters and a summer (~740 days).
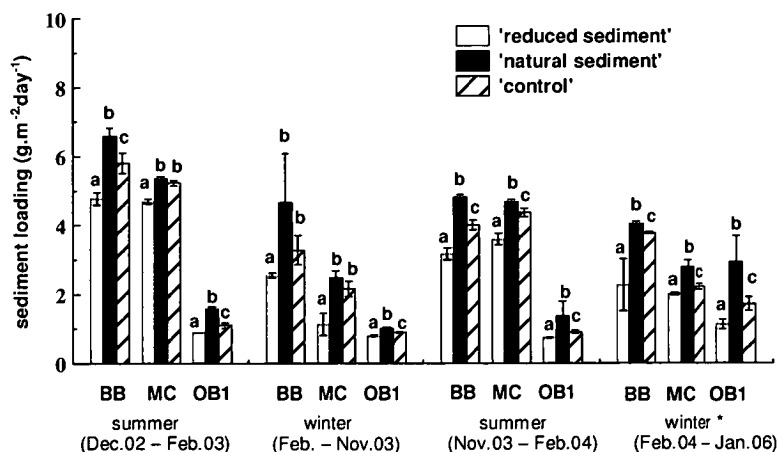
Figure 3.5   Sediment loads measured for each bay and treatment combination within the four time periods (±SE, n=4). Note that the second winter time period (*) includes two winters and the intervening summer. BB=Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1. For each bay within sampling period, the letters above the bars refer to groupings designated by Tukey HSD results where bars with similar letters are not significantly different

Despite evidence of some advection of sediments onto the 'shielded' tiles, accumulated sediment within the treatments at all time and bay combinations (*Fig.3.5*) revealed a significant treatment effect ($F_{6,72}=2.5243, P=0.0370$) in that the sediment load on tiles within 'reduced sedimentation' treatments at all bays was significantly less than that reaching tiles in 'natural sedimentation' and 'experimental control' treatments. Tiles within the 'experimental control' treatment were also exposed to significantly less sediments than tiles within the 'natural sedimentation' treatment at most bays.

A posteriori comparison of multivariate recruitment data for tiles within the sediment treatments indicated that the effect of experimental unit within bays was highly non-significant (PERMANOVA, $F_{3,48}=1.0219$, $P=0.4467$), and subsequent pairwise comparisons were undertaken after *post hoc* pooling of tiles across experimental units within each treatment in each bay. Due to the low number of unique permutations for each pairwise comparison, Monte Carlo *P*-values were used (Anderson 2005).

Significant interactions (PERMANOVA) were apparent between the main effects of deployment time, bay and sediment treatment for multivariate community structure on horizontal tiles ($F_{6,72}=2.0443$, $P=0.0036$) and *a posteriori* pairwise comparisons (PERMANOVA, 9999 permutations) indicated significant differences in recruitment across a variety of groupings (*Table 3.10*).

Highly significant differences between tiles deployed for 13 and 37 months were observed for all bay and treatment combinations. Similarly, significant differences between each bay pair were apparent within each time x treatment combination, with the exception of McGrady Cove *vs.* O'Brien Bay 2. Importantly, significant differences in multivariate recruitment to tiles within the reduced sediment *vs.* natural sediment treatments were only apparent at Brown Bay after 13 months deployment. However, significant differences were also indicated for reduced sediment *vs.* control treatments at Brown Bay and McGrady Cove after 13 months.

Table 3.10   *Results of a posteriori pairwise comparisons across times, bays and sediment treatments (PERMANOVA, 9999 permutations). Data was fourth root transformed using Bray – Curtis dissimilarity measures, Monte Carlo P-values were used due to low number of unique values (35 in each case), BB = Brown Bay, MC = McGrady Cove, OB1 = O'Brien Bay 1, OB2 = O'Brien Bay 2 Level of significance: * P < 0.05, ** P < 0.01*

Time *(13 months vs. 37 months)*

Groups	Reduced Sediment		Natural Sediment		Control	
	t	P	t	P	t	P
BB	4.0224	0.0013**	3.6916	0.0011**	3.6370	0.0013**
MC	3.1526	0.0028**	2.6931	0.0030**	3.7138	0.0020**
OB1	3.6008	0.0021**	3.5881	0.0013**	2.3455	0.0128*
OB2	2.0891	0.0252*	2.6751	0.0041**	2.6516	0.0051**

Bays
After 13 months

Groups	Reduced Sediment		Natural Sediment		Control	
	t	P	t	P	t	P
BB *vs.* **MC**	2.8105	0.0053**	2.9269	0.0038**	3.3214	0.0023**
BB *vs.* **OB1**	5.1185	0.0010**	3.3865	0.0022**	2.8898	0.0055**
BB *vs.* **OB2**	2.4962	0.0091**	3.8851	0.0006**	3.0833	0.0500
MC *vs.* **OB1**	2.9761	0.0042**	2.3001	0.0130*	3.1612	0.0025**
MC *vs.* **OB2**	1.5699	0.0956	1.1960	0.2611	1.6237	0.0660
OB1 *vs.* **OB2**	2.8254	0.0044**	2.3915	0.0085**	2.9870	0.0033**

After 37 months

Groups	Reduced Sediment		Natural Sediment		Control	
	t	P	t	P	t	P
BB *vs.* **MC**	2.6162	0.0099**	2.1106	0.0256*	2.7235	0.0050**
BB *vs.* **OB1**	3.3606	0.0022**	4.0916	0.0008**	3.3025	0.0020**
BB *vs.* **OB2**	2.7028	0.0101*	3.1021	0.0041**	2.2137	0.0211*
MC *vs.* **OB1**	2.6483	0.0105*	3.5158	0.0013**	2.8412	0.0062**
MC *vs.* **OB2**	1.2768	0.2164	1.6230	0.0745	3.1963	0.0040**
OB1 *vs.* **OB2**	2.4732	0.0123*	3.9496	0.0008**	3.5657	0.0019**

Sediment Treatments

Groups	Reduced vs. Natural		Reduced vs. Control		Natural vs. Control	
	t	P	t	P	t	P
BB – 13 months	2.2413	0.0296*	2.0101	0.0425*	1.0322	0.3835
BB – 37 months	1.0782	0.3439	0.9680	0.4225	1.3554	0.1835
MC – 13 months	1.1216	0.3129	2.0109	0.0317*	1.1992	0.2543
MC – 37 months	1.0098	0.4064	1.5344	0.1075	1.7742	0.0670
OB1 – 13 months	1.7486	0.0564	1.6741	0.0806	1.2922	0.1962
OB1– 37 months	1.1050	0.3445	1.0820	0.3453	1.1299	0.3120
OB2 – 13 months	1.2437	0.2323	1.5068	0.1320	0.9033	0.4859
OB2 – 37 months	1.8852	0.0557	1.7772	0.0802	0.5888	0.7782

Mean number of taxa

Univariate analysis (ANOVA) of mean number of taxa recruiting to tiles *(Fig.3.6a)*

identified a highly significant time x bay interaction *(Table 3.11)* and bay x treatment

interaction. Across all sediment treatments, significantly more taxa recruited to Brown Bay

tiles after 37 months deployment compared to tiles deployed for 13 months *(P<0.01)*

whereas at all other bays, the number of taxa recruiting to tiles was significantly greater

(P<0.01) at 13 months than at 37 months.

Table 3.11   Results of ANOVA for Mean Number of Taxa – Horizontal Tiles (P<0.05)

Source	SS	df	MS	F	P	Error
Time	17.51	1	17.51	0.43	0.5572	Time x Bay
Bay	301.61	3	100.54	63.36	0.0000	Residual
Treatment	0.02	2	0.01	0.00	0.9983	Bay x Treatment
Time x Bay	121.11	3	40.37	25.44	0.0000	Residual
Time x Treatment	3.52	2	1.76	0.83	0.4807	Time x Bay x T'ment
Bay x Treatment	37.73	6	6.29	3.96	0.0018	Residual
Time x Bay x T'ment	12.73	6	2.12	1.34	0.2521	Residual
Residual	114.25	72	1.59			
Total	608.49	95				

At Brown Bay, significantly more taxa recruited to tiles exposed to 'reduced

sediment' compared to tiles exposed to either a 'natural sediment' regime or the 'control'

treatment *(P<0.05)*. At McGrady Cove and O'Brien Bay 1, the number of taxa recruiting

to tiles was similar for all sediment treatments, whereas after 37 months at O'Brien Bay 2,

fewer taxa recruited to tiles within the 'reduced sediment' treatment compared to tiles

within either the 'natural sediment' or 'control' treatments *(P<0.05)*.

Mean number of individuals

Univariate analysis (ANOVA) of mean number of individuals recruiting to tiles

(Fig.3.6b) identified a highly significant time x bay x treatment interaction *(Table 3.12)*.

After 13 months of deployment, the number of individuals recruited to tiles was similar

within each of the three sediment treatments at Brown Bay, O'Brien Bay 1 and O'Brien

Bay 2; however, fewer individuals recruited to tiles within the 'reduced sediment' treatment

compared to the other treatments at McGrady Cove.

After a 37 month deployment period, a similar number of individuals recruited to tiles within the three sediment treatments at both Brown Bay and O'Brien Bay 1, whereas fewer individuals recruited to tiles within the 'control' treatment at McGrady Cove and the 'reduced sediment' treatment at O'Brien Bay 2, compared to the other treatments at each bay.

(a)

(b)

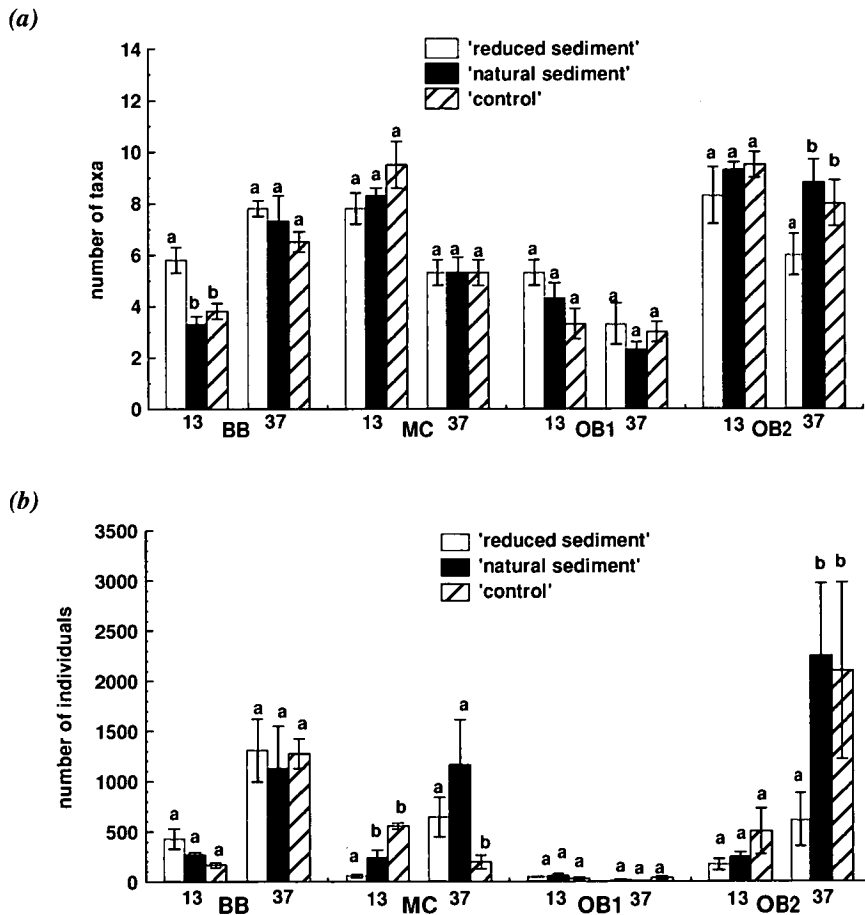*Figure 3.6   Mean number of (a) taxa and (b) individuals recruiting to horizontal tiles within three sediment treatments deployed for 13 and 37 months at Brown Bay (BB), McGrady Cove (MC), O'Brien Bay 1 (OB1) and O'Brien Bay 2 (OB2) (n=4, ±SE). For each deployment time at each bay, letters above bars refer to groupings designated by Tukey HSD results; bars with similar letters are not significantly different*

Table 3.12   Results of ANOVA for Mean Number of Individuals (transformed Ln(X+1), P<0.05)

Source	SS	df	MS	F	P	Error
Time	10.76	1	10.76	1.06	0.3790	Time x Bay
Bay	169.39	3	56.46	99.97	0.0000	Residual
Treatment	2.58	2	1.29	1.01	0.4179	Bay x Treatment
Time x Bay	30.47	3	10.16	17.98	0.0000	Residual
Time x Treatment	0.01	2	0.01	0.00	0.9991	Time x Bay x T'ment
Bay x Treatment	7.65	6	1.27	2.26	0.0472	Residual
Time x Bay x T'ment	22.38	6	3.73	6.60	0.0000	Residual
Residual	40.67	72	0.56			
Total	283.92	95				

Discussion:

The overall rate of recruitment to artificial hard substrata was variable between bays and was considered to be relatively slow compared to temperate recruitment. Only 5-20% of available tile surfaces were colonised by sessile invertebrates after 37 months. Recruiting assemblages were numerically dominated by spirorbid polychaetes and encrusting bryozoan species, indicating that these faunal groups are opportunistic recruiters in Antarctic coastal waters. These recruitment patterns along the Windmill Islands coast are similar to findings from studies utilising artificial substrata elsewhere in the Antarctic (Dayton 1989, Pearse & Pearse 1991, Bowden 2005b, Webster *et al.* 2006). The wide distribution of these few studies around the Antarctic (i.e. at longitudes 110°E, 170°E, and 68°W), and the range in latitude at which the studies were conducted (between 66°S and 75°S), lend support to a circum-Antarctic trend of relatively slow recruitment to hard substrata in shallow marine environments.

Recruitment patterns

Taxa observed on tiles after 13 month deployment in late summer must have recruited to tiles during winter or early summer. Bowden (2005b) suggests that invertebrate taxa recruit throughout the year following predictable annual patterns, concluding that the larvae of many common sessile taxa preferentially settle during winter in order to commence growth (feeding on nanoplankton) and attain a size that allows them to utilise the summer blooms of larger phytoplankton. Stanwell-Smith & Barnes (1997) also report late winter to early summer recruitment peaks for Antarctic cheilostome

bryozoans. Such patterns of recruitment likely explain the abundance of spirorbids and bryozoan species in assemblages on tiles deployed for the 13 month period in the Windmill Islands region.

Bryozoan species (15) accounted for more than half of all taxa (25) in the recruiting assemblages. However, almost half of the bryozoan species were rare in that their total counts did not exceed 10 individuals (indeed, most of the rare species were only counted once or twice across 144 tiles). Only four bryozoan species, *Celleporella antarctica, Inversiula nutrix, Micropora brevissima,* and an unidentified "cup bryozoan" had mean abundances exceeding one colony per tile. Similarly, on the Antarctic Peninsula, Bowden (2005b) found 17 species of cheilostome bryozoans out of 32 taxa recruiting to his acrylic panels deployed into 8 m at several locations, and more than half of these were counted infrequently. Barnes & Arnold (2001) studied growth rates of the most common species of bryozoans along a latitudinal gradient on the Antarctic Peninsula, and concluded that, compared with temperate species, Antarctic bryozoa grow up to one order of magnitude more slowly.

Most previous recruitment studies in the Antarctic have deployed artificial substrata for 12 months; however this study continued the observation period to 37 months. Interestingly, the longer recruitment period only resulted in an increase in the number of individuals of most species already present after 13 months; a pattern that has been commonly observed (Connolly & Roughgarden 1999) and suggests that for the period of observation (13 – 37 months), competition between species that have already settled on hard substrata is not an important factor in community development at these study locations. Spirorbid polychaetes and bryozoan species remained numerically dominant members of the sessile community with mean increases in abundance per tile over the period 13-37 months after tile deployment of 236% and 30%, respectively.

Recruitment of macroalgae in the Windmill Islands was slower than for invertebrates. None of the rhodophyte and chlorophyte recruits were present on tiles deployed for 13 months. The number of rhodophyte basal discs (some with short shoots)

exceeded the spirorbid polychaetes on many tiles collected after 37 months. The total absence of these basal discs on tiles deployed for 13 months suggests either a time lag or inter-annual variability in the recruitment of macroalgae to available hard substrata. These basal discs are thought to be early stages of *Palmaria decipiens* which grows abundantly on natural hard substrata in the region. The lifecycle of *P.decipiens* includes a gametophyte stage that requires two seasons to develop male gametes, followed by a sporophyte stage (Wiencke & Clayton 2002), which may contribute to the observed delay in recruitment. Interestingly, this alga recruited to tiles at all bays despite the complete absence of adult algae at any of the bays; the closest known algal beds were ~3 km distant from several of the tile deployment sites. Therefore, this particular species must undertake broad scale dispersal of reproductive cells.

Recruitment to horizontal and vertical tiles differed at each bay, with significantly more individuals found on vertical tiles. This pattern is typical of similar studies in temperate locations (Glasby 2000, Glasby & Connell 2001). This is the first report of the affect of surface orientation on recruitment to hard substrata in Antarctica because other studies of recruitment in the Antarctic either only looked at horizontal surfaces (Bowden 2005b), or did not specify the orientation of substrata (Pearse & Pearse 1991, Webster *et al.* 2006). In the Windmill Islands, two species of bryozoa (*Aimulosia antarctica*, *Escharella watersi*) were only found on vertical tiles, as was the unidentified black polyp, but the overall diversity was not significantly different between tiles of different orientations.

The supply of recruits to available substrata is long recognised as being highly variable (e.g. Underwood & Fairweather 1989), yet vital to the establishment and maintenance of sub tidal marine communities. In the past, it has been suggested that many Antarctic benthic species have relatively short planktonic life stages or are brooders, and consequently that larvae (or juveniles) are dispersed over short distances (Thorson 1950, Holme 1962, Clarke 1996). However, recent studies of Antarctic plankton (e.g. Stanwell-Smith *et al* 1999, Freire *et al.* 2006) have identified large numbers of planktotrophic larvae; suggesting that long distance dispersal of larvae is not as uncommon among Antarctic

species as first thought. Indeed, results from the Windmill Islands indicate that juveniles of species (e.g. the annual rhodophyte, *Palmaria decipiens*) were commonly detected on recruitment tiles in bays where adults were not observed, and therefore are able to recruit to newly available substrata over distances of several kilometres or more from the nearest source of reproduction.

Sediment impacts

Sedimentation rates were significantly reduced at all bays through using Plexiglas shields, yet significant increases in total number of taxa in response to reduced sedimentation was only apparent at Brown Bay. This suggests that a reduction in sediment loading in Brown Bay could potentially allow more species to recruit to available hard substrata than are currently recruiting under 'natural' sediment loads, and/or sediment loads at bays other than Brown Bay are not sufficient to cause reduced diversity in recruitment. Clearly, sediment is causing a measurable effect on recruitment to hard substrata in Brown Bay but not at other bays.

Brown Bay had a relatively depauperate community recruiting to the tiles, with fewer overall species, and fewer bryozoan species than the other bays after 13 months. Only the most common taxa were found on tiles from Brown Bay, except for the single chlorophyte species (which was found only at Brown Bay). Natural sediment loading in Brown Bay was measured as 30% higher than in McGrady Cove, and 190% higher than in O'Brien Bay 1. Consequently, recruitment at Brown Bay was slower than at other bays, with the number of taxa recruiting to tiles in Brown Bay increasing over the 37 month deployment period whereas the number of tax stayed approximately similar over the same time period at the other bays, and diversity (H') and evenness (J') indices for Brown Bay were significantly lower after 13 months compared to the other bays and only reached similar values after 37 months.

O'Brien Bay 1 was exceptional in that it had fewer individuals than the other three bays, despite a lower sedimentation regime. This difference could be due in part to the noticeably higher diatom cover observed at this site compared to the other sites

(unpublished data). At the times of collection, tiles were heavily covered with diatoms

(mainly *Achnanthes* sp., *Nitzschia stellata, Trigonium arcticum, Trachyneis aspera* - Scott

& Marchant 2005) that could have prevented settlement of new recruits, and/or smothered

those already attached. Indeed, it is likely that significantly lower sediment loading (and

higher benthic irradiation) within O'Brien Bay may assist the growth of benthic diatoms

which in turn hinders the recruitment of invertebrates. Webster *et al.* (2006) suggest that

reduced diversity of recruits at one of their bays could be attributed to the observed higher

diatom abundance which out-competed other recruits for available space.

Sedimentation is often stated as a reason why vertical surfaces recruit richer

assemblages than horizontal surfaces (Irving & Connell 2002). Sediment does not settle as

readily on vertical surfaces and therefore is certainly less likely to smother individuals.

This study shows that very few species are specifically targeting vertical over horizontal

surfaces. Yet, even at sites where sedimentation rates are low (e.g. O'Brien Bay 1), there

are measurable differences between horizontal and vertical surfaces (i.e. sponges and the

erect bryozoan, *Beania challengeri* were only observed on vertical tiles at OB1). Assuming

that the low rates of sedimentation at O'Brien Bay 1 had little effect on recruitment, this

suggests that observed differences between substratum orientation cannot be totally

explained by sedimentation pressures, and that some taxa are preferentially selecting

vertical surfaces (Glasby 2000, Glasby & Connell 2001). Other reasons for actively

selecting vertical surfaces might be avoidance of direct light, or avoidance of competition

with taxa that actively seek well lit areas (e.g. diatoms), or in polar regions, to avoid the

effects of ice scour. Algal recruits tended to preferentially settle on horizontal surfaces

where irradiance levels are presumably more conducive for growth.

The absence of large river discharges in Antarctica, which is a common feature of the

Arctic, keeps sedimentation rates naturally low (e.g. 1.7 to 5.1 $g.m^{-2}.day^{-1}$ in the Windmill

Islands). However, localised events can and do cause significant sediment loading of

benthic assemblages in the Antarctic (Slattery & Bockus 1997). Similar events have been

observed at bays in the Windmill Islands, where the destabilisation and subsequent collapse

of ice cliffs in the summer months cause shock waves through sea ice and water that lead to resuspension of marine sediments on the scale of hundreds of metres (unpublished data). Such events, while undoubtedly common, are probably not as significant as the continuous input of anthropogenically elevated sediment loads at places such as Brown Bay which occur over many weeks every summer.

Conclusion:

Recruitment of rarer species to artificial substrata varies between bays while most of the abundant species recruit at consistent densities across scales of tens of kilometres. It is likely that the success of these more common species in recruiting to available substrata is directly related to their propensity for broadcast reproductive strategies.

The recruitment trends identified in this study suggests that researchers should be cautious about concluding too much about recruitment patterns from experiments that are undertaken over periods of 12 months or less. Recruitment in Antarctic waters is slow and, while potential sediment-induced effects were identified over the short term (13 months), the longer term trends do not follow the same patterns. Nonetheless, this study has shown that an elevated sedimentation rate in Antarctica, in this instance associated with human activities, can reduce the diversity of sessile species recruiting to hard substrata.

Chapter 4
Effects of sedimentation and irradiation on spore settlement and early post-settlement gametophyte growth of *Himantothallus grandifolius* (Desmarestiales, Phaeophyceae) in Antarctica

Abstract:

Elevated sedimentation rates and low benthic irradiance levels are known to affect development of macroalgal assemblages, with the most susceptible stage likely to be at settlement and initial growth of sporelings. However, the influence of sedimentation and irradiance on Antarctic macroalgae is unknown. The zoospore settlement success and early post-settlement growth of an endemic Antarctic brown alga, Himantothallus grandifolius *(Desmarestiales, Phaeophyceae), were assessed in laboratory experiments using 'contaminated' and 'clean' sediments under a variety of sedimentation and irradiance levels. The presence of a layer of sediment as little as 0.5 mm thick effectively prevented spores from attaching successfully to the substratum irrespective of sediment quality and levels of irradiance. Furthermore, spores were able to attach to glass substrata in areas where sediments were disturbed, and they successfully extended germ tubes even when sediments (contaminated or otherwise) were immediately adjacent to the site of attachment. Smothering of attached early stage gametophytes by a thin layer of sediment significantly reduced the growth rate of germ tubes compared to gametophytes not smothered. A distinct increase in the growth of gametophyte germ tubes occurred when irradiance levels reached 12 $\mu mol\ photons.m^{-2}.sec^{-1}$, suggesting a potential threshold irradiance level necessary for significant growth of* H.grandifolius *gametophytes. Overall, the results indicate that the sedimentation regime is likely to be a significant determinant in the development of macroalgal assemblages in Antarctic nearshore environments.*

Introduction:

Elevated sedimentation rates are recognised as an increasing threat to coastal marine communities (Rogers 1990, Fabricius 2005). Research into the effects of elevated sedimentation at some locations in the Mediterranean has shown a shift in macroalgal communities towards turf-dominated assemblages that are able to withstand increased sediment loads (Airoldi 1998, Airoldi & Virgilio 1998, Balata *et al.* 2005), suggesting some

non-turf algal species are disadvantaged by elevated sedimentation at some stage of their life cycle. The most susceptible stage is likely to be at settlement and initial growth of sporelings due to the microscopic size of the early development stages of most macroalgal species (Santelices 1990, Coelho *et al.* 2000) and their need for a stable substratum and adequate light levels. Indeed, Vadas *et al.* (1992) state that these early life stages suffer "*considerable stress and mortality from silt and sediments*", and that survival of early post settlement phases is instrumental in the establishment and maintenance of benthic marine communities.

Spore settlement

Spores from many macroalgae species are released *en masse* into the water column and suffer significant mortality within the first few hours (Santelices 1990). Surviving spores must then re-enter the benthic boundary layer (Fletcher & Callow 1992) and make physical contact with the substratum. Spores of some algal species are flagellate and therefore able to actively select suitable substrata, while many other algal species have non-motile spores with little or no potential for unassisted movement. Spores are able to detect and respond to environmental cues that will enhance survival success, such as light, nutrients levels, and surface characteristics of the substratum (Fletcher & Callow 1992). Paradoxically, the calm water movement conditions that allow algal spores to settle onto substrata are also favourable for settlement of sediment (Santelices 1990). Sediment settling onto hard substrata is known to inhibit the initial attachment of macroalgal spores (Devinny & Volse 1978, Kendrick 1991, Airoldi & Cinelli 1997, Airoldi 2000), smother or scour successfully attached spores (Norton 1978, Umar *et al.* 1998), and reduce the growth of germinating algae by reduction of available light (Chapman & Fletcher 2002).

Spores in benthic research

Macroalgal spores and embryos make ideal subjects for *in vitro* or *in aquaria* experimental manipulation of environmental conditions, and have been used to help determine the effects of ultraviolet radiation on survival and growth (Dring *et al.* 1996, Wiencke *et al.* 2004, Veliz *et al.* 2006, Wiencke *et al.* 2006), increased sedimentation

(Chapman & Fletcher 2002) and even the effects of sewage effluent (Doblin & Clayton 1995, Kevekordes 2001) on temperate marine algae.

Selected species of Antarctic macroalgae have been cultured successfully through the early development stages of their lifecycles (e.g. Mueller *et al.* 1990, Wiencke & Clayton 1990, Dummermuth & Wiencke 2003), and subsequently used for *in vitro* physiological research such as determination of relationships between irradiance and photosynthetic pigment concentrations (Wiencke 1990a, 1990b, Lüder *et al.* 2001). However, there are no known studies using early developmental stages of Antarctic macroalgae to determine potential impacts of human activities.

Sedimentation and Antarctic benthic environments

The Antarctic coastal marine environment has distinct seasonality with many areas completely covered by sea ice for more than nine months of the year, followed by a brief one to three month period of open water. During the summer months, intense solar radiation over long day lengths and above-zero temperatures cause snow and ice to melt, and result in melt streams and/or broad scale movement of water through terrestrial catchments to the marine environment. In areas within or adjacent to weathered bedrock, flowing water can entrain terrestrial sediments that are subsequently deposited into the marine (or lacustrine) environment; however, natural sedimentation rates in Antarctic coastal waters are considered low (Isla *et al.* 2001).

Human activities associated with research stations in Antarctica require the development of infrastructure such as roads to allow movement of cargo to and from supply vessels during the brief summer period. Each year at Australia's Casey Station, a one kilometre road is graded and stabilised with crushed local rock to allow heavy machinery to transfer food and supplies from the wharf to storage areas. In addition, roads of crushed rock around the station buildings are maintained throughout the summer. For a period of ~six weeks from mid-December, the mean daily maximum temperatures at Casey Station are often above freezing, and meltwater flows off the station roads, down the catchment gradients and into Brown Bay. An abandoned rubbish disposal site is located on

the western shore of Brown Bay, through which the main meltwater stream runs. At peak flow, surface sediment plumes are visible at the interface of the meltwater and seawater in Brown Bay, extending out into the bay for at least 100 m. Within a ten year period from 1996, no sediment plumes have been observed entering the marine environment in the Casey region at any location other than Brown Bay.

Himantothallus grandifolius

The large kelp-like alga, *Himantothallus grandifolius* (A & E Gepp) Zinova 1959, O.Desmarestiales, is endemic to Antarctica (Wiencke & Clayton 2002). Growing to more than 10 m long and over 0.6 m wide, the brown leathery blades of the sporophyte are attached by holdfasts to hard substrata in shallow (<70 m) coastal environments of eastern and western Antarctica. This species is known to be strongly shade and cold adapted (Wiencke & Clayton 2002), and thrives in the low light conditions typical under coastal sea ice (Schwarz *et al* 2003). *H.grandifolius* releases masses of 5 µm diameter meiospores from visibly raised and darkened sori on the thallus in early summer (Drew & Hastings 1992). This phenomenon has been successfully exploited in reproductive and life history studies in which spontaneous spore release is stimulated *in vivo*, allowing subsequent culture of gametophytes and sporophytes (Wiencke & Clayton 1990).

In the Windmill Islands area of eastern Antarctica, *H.grandifolius* is widespread along exposed areas of coast, and within many shallow (<10 m), semi-enclosed bays. However, the species is also noticeably absent in the inner reaches of bays in the vicinity of Casey Station, including Brown Bay where summer sediment plumes have been observed over the past ten years. The absence of *H.grandifolius* in these bays could be a natural pattern due to the specific characteristics of the local environment such as persistent sea ice (and therefore reduced irradiance) and the hydrodynamics of the bays; however, elevated sedimentation rates could also be a contributing factor. Little is known about the sensitivity of *H.grandifolius* spores and gametophytes to elevated sedimentation rates associated with station activity, and or to sediments contaminated with heavy metals.

The overall goal of this current study was to determine the effect of sedimentation and irradiance on the settlement success of *H.grandifolius* spores and subsequent early growth of gametophytes. The aims of this study were threefold:

(1) to determine whether different thicknesses of 'clean' and 'contaminated' sediments overlying otherwise suitable substrata would affect the settlement success of spores and subsequent early growth of gametophytes while exposed to different irradiance levels;

(2) to determine whether the presence of sediment ('clean' or 'contaminated') *adjacent* to otherwise suitable substrata has an effect on the settlement success of spores and subsequent early growth of gametophytes while exposed to different irradiance levels; and

(3) to determine whether the growth of early post-settlement gametophytes is affected by smothering of thin layers of 'clean' or 'contaminated' sediments while exposed to different levels of irradiance.

Materials and Methods:

Algal zoospores

Samples of reproductively active thallus of *Himantothallus grandifolius* were collected in December 2003 by divers from a shallow embayment (Sparkes Bay) on the southern side of the Mitchell Peninsula, near Casey Station, East Antarctica (66.34°S, 110.54°E). Large pieces of mature thallus with visibly raised sori were excised underwater and placed into mesh collecting bags. At the surface, the thallus pieces were transferred to dry, plastic ziplock bags, and then placed on fresh snow inside a 30 L black plastic drum to avoid light and temperature shock before being transported to the Casey Station laboratory.

In the laboratory, the entire plastic drum containing the thallus pieces was placed inside a refrigerator set at 0°C. Early trials revealed that thallus sections could be kept in the dark and 'on ice' for at least 24 hrs without detriment to subsequent zoospore release. Within 12 hrs of collection, sections of thallus were wiped gently with damp paper towel to remove adherent diatoms and fauna, before a 60 mm disc of algal tissue was cut from each

of several thalli on a Teflon cutting board using a new scalpel blade. The excised discs were placed into new plastic petri dishes, and irrigated slowly with cold, filtered seawater (0°C, 35 ppt) until the algal discs were immersed. The petri dishes were placed into a growth cabinet set at 0°C with multiple Sylvania/GroLux F18W/GRO fluorescent tubes.

Masses of flagellate zoospores were released from the algal discs within 3 – 5 hrs. Zoospores were transferred by pipette to a 1 L glass beaker containing 500 mL of Provasoli enriched seawater medium (Starr & Zeikus 1987) at 0°C. The resulting zoospore mixture was stirred gently and continuously while 2 mL aliquots were used to seed each experimental unit.

Experimental set-up

New 100 mL Pyrex crystallising dishes (70 mm diameter, 40 mm depth) were used as experimental units. The outside base and walls of the dishes were covered with black adhesive contact film to eliminate contaminating light from the sides and bottom. The dishes were numbered and then soaked in distilled water for seven days before being air dried. A single glass microscope slide (cut to 60 mm length and soaked in distilled water for one month, and then air dried) was placed into each dish. Enriched seawater medium (Starr & Zeikus 1987) was produced less than 7 days before use and stored in the dark at 0°C. A 50 mL aliquot of the enriched seawater medium was used in each experimental unit.

To stabilise the experimental temperature within the range of natural Antarctic water temperatures, a system of four chilled hyper-saline water baths with constantly circulating water (-1°C, 60 ppt) was established. The experimental units (crystallising dishes) were placed on racks within the water baths thus ensuring the seawater medium within the dishes was kept at a constant low temperature between -1 and 0°C. Ambient room temperature varied from 0 to 5°C.

Irradiance

The experiment was illuminated by metal halide lamps (Osram Powerstar HQI-TS 150W/NDL UVS) in weatherproof housings (GEC Civic Flood). Blue-green filters were used to modify incident light to characteristics found at 5 - 10 m depth (S.Wright, pers

comm.). Ambient photon irradiance above the experimental units (100%) was measured as 98.31 μmol photons.sec^{-1}.m^{-2}. Light treatments of 0%, 6%, 12%, 25%, and 90% of ambient incident light were established using neutral density (ND) filter films, with black plastic film used to eliminate light intensity in the '0%' treatments. ND filter films (attached to supporting frames of 5 mm thick acrylic sheet) were placed across the tops of the crystallising dishes to reduce the photosynthetically active radiation (PAR) incident light intensity but allow broad spectrum incidence, even into the UV and close IR wavelengths (330 - 700 nm). Photoperiod was kept at 24 hrs of light which approximated natural conditions at the time of the experiments.

Levels of PAR (400 - 700 nm) reaching the glass slides within each experimental unit were measured at the beginning and end of the experiments using a series of underwater quantum sensors (Li-Cor LI-192SA) connected to a multi-channel data logger (Li-Cor LI-1400). These sensors measured continuous running averages of instantaneous readings over 15 sec intervals. Simultaneous measurements of irradiance levels (μmol photons.m^{-2}.sec^{-1}) above the light filters (i.e. 100% ambient irradiance), and at the slide depth beneath the light filters within the experimental units were logged.

Sediment

Two types of sediment were used in the experiments. Contaminated sediment was collected from the abandoned Thala Valley rubbish disposal site that is located on the shore of Brown Bay, and is the likely source of contaminated sediment that is implicated in anthropogenic impacts on marine communities within the bay (Duquesne & Riddle 2002, Stark *et al* 2005). Sediment was sampled from near the edge of the bay, adjacent to where the sediment plumes are evident each summer. Clean (control) sediment was collected from the Casey Station quarry that is located less than 600 m from the Thala Valley, with similar geology but none of the contaminant loading of the Thala Valley sediment (*Table 4.1*). Both sediment types were collected in bulk, sieved (0.5 mm) and dried before use. Chemical and grain size analysis was undertaken on five replicate samples of both sediments.

Sediments were added to the experimental units using a mesh overlay that allowed an even coating of sediment to settle onto the glass slides within the crystallising dishes. A known volume of sediment was added to each experimental unit depending upon whether the treatment called for a thin or thick layer of contaminated or clean sediment. Trial applications of known volumes of each sediment type onto glass slides were conducted and the thickness of sediment overlying the glass slides subsequently measured. Within the experiments, a thin layer equated to 0.5 mm (SE±0.1) thickness (~1.3 g.m^{-2} ±0.3), a thick layer equated to 1.5 mm (SE±0.1) sediment thickness (~4.7 g.m^{-2} ±0.3).

Each experimental unit therefore consisted of a single microscope slide sitting flat on the bottom of a numbered, blackened crystallising dish, within 50 mL of enriched seawater medium. The slide was treated with sediment as appropriate and the dish covered by a thin film of either ND filter or black plastic to create one of the light treatments.

Experimental design

Three experiments were conducted on *H. grandifolius* zoospores using similar set-ups to those described above, but with slightly different aims and treatments.

Experiment 1   Direct effect of sediment and irradiance

The aim was to determine whether a layer of sediment overlying hard substrata could influence the settlement success and subsequent growth of macroalgal zoospores, and whether the effect of sediment was dependent on irradiance levels. Two sediment layer thicknesses were investigated (arbitrarily referred to as 'thin' and 'thick'), using both 'contaminated' and 'clean' sediment, and substrata without sediment acted as the control. Five irradiance levels were investigated to determine whether synergistic effects of sediment and irradiance were apparent. In summary, the layout of *Experiment 1* consisted of five sediment treatments crossed with five irradiance treatments (25 combinations) with three replicate experimental units of each treatment combination. Each of the 75 experimental units (crystallising dishes) was randomly allocated a position within the four hyper-saline water baths.

Experiment 2   Effects of sediment adjacent to zoospores

The aim was to determine whether a thin layer of sediment overlying a section of

hard substrata could influence the settlement and growth of zoospores on an adjacent

section of hard substratum that is free of sediment, i.e. whether there are any chemical or

physical deterrents to settlement resulting from nearby sediments. Sediment was added to

the microscope slides as for *Experiment 1*, and two diagonally opposite quarters of each

microscope slide were then scraped clean of sediment using the end of a glass slide. This

resulted in the presence of two non-sedimented areas for zoospore settlement adjacent to

two sedimented areas on each slide. Contaminated sediments were compared with 'clean'

sediments to determine whether contaminants released from contaminated sediments have

an added impact on settlement success. Only thin sediment layers (0.5 mm) were

investigated given results from *Experiment 1* which showed that both thicknesses of

sediment equally reduced sporeling settlement and growth. Treatments without any added

sediment were also included as a control. All sediment treatments were subjected to the

five irradiance treatments as described for *Experiment 1* to assess the possibility of

interactions between light and sediment. There were three replicates of each treatment

combination. Each of the 45 experiment sediment/irradiance combinations was randomly

allocated to positions in the four hyper-saline water baths.

Experiment 3   Smothering effects

The aim was to assess whether growth of zoospores that had already settled

successfully is affected by subsequent smothering by sediment. Zoospores were added to

enriched seawater medium overlying clean glass slides as for all other experiments. The

experimental units were all covered with 90% ND filters, placed in the hyper-saline water

baths and left to allow the zoospores to settle onto the glass slides. After four days, a thin

layer (0.5 mm) of 'contaminated' or 'clean' sediment was added to three replicate

experimental units for each of the five irradiance treatments, and allowed to germinate for a

further six days. The 30 experimental units of the sediment/irradiance treatment

combinations were allocated randomly to positions within the four hyper-saline water

baths. The results from these treatments were compared to the 'no sediment' treatment

replicates used for *Experiment 2* since the two experiments ran simultaneously within the same water baths.

Experiment 1 ran over 10 days between 29 December 2003 and 8 January 2004.

Experiments 2 and *3* ran simultaneously over 10 days from 12 to 22 January 2004.

At the conclusion of experiments, each glass slide was rinsed with filtered seawater to remove non-adherent spores and sediment, before being viewed under a dissecting microscope (Zeiss Axioskop 10x optical, 40x power, ocular graticule). For each slide, the number of attached zoospores, and the number and length of sporelings was counted in 12 random fields of view (490 μm diameter). In *Experiment 2*, where alternate quarters of each slide were either sedimented or not, six fields of view were counted in each of the non-sedimented quarters giving a total of 12 fields of view on each slide. Zoospores/sporelings were categorised into one of three development stages:

- Type 1   attached spores with no visible germ tube;

- Type 2   germ tube length < diameter of zoospore, or

- Type 3   germ tube length > diameter of zoospore. The length of germ tube was subsequently measured using an ocular graticule.

Statistical analysis

Univariate statistical analysis (GMAV, Underwood & Chapman 1998) was undertaken on the mean number of each type of zoospore/sporeling, and on the mean lengths of Type 3 germ tubes. Means were calculated from the counts of 12 replicate fields of view within each experimental unit. Treatment effects within each of the three experiments were identified using ANOVA, and where significant, were further identified using the Tukey HSD (honestly significant difference) test.

Experiment 1   Direct effect of sediment and irradiance levels

A two factor ANOVA design was used to test for differences between zoospore settlement and growth of gametophyte germ tubes under different sediment treatments (5 levels, fixed) and different irradiance levels (5 levels, fixed, orthogonal), using the means of 12 counts within each of 3 independent replicate experimental units per treatment

combination. Due to the almost complete absence of sporeling settlement and growth within treatments with added sediment, it was not possible to investigate possible interactions between sediment type and thickness.

Experiment 2   Effects of sediment adjacent to zoospores

A two factor ANOVA design was used to test for differences between zoospore settlement and growth of gametophyte germ tubes on substrata adjacent to different sediment treatments (3 levels, fixed) and under different irradiance levels (5 levels, fixed, orthogonal), using the means of 12 counts within each of 3 independent replicate experimental units per treatment combination.

Experiment 3   Smothering effects

A two factor ANOVA design was used to test for differences between zoospore settlement and growth of gametophyte germ tubes under different sediment treatments (3 levels, fixed) and different irradiance levels (5 levels, fixed, orthogonal), using the means of 12 counts within each of 3 independent replicate experimental units per treatment combination.

Results:

The 'clean' sediment from the Casey Station quarry had low concentrations of metals and undetectable concentrations of total petroleum hydrocarbons (TPH) (*Table 4.1*). The 'contaminated' sediment from the Thala Valley had a higher percentage of sand and lower percentage of silt than the quarry sediment, and contained higher levels of contaminants, including copper (Cu), iron (Fe), lead (Pb), nickel (Ni) and zinc (Zn), and TPH.

The mean PAR light levels characterising the five irradiance treatments were 0.04, 7.12, 12.08, 24.97, and 93.63 μmol photons.m^{-2}.sec^{-1} which equate to 0, 7, 12, 25, and 95% of ambient irradiance respectively. Equating those irradiance levels to 'real world' levels, <2 μmol photons.m^{-2}.sec^{-1} was measured at 6 m depth beneath 1.3 m (SE ±0.01) of sea ice, with 0.24 - 0.29 m (SE ±0.01) of overlying snow in several local Windmill Island bays.

Table 4.1   *Characteristics of sediments used within experiments (n=5)*

	clean sediment	contaminated sediment
	mean±SE (mg.kg⁻¹)	mean±SE (mg.kg⁻¹)
arsenic (As)	0.63 ± 0.00	2.38 ± 0.05
cadmium (Cd)	0.06 ± 0.00	13.51 ± 0.43
copper (Cu)	6.65 ± 0.86	1227.36 ± 49.35
iron (Fe)	2494.78 ± 24.32	24210.00 ± 601.23
lead (Pb)	4.38 ± 0.91	4854.23 ± 127.12
nickel (Ni)	31.60 ± 1.49	83.85 ± 13.40
tin (Sn)	0.11 ± 0.01	78.50 ± 1.02
zinc (Zn)	14.04 ± 0.86	2708.48 ± 55.71
TPH	< 200 ± 100	1820 ± 100
size fraction	% of sample	% of sample
> 63 μm	38.0 ± 3.99	57.7 ± 1.67
2 to 63 μm	60.9 ± 4.31	41.6 ± 3.25
< 2 μm	1.1 ± 0.36	0.7 ± 0.35

Experiment 1 Direct sediment effects

Zoospores attached to glass slides and developed gametophyte germ tubes (collectively called sporelings) at high densities (*Table 4.2*) on all slides within the 'no sediment' treatments at all irradiance levels, but rarely occurred on slides with added sediment (*Fig.4.1*).

Table 4.2   *Results of ANOVA for Total Number of Sporelings (untransformed, P<0.01)*

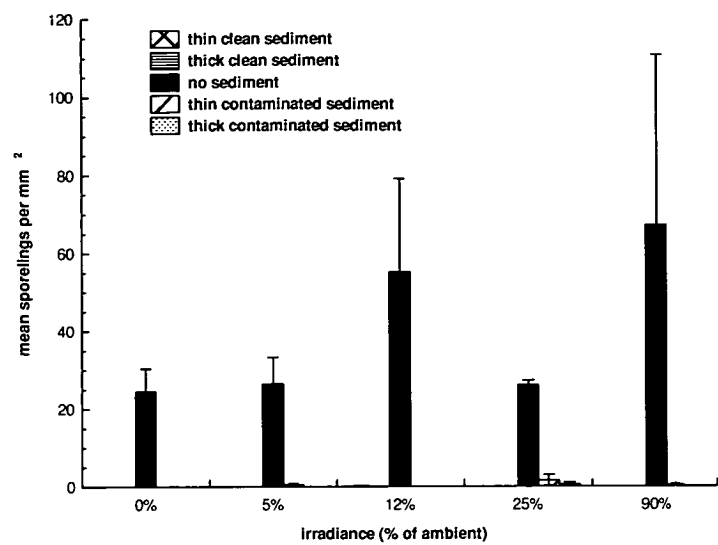| Source	SS	df	MS	F	P	Error
Sediment	667.22	4	166.80	15.35	0.0000	Residual
Irradiance	32.52	4	8.13	0.75	0.5638	Residual
Sed x Irrad.	135.95	16	8.50	0.78	0.6974	Residual
Residual	543.22	50	10.86			
Total	1378.91	74				

Figure 4.1   *Mean total number of sporelings per mm² that attached to glass slides within the five sediment treatments under five irradiance levels, Experiment 1 (±SE, n=3).*

The few sporelings counted within 'contaminated sediment' treatments were located within small patches of disturbed sediment where the glass substrate was exposed, and therefore are not representative of the true sediment treatment.

Within the 'no sediment' treatment (*Fig.4.2*), the mean density of Type 1 sporelings did not vary significantly with irradiance (*Table 4.3*), although fewer sporelings were counted for 25% irradiance.

Table 4.3   *Results of ANOVA for Total Number of Type 1 Sporelings (untransformed, P<0.01)*

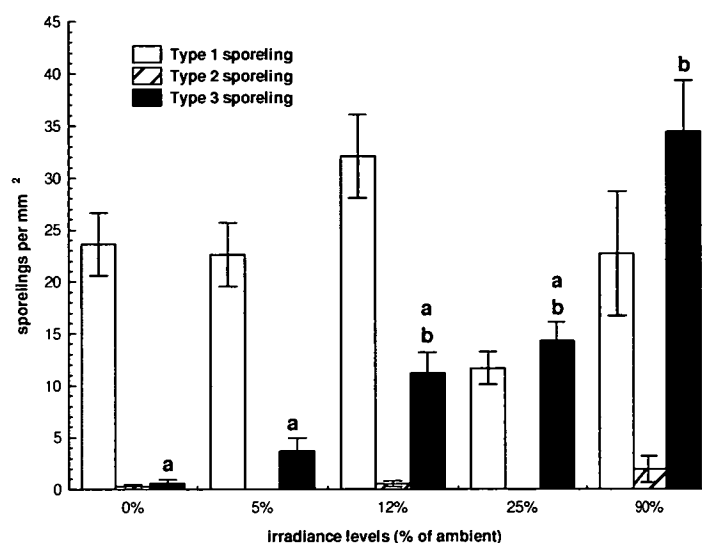| Source	SS	df	MS	F	P	Error
Sediment	263.58	4	65.89	18.24	0.0000	Residual
Irradiance	8.78	4	2.20	0.61	0.6588	Residual
Sed x Irrad.	34.76	16	2.17	0.60	0.8676	Residual
Residual	180.62	50	3.61			
Total	487.74	74				

Figure 4.2 **Mean number of each sporeling type per mm² across the five irradiance levels within the 'no sediment' treatment (±SE, n=3).** *Letters above Type 3 sporeling bars represent groupings designated by Tukey HSD test results; bars with similar letters are not significantly different.*

Type 2 sporelings were rarely counted and did not exhibit a trend across the range of irradiance levels (*Table 4.4*). Despite an apparent increasing abundance of Type 3 sporelings with increasing irradiance levels (*Fig.4.2*), significant differences were only apparent between 0% and 90% irradiance and between 5% and 90% irradiance ($F_{4,10}=5.39$, $P=0.0141$).

Table 4.4 **Results of ANOVA for Total Number of Type 2 Sporelings (untransformed, $P<0.01$)**

Source	SS	df	MS	F	P	Error
Sediment	0.18	4	0.05	1.86	0.1314	Residual
Irradiance	0.08	4	0.02	0.80	0.5294	Residual
Sed x Irrad.	0.33	16	0.02	0.85	0.6224	Residual
Residual	1.23	50	0.02			
Total	1.82	74				

Table 4.5 **Results of ANOVA for Total Number of Type 3 Sporelings (untransformed, $P<0.01$)**

Source	SS	df	MS	F	P	Error
Sediment	84.12	4	21.03	12.20	0.0000	Residual
Irradiance	18.41	4	4.60	2.67	0.0426	Residual
Sed x Irrad.	72.58	16	4.54	2.63	0.0047	Residual
Residual	86.17	50	1.72			
Total	261.27	74				

Type 3 sporeling germ tubes were significantly longer (*Table 4.6*) for all irradiance

levels above 5% compared to lengths for the 0% irradiance treatment ($F_{4,10}=7.40$,

$P=0.0049$).

Table 4.6   Type 3 Sporeling Germ Tube Lengths (Experiment 1).

Irradiance (% of ambient)	Mean length (μm)	SE	n
0%	4.8	0.60	3
5%	7.5	0.53	12
12%	7.3	0.47	21
25%	8.7	0.32	29
90%	9.9	0.17	33

Experiment 2 Effects of adjacent sediment

The mean number of sporelings (of all types) counted on glass slides varied across

the sediment and irradiance treatment combinations (*Fig.4.3*). There were no significant

differences in sporeling density among sediment treatments within each irradiance level

(*Table 4.7*) but a highly significant effect of irradiance was apparent overall.   Fewer

sporelings were counted on slides with 0% irradiance than at all other irradiance levels, and

on slides with 5% irradiance compared to irradiances of 12% and above; whereas similar

numbers of sporelings were counted on slides with 12, 25 and 90% irradiance.

Table 4.7 Results of ANOVA for Total Number of Sporelings – Experiment 2 (P<0.05)

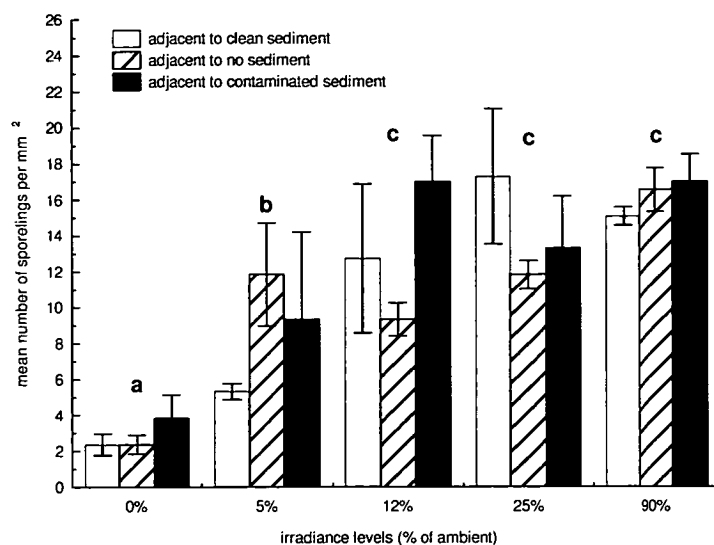| Source	SS	df	MS	F	P	Error
Sediment	1.01	2	0.50	0.80	0.4572	Residual
Irradiance	35.74	4	8.94	14.27	0.0000	Residual
Sed x Irrad.	6.72	8	0.84	1.34	0.2620	Residual
Residual	18.78	30	0.63			
Total	62.24	44				

Figure 4.3 **Mean counts of sporelings (all types grouped) per mm^2 on glass slides within the**
three sediment treatments, across five irradiance levels ($\pm SE$, n=3). Letters above bars represent
irradiance groupings designated by Tukey HSD test results; groups with similar letters are not
significantly different.

Mean density of Type 1 sporelings under the different sediment treatments (*Fig.4.4*)
were significantly different (*Table 4.8*) in that for all irradiance levels except 5%, Type 1
sporelings were not counted on glass slides adjacent to no sediment. In addition, an
irradiance effect was apparent for Type 1 sporelings due to their absence on all slides with
90% irradiance.

Table 4.8 Results of ANOVA for Total Number of Type 1 Sporelings – Experiment 2 (transformed
Sqrt (X+1), P<0.05)

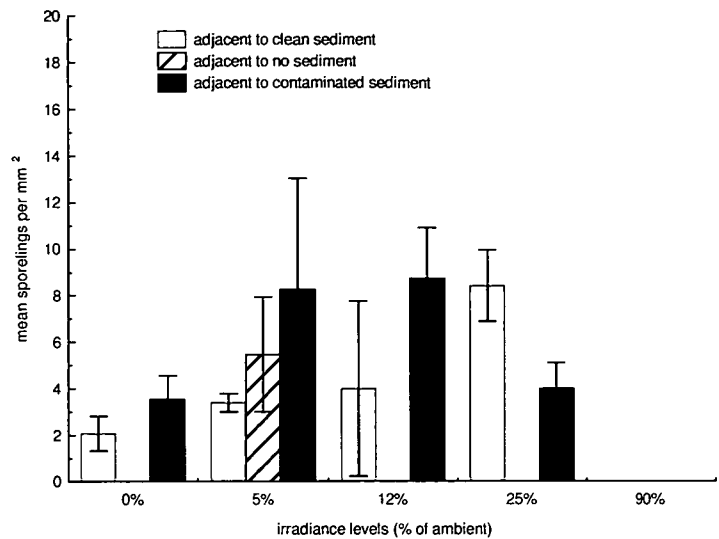| Source	SS	df	MS	F	P	Error
Sediment	0.45	2	0.22	5.09	0.0125	Residual
Irradiance	0.93	4	0.23	5.28	0.0024	Residual
Sed x Irrad.	0.64	8	0.08	1.82	0.1121	Residual
Residual	1.32	30	0.04			
Total	3.33	44				

Figure 4.4   Mean counts of Type 1 sporelings per mm² on glass slides within the three sediment treatments, across five irradiance levels, Experiment 2 (±SE, n=3).

Type 2 sporelings were not counted on any of the slides in *Experiment 2*. However, density of Type 3 sporelings was significantly influenced by both sediment and irradiance (*Fig.4.5*). Type 3 counts were slightly higher on glass slides adjacent to no sediment compared to slides adjacent to either clean or contaminated sediments (*Table 4.9*) but only at 0 and 5% irradiances. Increasing irradiance levels led to higher densities of Type 3 sporelings, with each irradiance treatment significantly different from the others, with the exception of 12 and 25% which had similar Type 3 counts.

Table 4.9 Results of ANOVA for Total Number of Type 3 Sporelings – Experiment 2 (P<0.05)

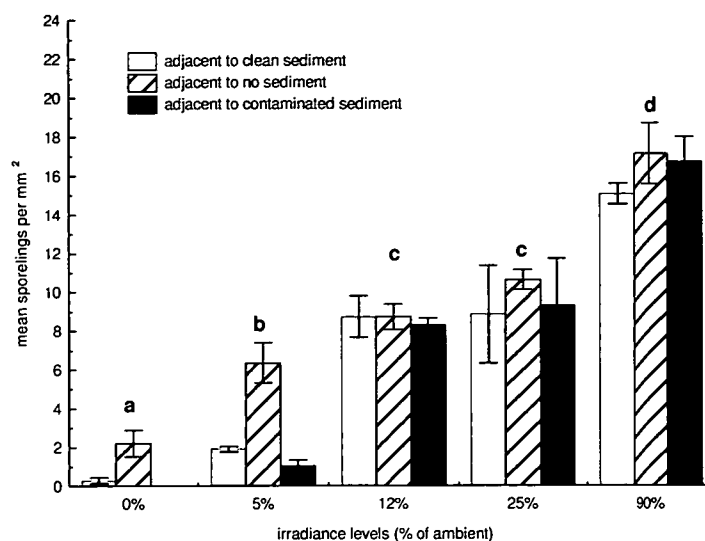| Source	SS	df	MS	F	P	Error
Sediment	1.38	2	0.69	4.71	0.0166	Residual
Irradiance	46.46	4	11.61	79.43	0.0000	Residual
Sed x Irrad.	1.09	8	0.14	0.93	0.5042	Residual
Residual	4.39	30	0.15			
Total	53.31	44				

Figure 4.5 **Mean counts of Type 3 sporelings per mm² on glass slides within three sediment treatments, across five irradiance levels in Experiment 2 (±SE, n=3).** Letters above bars represent irradiance groupings designated by Tukey HSD test results; groups with similar letters are not significantly different.

The length of germ tubes of Type 3 sporelings (*Fig.4.6*) increased significantly with irradiance (*Table 4.10*), but was not significantly affected by the sediment treatments at each irradiance. The mean germ tube lengths increased significantly with each higher irradiance level, with the exception that germ tube lengths at 12 and 25% irradiance were similar.

Table 4.10 Results of ANOVA for Total Number of Type 3 Germ Tube Lengths – Experiment 2 (untransformed, P<0.01)

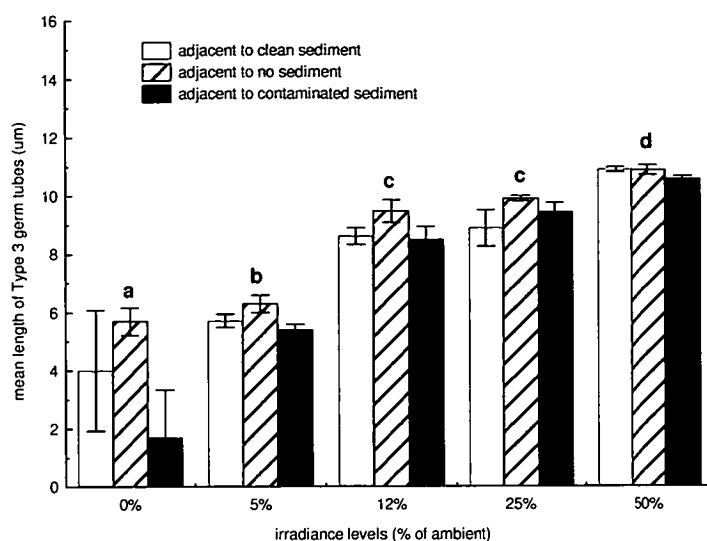| Source	SS	df	MS	F	P	Error
Sediment	13.75	2	6.88	4.04	0.0280	Residual
Irradiance	293.56	4	73.39	43.09	0.0000	Residual
Sed x Irrad.	15.51	8	1.94	1.14	0.3674	Residual
Residual	51.10	30	1.70			
Total	373.93	44				

Figure 4.6   Mean length of Type 3 sporeling germ tubes measured on glass slides within the three sediment treatments under five irradiance levels, Experiment 2 (±SE, n=3). Letters above bars represent irradiance groupings designated by Tukey HSD test results; groups with similar letters are not significantly different.

Experiment 3 Smothering effects

There was a significant interaction (*Table 4.11*) in the effects of sediment smothering and irradiance treatments on sporeling density (all types combined) on the slides (*Fig.4.7*). Sporeling density was generally similar across the three sediment treatments within each irradiance level except that there were significantly lower densities on slides with no sediment at 12% irradiance, and at 5% irradiance fewer sporelings grew on slides subject to clean sediment than contaminated sediment. Sporeling counts were significantly lower for 0% irradiance than all other irradiance levels, whereas counts for irradiance levels >5% were not significantly different from each other.

Table 4.11 Results of ANOVA for Total Number of Sporelings – Experiment 3 (P<0.05)

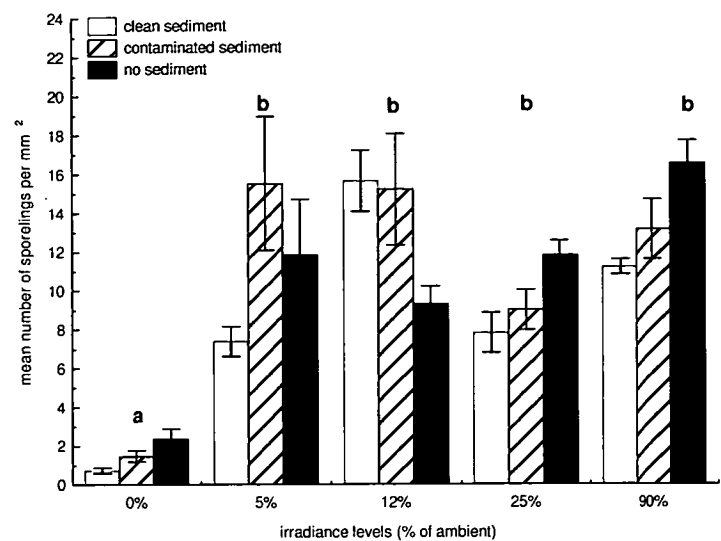| Source	SS	df	MS	F	P	Error
Sediment	1.48	2	0.74	2.53	0.0964	Residual
Irradiance	31.33	4	7.83	26.89	0.0000	Residual
Sed x Irrad.	7.35	8	0.92	3.15	0.0104	Residual
Residual	8.74	30	0.29			
Total	48.90	44				

Figure 4.7   Mean counts of sporelings (all types) per mm² on glass slides within three sediment treatments, across five irradiance levels in Experiment 3 (±SE, n=3). Letters above bars represent irradiance groupings designated by Tukey HSD test results; groups with similar letters are not significantly different.

Few Type 1 sporelings and no Type 2 sporelings were counted on the glass slides in this experiment reflecting the advanced development of most sporelings over the four days prior to treatment with sediment.

The mean number of Type 3 sporelings did not differ significantly (*Table 4.12*) between each of the sediment treatments at each irradiance level (*Fig.4.8*), although there was a slightly higher count on slides not subject to sediment at 90% irradiance. In contrast, irradiance level strongly affected sporeling density with the fewest Type 3 sporelings occurring on slides with 0% irradiance, highest densities developing on slides under 90% irradiance, and with intermediate (and similar) densities on slides subject to 5, 12 and 25% irradiances.

Table 4.12 Results of ANOVA for Type 3 Sporelings – Experiment 3 (P<0.05)

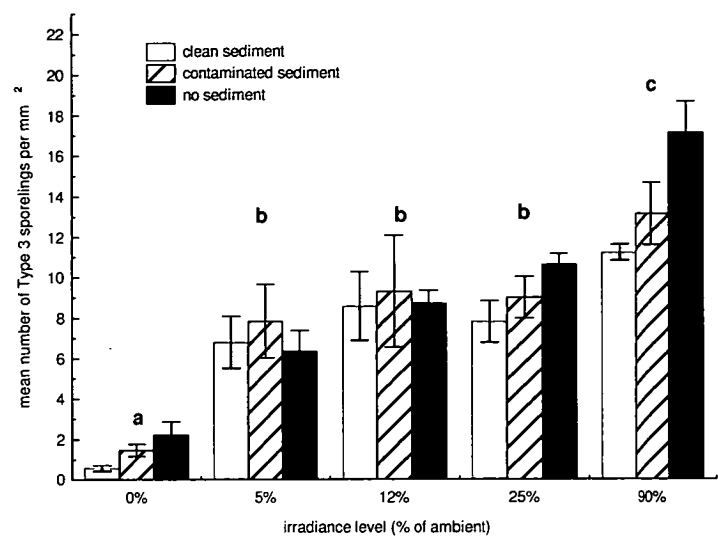| Source	SS	df	MS	F	P	Error
Sediment	1.01	2	0.51	2.70	0.0834	Residual
Irradiance	25.63	4	6.41	34.24	0.0000	Residual
Sed x Irrad.	1.56	8	0.20	1.05	0.4258	Residual
Residual	5.61	30	0.19			
Total	33.82	44				

Figure 4.8   Mean counts of Type 3 sporelings per mm^2 on glass slides within three sediment treatments, across five irradiance levels in Experiment 3 (±SE, n=3). Letters above bars represent irradiance groupings designated by Tukey HSD test results; groups with similar letters are not significantly different.

The mean length of Type 3 germ tubes exhibited a highly significant interaction (*Table 4.13*) between sediment and irradiance treatments (*Fig.4.9*). At the 0 and 5% irradiances there were no significant differences between the three sediment treatments. However, at 12, 25 and 90% irradiance, the length of germ tubes of Type 3 sporelings were significantly longer on slides not smothered with sediment compared with those smothered with clean or contaminated sediment.

Table 4.13 Results of ANOVA for Type 3 Sporeling Germ Tube Lengths – Experiment 3 (P<0.05)

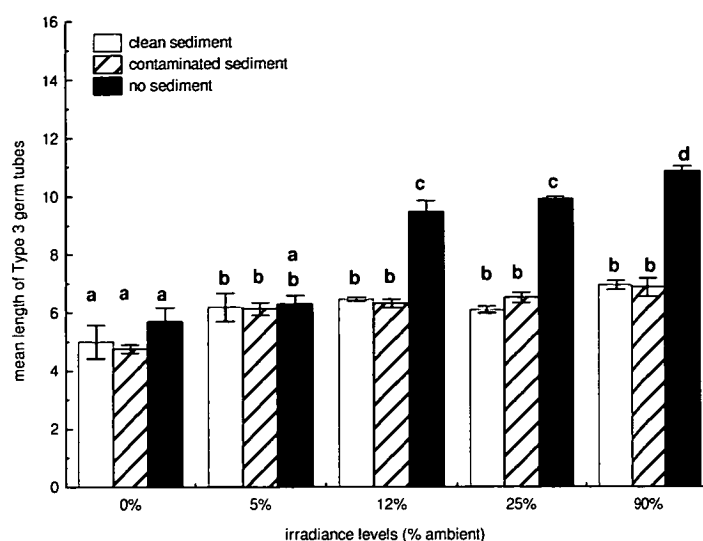| Source	SS	df	MS	F	P	Error
Sediment	53.86	2	26.93	102.57	0.0000	Residual
Irradiance	53.64	4	13.41	51.07	0.0000	Residual
Sed x Irrad.	24.31	8	3.04	11.57	0.0000	Residual
Residual	7.88	30	0.26			
Total	139.68	44				

Figure 4.9   Mean length of Type 3 sporeling germ tubes measured on glass slides within the three sediment treatments and five irradiance levels in Experiment 3 (±SE, n=3). Letters above bars represent groupings designated by Tukey HSD test results; bars with similar letters are not significantly different.

Overall, germ tubes were significantly shorter on Type 3 sporelings smothered with clean or contaminated sediment and exposed to 0% irradiance compared with those sporelings that were smothered and exposed to higher irradiances. For Type 3 sporelings not smothered with sediment, those exposed to 0 and 5% irradiance had the shortest germ tubes, while those exposed to 90% had the longest.

Discussion:

Sedimentation has a significant negative impact on *Himantothallus grandifolius* spore settlement and subsequent early gametophyte growth. The presence of a layer of sediment as little as 0.5 mm thick effectively precludes the spores from attaching successfully to the substratum. Spores are able to attach to the glass substratum in areas where sediments are disturbed, and they successfully extend germ tubes even when sediments are adjacent to the site of attachment. Smothering of attached early stage gametophytes by a thin layer of sediment significantly reduces the growth rate of germ tubes compared to gametophytes not smothered.

Settlement inhibition

Layers of sediment overlying hard substrata are known to inhibit the initial attachment of macroalgal spores (Devinny & Volse 1978, Airoldi & Cinelli 1997, Airoldi 2000). Settlement inhibition is thought to be due to the relative dimensions of spores, sediment grains and sediment layer thickness. *H.grandifolius* spores are 5 µm in diameter, and a layer of sediment 0.5 mm thick is therefore 100 times the spore diameter, which provides a significant barrier to attachment. In addition, more than 90% of the grains within the sediments used in these experiments are greater than the size of the spores and could therefore themselves provide a suitable substratum for initial attachment. Spores attaching to unstable substrata such as loose sediment grains are more likely to be washed away with sediments during periods of water movement and are prone to abrasion and physical damage by other sediment grains (Norton 1978, Santelices 1990). *H.grandifolius* spores settling in areas where sediment layers overlay hard substrata are therefore disadvantaged and are less likely to recruit successfully.

Sediment layer irregularity

Sediment layers are not typically uniform in thickness and are often transient in nature. Substratum irregularities, microscale variations in sediment settling conditions, subsequent disturbance of sediment layers by faunal activity and wave or current action, lead to sediment layers that are variable in thickness and persistence. Results of this study illustrate that even small scale disturbances to sediment layers provide opportunities for successful spore settlement and subsequent growth. Yet, under Antarctic conditions, the inner most reaches of bays are covered by sea ice for long periods of time (e.g. up to 11 months in the Windmill Islands) and therefore are not subjected to wind-driven waves and swell that are common on more temperate coasts. Unbroken layers of fine sediment are observed on hard substrata in the calm protected areas of the Windmill Islands where dispersal by water movement is less frequent than on exposed coasts. In these protected bays, sediment is likely to inhibit successful macroalgal spore settlement for much of the year. Substratum surface irregularities and faunal disturbance to sediment layers (e.g.

echinoderm grazing) are therefore likely to be particularly important features to facilitate

successful settlement of spores in the low energy environments of Antarctic coastal bays.

Physical versus chemical inhibition

Inhibition of *H.grandifolius* spore settlement by sediment at a thickness of 0.5 mm is

due to physical effects rather than the chemical characteristics of the sediments. The results

illustrate clearly that a thin layer of sediment will prevent spore settlement irrespective of

whether it is 'clean' or 'contaminated' by heavy metals and hydrocarbons. The physical

barrier formed by even relatively thin sediment layers is sufficient to prevent spores

successfully attaching to stable substrata and results in poor settlement success. The

success of spores settling on exposed substrata adjacent to sediments was not significantly

different from settlement success on sediment free substrata, and subsequent growth of

gametophytes was not affected by the presence of 'clean' or 'contaminated' sediments

nearby. This further supports the conclusion that inhibition of spore attachment and early

gametophyte growth by sediments is a physical rather than chemical phenomenon.

Smothering effects

Rates of sedimentation vary with time in response to natural cyclical fluctuations

such as seasonal storm activity and snow melt, or unnaturally due to modification of

sediment fluxes through human activities. In either case, pulses of sediment can smother

spores and gametophytes that have recently attached to available substratum. Smothering

by sediment in a layer 0.5 mm thick did not reduce the number of attached spores and

gametophytes in the short term but led to significantly reduced growth rates of

gametophytes. The rate of gametophyte growth under a thin layer of sediment is similar to

non-sedimented gametophytes under low irradiances (0 and 5% of ambient). Chapman &

Fletcher (2002) found similar results from smothering trials of *Fucus serratus* embryos,

where they concluded that the survivorship of embryos was not affected by smothering but '

that growth of the parenchymatous embryos was. Clearly, the physical presence of an

overlying sediment layer significantly reduces the amount of available light to

gametophytes (and embryos), resulting in a slowing of growth. The presence of a sediment

layer may also reduce gametophyte exposure to oxygen and nutrients due to altered

boundary water flow, resulting in lower growth rates.

Influence of irradiance

The phenology of Antarctic macroalgae is primarily regulated by the light regime

(Wiencke 1990a). Irradiance has a strong influence on the success of spore settlement and

subsequent growth of gametophytes (Santelices 1990, Miller & Pearse 1991). Results from

this study illustrate that there is significantly less spore settlement at irradiances of 0.04

μmol photons.m^{-2}.sec^{-1} than at all other irradiance treatments tested. Even at extreme low

light levels (0%), *H.grandifolius* spores are able to settle and successfully attach to

available hard surfaces. However, subsequent growth of early stage gametophytes is more

highly light dependent, and results indicated that an irradiance level >7 μmol photons.m^{-2}.sec^{-1} is required to promote growth significantly greater than zero. In addition, there is a

distinct increase in the growth of gametophyte germ tubes when irradiance levels reached

12 μmol photons.m^{-2}.sec^{-1}, suggesting this is around a threshold irradiance level necessary

for significant growth of *H.grandifolius* gametophytes.

Interestingly, the mean benthic irradiance level at 6 m depth under sea ice in mid-

summer, in four Windmill Island bays was measured as 0.03, 0.73, 1.76, and 7.75 μmol

photons.m^{-2}.sec^{-1} (author's unpublished data). Of the four bays, the only one supporting

macroalgae species, including *H.grandifolius*, was the bay with the highest irradiance level.

The minimum light requirements for the completion of *H.grandifolius* life-cycle is believed

to be as low as 2 μmol photons.m^{-2}.sec^{-1} (Kirst & Wiencke 1995), thus it is not surprising

that, given the measured light levels, three of the four Windmill Island bays did not contain

this alga. Bays without *H.grandifolius* had maximum irradiance levels under ice below the

minimum light requirement for germination and growth of *H.grandifolius* gametophytes.

Seasonality of H.grandifolius spore release

In the Windmill Islands, spontaneous spore release in *H.grandifolius* was observed in

thallus pieces collected from under ice in late December, yet spore release was not apparent

in thallus pieces collected from open water at the same bay in mid-January. Clearly,

H.grandifolius has a distinct seasonal reproductive cycle that is related to the annual

4-25

presence of sea ice. Indeed, Drew & Hastings (1992) note that *H.grandifolius* at Signy

Island off the Antarctic Peninsula, have plentiful sporangial sori shortly before sea ice

break-out. This phenomenon is probably an adaptation to maximise dispersal of spores

during times of open water, when wind-driven waves and currents are more likely, and also

to provide the spores and gametophytes with maximum irradiance during the early post-

settlement phase. Seasonality of spore release has implications for research using spores of

H.grandifolius in that spore collection is most successful in early summer prior to sea ice

break-out.

Impacts of sedimentation in Antarctica

Elevated sedimentation rates resulting from human activities have the potential to

affect successful recruitment of macroalgae regardless of the source of sediment.

Environmental assessments of human impacts routinely measure the contaminant levels of

sediment entering marine environments and, while contaminants are known to negatively

affect Antarctic flora and fauna (Cunningham *et al.* 2005, Duquesne & Riddle 2002,

Thompson *et al.* 2006), the physical effect of increased sedimentation rates alone is clearly

sufficient to affect the long term persistence of coastal marine communities. Results from

this study confirm the impact potential of elevated sedimentation rates on Antarctic coastal

marine macroalgal assemblages, and suggest that increased sediment loading adjacent to

stations may be negatively influencing the ability of macroalgal recruitment to hard

substrata. In Brown Bay, the absence of *H.grandifolius* may be due to a combination of

low ambient irradiance caused by persistent sea ice and thick snow accumulation, and the

input of increased sediment in meltwater runoff as a result of seasonal road maintenance.

Given inter-annual variability in sea ice persistence and snow accumulation rates,

benthic irradiance may be sufficient in some years for *H.grandifolius* to successfully recruit

to hard substrata in Brown Bay. However, nearshore activities that cause an increase in

sediment loading have the potential to inhibit settlement success and therefore may prevent

successful recruitment in every year.

Knowledge of such mechanisms highlights the need to control sedimentation caused by human activities in coastal Antarctic locations because of physical impacts as well as potential chemical impacts associated with contaminants.

Conclusion:

Sediments have the potential to significantly affect the recruitment and growth of Antarctic macroalgae by creating a barrier to spore attachment, and reducing irradiance levels for subsequent growth. Non contaminated sediments are equally effective at deterring successful spore attachment as is sediment contaminated with heavy metals and hydrocarbons. Irradiance levels beneath sea ice are close to the limits of macroalgal survival and further reductions of available light by increased sediments in the water column or as sediment layers settling onto substrata have the potential to dramatically alter the natural distribution of algal assemblages.

Increasing temperatures associated with climate change have the potential to increase meltwater runoff (Anisimov *et al.* 2007) and further increase sedimentation rates in coastal areas disturbed by human activities. National Antarctic programmes should therefore minimise their operational footprint in Antarctica to alleviate additional stressors on marine flora and fauna that may be surviving at their physiological limits.

Chapter 5
Effects of sedimentation and irradiance levels on growth of an endemic Antarctic red alga, *Palmaria decipiens* (Reinsch) Ricker

Abstract:

Coastal marine macroalgal communities are recognised as valuable habitats, and the potential for human impacts, such as increased sediment runoff, to affect the long-term health and survival of coastal algal communities have been studied in detail. Nearshore Antarctic environments are exposed to highly seasonal benthic irradiance and naturally low rates of sedimentation. While research on the light requirements of Antarctic macroalgae is well advanced, the influence of sedimentation rates on the growth of Antarctic marine macroalgae is currently unknown. Human activities at Casey Station, East Antarctica each summer are thought to be causing elevated sedimentation rates in a local bay and the absence of macroalgae in that bay may be a result of station activities. A translocation experiment was undertaken in the vicinity of Casey Station using an endemic red alga, Palmaria decipiens (Reinsch) Ricker. Algae were allocated to three sediment treatments (natural, reduced and control) and translocated into each of three bays where the alga is not naturally found, including the bay potentially impacted by elevated sediment runoff from Casey. Compared to thalli lengths at initial deployment, translocated algae had mean thalli lengths that were 79.6 - 96.8% shorter (after 12 months) and 91.8 - 99.0% shorter (after 36 months), whereas algae returned to the source bay (as movement controls) had thallus lengths 31.6% and 12% longer for the same time periods, respectively. Reduction of sedimentation rates at the three translocation sites did not significantly affect the measured growth rates of algal thalli, suggesting that sedimentation rates at these bays are insufficient to negatively affect the growth of P.decipiens under the irradiances experienced at each location. Growth of P.decipiens under a variety of irradiances in aquaria did indicate a strong correlation between irradiance levels and thallus growth in the absence of sedimentation, even at irradiance levels as low as 10 μmol photons.m^{-2}.sec^{-1}.

Introduction:

Coastal marine communities are under increasing pressure from physical and chemical pollution resulting from the human modification of natural catchment areas (Rogers 1990, Edgar & Barrett 2000). Of particular concern are the increasing

sedimentation rates in coastal environments which are rising as a consequence of continued population growth, related land clearing and agricultural practices. Terrestrial runoff, and thus associated sedimentation and other pollution, is predicted to increase further with the higher storm frequencies associated with climate change (GESAMP 1994, Anisimov *et al.* 2007).

Coastal marine macroalgal communities are widely recognised as valuable habitats for a rich diversity of vertebrate and invertebrate species, and for commercially important species of scalefish and shellfish. Potential human impacts, including sedimentation, on the long-term health and survival of coastal algal communities have been studied in detail (e.g. Daly & Mathieson 1977, Littler *et al.* 1983, Schaffer & Parkes 1994, Airoldi & Cinelli 1997, Renaud *et al.* 1997, Irving & Connell 2002, Johansson 2002, Connell 2005, Valentine & Johnson 2005). Researchers in the Mediterranean suggest that an increase in sedimentation within coastal macroalgal communities results in decreased growth of sensitive algal species due to shading effects of sediment in the water column and on algal surfaces (Airoldi 1998, Piazzi & Cinelli 2001). Conversely, many algal turfs are particularly adapted to survive in elevated sedimentation environments (Airoldi 1998, Airoldi & Virgilio 1998) and recent research has shown that invasive turf species are out-competing native turf and non-turf species in sediment-affected environments (Piazzi & Cinelli 2001). Similarly, Valentine & Johnson (2005) found that increased sedimentation, bound in a semi-consolidated matrix by filamentous red algae, led to persistence of an invasive species, *Undaria pinnatifida*, by preventing the regrowth of native algal species after severe urchin grazing. Decreasing irradiance levels due to increased sedimentation can also result in the migration of algal species into shallower waters, thereby increasing competition with shallow-water species (Johansson 2002), and potentially changing the coastal community structure and the distribution of algal species.

Coastal Antarctica is considered an environment with low natural rates of sedimentation (Isla *et al.* 2001), due largely to the high percentage of ice covered terrain (an estimated 96% of total land mass) and the total absence of large river systems. However,

the Antarctic coastal marine environment has distinct seasonality with many areas completely covered by sea ice for more than nine months of the year, followed by a brief one to three month period of open water during summer when high productivity within the water column reduces water clarity. During the summer months, intense solar radiation over long day lengths and above-zero temperatures cause snow and ice to melt, and result in melt streams and/or broad scale movement of water through terrestrial catchments to the marine environment. The majority of meltwater flows across ice covered terrain and therefore contains little terrigenous sediment. However, in areas within or adjacent to weathered bedrock, flowing water can entrain terrestrial sediments that are subsequently deposited into the marine (or lacustrine) environment.

Human activities associated with research stations in Antarctica require the development of infrastructure such as roads to allow movement of cargo to and from supply vessels during the brief summer period. Each year at Australia's Casey Station, a one kilometre road is graded and stabilised with crushed local rock to allow heavy machinery to transfer food and supplies from the wharf to storage areas. In addition, roads of crushed rock around the station buildings are maintained throughout the summer. For a period of approximately six weeks from mid-December, the mean daily maximum temperatures at Casey Station are often above freezing, and meltwater flows off the station roads, down the catchment gradients into a small valley and into Brown Bay. At peak flow, surface sediment plumes are visible at the interface of the meltwater and seawater in Brown Bay. Within a ten year period from 1996, no sediment plumes have been observed entering the marine environment in the Casey region at any site other than Brown Bay.

Antarctic macroalgae has relatively low species richness compared with lower latitudes, with an estimated 120 - 130 known species (Wiencke & Clayton 2002), and high endemism (Clayton 1994). The distribution of macroalgae in Antarctica is known to vary in response to local environmental conditions such as sea ice development and persistence, ice scour, and water movement (Zaneveld 1965, Moe & DeLaca 1976, Cormaci *et al* 1992, Amsler *et al* 1995, Gutt 2001). Research on Antarctic macroalgae has largely been

associated with ecophysiology and specific adaptations to widely varying irradiance resulting from seasonal sea ice and snow cover (see reviews by Kirst & Wiencke 1995, and Wiencke 1996).

Palmaria decipiens (Reinsch) Ricker is an endemic Antarctic red alga with a circumpolar distribution (Wiencke & Clayton 2002). Commonly forming high density, almost monospecific, beds on shallow (<20 m), sub-tidal hard bottom, *P.decipiens* is considered a pseudoperennial in that it develops new thalli each summer from a persistent basal disc. *P.decipiens* is well adapted to low light environments below sea ice, yet is able to survive the extremely high irradiance of shallow, clear Antarctic waters after summer sea ice break out (Weykam & Wiencke 1996). *P.decipiens* is also considered a 'season anticipator' (Wiencke 1990) due to its ability to start growing thalli in late winter/early spring under the low irradiances prior to, and therefore in anticipation of, the break-up of sea ice. The mechanism behind this phenomenon is thought to be synchronised with increasing daylength (Weykam & Wiencke 1996).

At Casey Station, *P.decipiens* (and most other macroalgae) are completely absent from the innermost reaches of Brown Bay where the annual sediment plumes occur. This study was designed to assess the potential impact of terrigenous sediments resulting from annual road development and other station activities at Casey Station on the natural distribution of *P.decipiens* on hard substrata in Brown Bay. The aims of this study were threefold: (1) to determine whether healthy, 'wild' individuals of *P.decipiens* translocated into Brown Bay and two other bays in the Casey region could survive and grow under natural conditions; (2) to determine whether a reduction in the naturally occurring sediment rates at each bay could significantly affect survival and growth of translocated *P.decipiens* individuals; and (3) to determine the relationship between irradiance levels and growth in *P.decipiens* in the absence of sedimentation.

Materials and Methods:

Description of bays

The experiment was undertaken in three shallow bays (<15 m deep) in the vicinity of

Australia's Casey Station (66.28°S, 110.53°E) within the Windmill Islands of eastern

Antarctica (*Fig.5.1*). The first bay (Brown Bay) was chosen due to observations of a

surface sediment plume, thought to result from station activities during the summer months.

The other bays (McGrady Cove and O'Brien Bay 1) were chosen as 'control' bays nearby

the station (2 - 3.5 km) but outside the influence of its activities. Macroalgae used in the

translocation experiments were sourced from Sparkes Bay on the southern side of the

Mitchell Peninsula (*Fig.5.1*).

Both Brown Bay and McGrady Cove are small embayments within the larger

Newcomb Bay. Brown Bay is 500 m north-east of Casey Station and is free of sea ice for

~4 wks per year. The bay receives most of the meltwater generated within the station

catchment area via melt streams that enter the bay from a small valley on the western shore.

Brown Bay's southern shore consists of low (3 - 4 m) ice cliffs, while the northern and

westerns shores are weathered outcrops of bedrock, boulders and cobble that continue into

the water. McGrady Cove is located in the eastern corner of Newcomb Bay ~2 km north-

east of Casey Station. The bay is ice free for ~4 wks per year, and receives meltwater via

streams flowing from the ice plateau below the Løken Moraines (*Fig.5.1*). The southern

and eastern shore consists of ice cliffs up to 8 m high, while the western shore is a

weathered bedrock ridge with boulders and cobble.

O'Brien Bay is 2 km south of Casey Station, and is similar in shape and size to

Newcomb Bay (*Fig.5.1*). O'Brien Bay 1 is a small embayment on the southern side of

O'Brien Bay, ~3.5 km from Casey Station. This bay is ice free for <4 wks per year, and

receives meltwater via a valley on the south-western shore. The northern and western shore

is exposed bedrock, with weathered boulders and cobble, while the southern shore consists
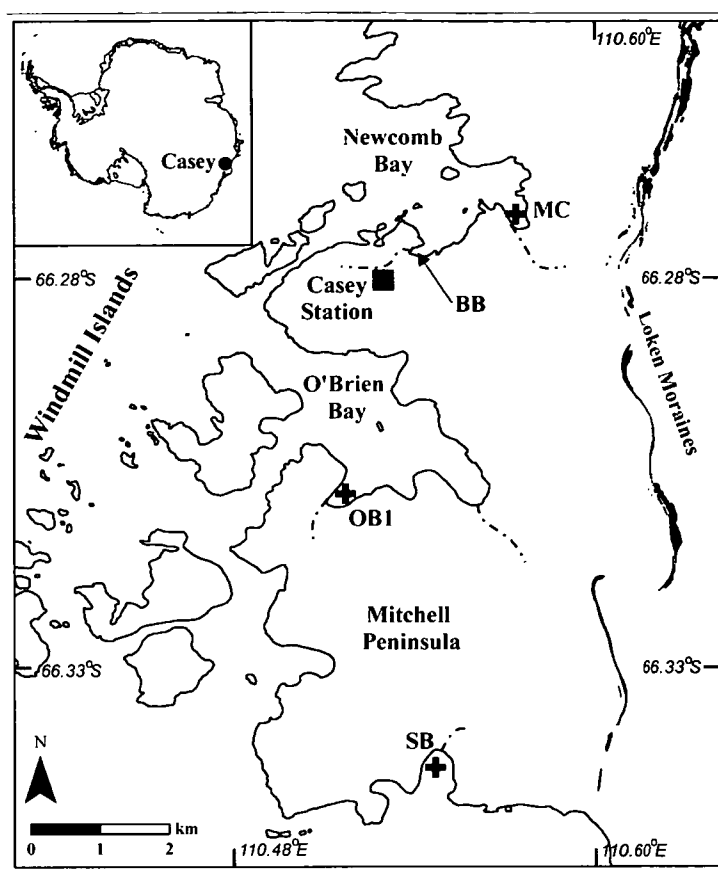
of 5 - 8 m ice cliffs.

Figure 5.1   Map of the Windmill Islands coastline near Casey Station illustrating bays where
experiments were deployed, and places mentioned in the text. BB=Brown Bay, MC=McGrady
Cove, OB1=O'Brien Bay 1, SB=Sparkes Bay. Approximate path of major melt stream entering each
bay is depicted by dashed lines.

All three bays were considered to have broadly similar environments in terms of area

(less than 0.4 km^2), shape (parallel sided, open bays), aspect (northerly facing), water flow

(sheltered, low energy, low current), and sea ice cover (1.3 m thick for >10 months each

year). Snow cover overlying the sea ice varied between bays, with Brown Bay having the

deepest snow cover (>1 m), and the other bays having a relatively thin cover of snow

(<0.3 m).

Sparkes Bay is a shallow bay (<12 m deep) on the southern side of the Mitchell

Peninsula, ~7 km south of Casey Station (*Fig.5.1*). The bay is free of ice for ~8 wks per

year, and receives meltwater via several streams on the north-western shore. The western

shore is weathered bedrock ridges, boulders and cobble that extend into the water, while the

north and eastern shore consists of 5 - 20 m ice cliffs.

Benthic environments within each bay consist of an irregular patchwork of isolated

boulders (20 - 35% cover) within fine grained sediment basins (~90% <500 μm). Hard

substratum is colonised to varying extents by encrusting invertebrate taxa such as sponges,

bryozoans, polychaetes, and ascidians. Macroalgae were not observed at any of the

deployment sites, but well-developed macroalgal-dominated communities were present at

Sparkes Bay. The bays chosen for placement of experimental units were essentially flat

sediment areas adjacent to naturally colonised hard substrata. All work at all sites was

undertaken at 6 m depth to avoid depth-related effects. This is the average depth at the

head of Brown Bay nearest the observed sediment plumes.

Experimental Design

A field experiment was designed to assess whether the distribution of the

rhodophyte, *Palmaria decipiens*, in the vicinity of Casey Station is determined by local

sedimentation rates. Translocation of healthy *P.decipiens* from a natural source into sites

where these macroalgae are not naturally found forms the basis of the experiment. At each

site, replicate cobbles with attached *P.decipiens* were exposed to three sediment treatments

to determine whether a reduction in sediment loading within the bays would significantly

alter algal growth over 12 and 36 months.

In addition, an aquarium experiment was designed to assess to what extent different

irradiance regimes could affect growth of *P.decipiens*. This experiment used a variety of

irradiances, independent of sedimentation, to determine the lower limit that would allow

discernable thallus growth. Change in thallus length relative to mean length of thalli at the

commencement of the experiment was used as a measure of growth.

Macroalgae translocations (field experiment)

Approximately 200 small cobbles (50 - 100 mm diameter) with attached thalli of

Palmaria decipiens were collected on 3 February 2003 by divers from a depth of 6 m in

Sparkes Bay. The 'algal cobbles' were placed carefully into shallow plastic trays underwater before being raised to the surface where the trays of cobbles were transferred into 52 L black plastic bins of cold, fresh seawater, and covered with black plastic lids to avoid light stress. The cobbles were transported to Casey Station, rinsed of adherent silt and motile fauna, and transferred into multiple 50 L glass aquaria containing fresh seawater (34 ppt) maintained at -0.5 ±0.3°C, via a recirculating hyper-saline jacket system.

Each algal cobble was subsequently photographed and numbered with a plastic tag attached to stainless steel wire. The length of each of the four longest *Palmaria decipiens* thalli was measured on each cobble. Once all cobbles were labelled and thalli measured, they were randomly allocated to treatments and bays. Within seven days of the initial collection, cobbles were deployed into the three translocation sites, with an additional suite of cobbles returned to Sparkes Bay as a check for algal damage/loss during cobble relocation (i.e. handling control).

Experimental units consisted of replicate 'algal cobbles' placed loosely into plastic trays that were attached to the uppermost side of each upturned, weighted 52 L plastic bins (645 x 413 x 276 mm). The configuration of experimental units prevented burial of the numbered cobbles within the sediments at each bay thus ensuring recollection of tagged cobbles at a later stage, and permitted uninterrupted water flow around the algae to promote health.

Three levels of sediment treatment were used: 'reduced sedimentation' (full Plexiglas shield), 'natural sedimentation' (no Plexiglas shield), and 'experimental control' (partial Plexiglas shield). Full sediment shields were made from sheets of 3 mm thick clear UV acrylic (Plexiglas Sunactive GS) that permits transmission of >70% of UV wavelengths (315 – 380 nm) and thus does not confound the effect of sedimentation with markedly reduced UV levels. Shields were cut to fully overhang the bins by 200 mm on each side to reduce the natural rain of sediment reaching the algae. The shields were attached to stainless steel rods protruding from each corner of the bin to a height of 200 mm above the surface of the algae. Partial Plexiglas shields were cut to enable them to attach to the

stainless steel rods but approximately 80% of the overlying shield was cut away to allow sediment to reach the algae. Experimental units within the 'natural sedimentation' treatment had no stainless steel rods or Plexiglas shield.

Six experimental units (two of each sediment treatment) were gently lowered by divers onto the sea bed at 6 m depth at each bay. The units were arranged haphazardly with random positioning of treatments within the group, with each unit ~2 m from its nearest neighbour. Once the units were positioned, eight predetermined (but randomly allocated) 'algal cobbles' were distributed between plastic trays on each experimental unit (i.e. 16 cobbles per treatment). At Sparkes Bay, eight labelled 'algal cobbles' were deployed on each of two experimental units without Plexiglas shielding (as for other sites) and in addition, 16 labelled cobbles were 'replanted' onto the sea bed adjacent to the experimental units in an area marked by weighted buoys to enable relocation. Those cobbles were otherwise treated in exactly the same way as the cobbles in the sediment treatments.

At each collection time, a random selection of four numbered cobbles from each experimental unit was handpicked by divers and placed into individual dark plastic jars. The jars were screwed closed while underwater to avoid light and temperature shock to the algae during transit back to the laboratory.

Cobbles with attached algae were deployed in early February 2003, and the first retrieval was during January/February 2004 (after 12 months), with final retrieval occurring in January/February 2006 (after 36 months). Divers scraped the Plexiglas shields clean of sediment approximately every 3 - 4 wks throughout the Antarctic summer, completely removed the shields at the end of each February when the snow melt had ceased, and reinstalled them early in the following December prior to the start of the summer melt.

Sea ice and the overlying snow thicknesses were measured at each deployment bay at the start of each summer, and sea ice break-out times were noted. Levels of photosynthetically active radiation (PAR, 400 - 700 nm) at 300 mm above the snow surface, underwater 30 mm below the bottom of the sea ice and 300 mm above the sea bed at 6 m depth were simultaneously recorded at solar noon on cloudless days in mid-summer

at each bay. These measurements (μmol photons.m^{-2}.sec^{-1}) were made using a series of underwater quantum sensors (Li-Cor LI-192SA) connected to a multi-channel, data logger (Li-Cor LI-1400). The sensors measured continuous running averages of instantaneous readings over 15 sec intervals.

Sedimentation monitoring

Local sedimentation was monitored throughout the experiment using collection jars installed in each experimental unit. Collection jars (30 mm diameter, 70 mm deep) were placed into holes cut into the upper surface of each experimental unit, in positions adjacent to the 'algal cobbles'. Jars were numbered and, during sampling, were capped underwater by divers, removed and replaced with a clean jar. Jars were sampled at ~6 wk frequency throughout the summer, and left in place throughout the nine month winter periods (March to November). Collected jars were taken to Casey Station for analysis.

Growth under varying irradiance levels (aquarium experiment)

Approximately 30 small cobbles (50 - 100 mm diameter) with attached thalli of *Palmaria decipiens* were collected in early December 2003 by divers from a depth of 6 m in Sparkes Bay. The cobbles were collected as described above. At Casey Station, the 'algal cobbles' were rinsed of adherent silt and motile fauna, and distributed randomly between ten 50 L glass aquaria of fresh, aerated seawater (34 ppt) that was maintained at -0.5 ±0.3°C, via a recirculating hyper saline jacket system. Each aquarium was illuminated from above with multiple Sylvania 50 W Biolux fluorescent tubes, providing ~86 μmol photons.m^{-2}.sec^{-1} ambient irradiance levels. A photoperiod varying from 20 - 22 hrs of light per day was used to mimic local ambient conditions. Initially, the aquaria were covered with opaque plastic lids to reduce light levels reaching the algae during the 1 wk acclimation period. Aquarium water quality (temperature and salinity) was monitored daily and partial water changes (~25% by volume) were made in each aquarium every two weeks throughout the experiment.

Five irradiance treatments (~0, 6, 12, 25, and 50% of ambient) were established using neutral density plastic film fixed within wooden frames. The neutral density filters

were selected to have broad spectrum transmission across the spectrum 330 - 700 nm. The 0% irradiance treatment was established using thick, black builder's plastic. The sides of all aquaria were wrapped in black builder's plastic to exclude reflected light. The irradiance treatments were randomly allocated to the ten aquaria, with two aquaria per treatment. At the commencement of the experiment, each aquarium was covered with the allocated irradiance treatment filter frame, and the algae were left undisturbed for 8 wks.

Levels of photosynthetically active radiation (PAR, 400 - 700 nm) reaching the cobbles within each treatment aquaria were measured at the beginning and end of the experiment using a series of underwater quantum sensors (Li-Cor LI-192SA) connected to a multi-channel data logger (Li-Cor LI-1400). These sensors measured continuous running averages of instantaneous readings over 15 sec intervals. Simultaneous measurements of irradiance levels (μmol photons.m^{-2}.sec^{-1}) above the light filters (i.e. ambient irradiance), and at cobble depth beneath the light filters within the aquaria were logged.

Laboratory analysis

Macroalgae translocations

At Casey Station, the 'algal cobbles' sampled from the experimental units at each bay were stored temporarily in their sealed jars within a darkened refrigerator before being photographed and rinsed of sediment. The four longest thalli of *P.decipiens* on each cobble were measured, along with a general description of thalli appearance.

Sedimentation monitoring

Sediment collected in jars from each experimental unit was vacuum filtered onto either glass fibre or cellulose acetate filter papers, depending on sediment volumes, oven dried at 30°C for 24 hrs, then weighed to the nearest 0.1 mg. Distinction between sediment source (marine versus terrestrial) was not possible due to the small amounts present.

Growth under varying irradiance levels

At the commencement of the aquarium experiment, the four longest *P.decipiens* thalli were measured on each of a random selection of 12 cobbles. These measurements provided a mean thallus length for cobbles at the beginning of the experiment (*Time 0*).

Cobbles used for this baseline determination were not used any further in the aquarium experiment. To establish a baseline, algal lengths were measured on the 12 random cobbles rather than for each cobble being used in the experiment because low ambient temperatures at the time were causing freezing of the algae during length measurements and it was considered likely that the algae could be damaged and potentially affect the experimental results. The baseline was deemed representative of the range of algal lengths on all cobbles used in the experiment since the baseline cobbles were randomly selected from the suite of available cobbles.

At the end of the experiment, each cobble from the ten aquaria was photographed and the length of the four longest *P.decipiens* thalli on each cobble was measured to the nearest mm.

Statistical analysis

Univariate statistical analysis was undertaken using GMAV (Underwood & Chapman 1998) with treatment effects identified using ANOVA, and where significant, multiple pairwise comparisons using the Tukey HSD (honestly significantly different) test.

Macroalgae translocations

A three factor nested ANOVA design (GMAV, Underwood & Chapman 1998) was used to test for differences between *P.decipiens* thallus growth under 'natural sedimentation', with main effects of time (3 levels, fixed), site (4 levels, random, orthogonal), and experimental unit (2 levels, random, nested within site), using the mean thallus length on four cobbles per experimental unit (n=8).

A four factor nested ANOVA design was initially used to test for differences due to sedimentation treatments at each site. Sparkes Bay data was excluded from this analysis due to an unbalanced design, thus resulting in main effects of time (3 levels fixed), site (3 levels, random), sedimentation treatment (3 levels, fixed), and experimental unit (2 levels, random, nested within site x sedimentation treatment), using the mean of four thallus lengths on each of four cobbles per experimental unit.

Sedimentation monitoring

Daily sedimentation rates ($g.m^{-2}.day^{-1}$) were calculated for each sediment jar at each of four sites. The mean length of time within each sampling period is: 293 days (Feb. – Nov.03), 60 days (Nov.03 – Feb.04), and 724 days (Feb.04 – Jan.06).

A three factor nested ANOVA was used to identify differences between and within sampling periods and translocation sites, with main effects of time (3 levels, fixed), site (3 levels, random, orthogonal), and experimental unit (2 levels, random, nested within site), using mean sediment weights from two sediment jars per experimental unit. Differences due to the sedimentation treatments were then identified using a four factor nested ANOVA with main effects of time (3 levels, fixed), site (3 levels, random), sedimentation treatment (3 levels, fixed), and experimental unit (2 levels, random, nested within site x sedimentation treatment), using mean sediment weights from two sediment jars per experimental unit.

Growth under varying irradiance levels

Mean thallus growth was calculated by subtracting the mean thallus length at the start of the experiment from the mean thallus length measured at the end of the experiment. The mean thallus growth per cobble was obtained by averaging the growth measurements of the four thalli obtained for each cobble. A two factor nested ANOVA was used to compare mean thallus growth of *P.decipiens* per cobble among the five irradiance treatments (5 levels, fixed) and aquaria (2 levels, random, nested within treatment), using mean thallus growth from three cobbles per aquarium.

Results:

Algal translocation experiment

A total of 144 labelled cobbles with attached *Palmaria decipiens* were translocated. Over the 36 month duration, one experimental unit was partially crushed beneath a boulder that rolled down the slope at McGrady Cove, resulting in the loss of two 'algal cobbles' and one sediment jar, and two algal cobbles 'replanted' at Sparkes Bay were not relocated.

Overall growth patterns

The initial 'algal cobbles' collected from Sparkes Bay had mean *P.decipiens* thalli lengths varying between 65 and 95 mm. Random allocation of cobbles to treatments within the three experiment sites minimised difference in mean thallus length between sites during initial deployment (*Fig.5.2*).

ANOVA comparison of mean thallus lengths revealed a significant interaction between time and site (*Table 5.1*) with algae replanted at Sparkes Bay significantly longer at the time of deployment than those used in the experiments at Brown Bay and McGrady Cove despite random selection from the available cobbles. After 12 and 36 months, mean thallus lengths at Sparkes Bay were largely unchanged whereas at all other bays the mean thallus length at deployment was significantly greater than mean lengths after 12 and 36 months, and for O'Brien Bay 1 the mean thallus length after 12 months was also significantly greater than mean thallus length after 36 months.
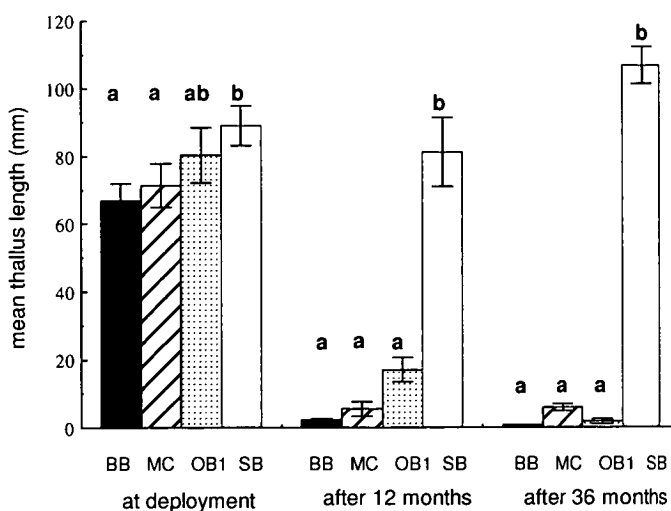

Figure 5.2   *Mean thallus lengths at each site at the time of deployment, and after 12 and 36 months (±SE, n=8). BB=Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1, SB=Sparkes Bay. Within each time period, letters above bars refer to groupings determined by Tukey HSD test results, bars with similar letters are not significantly different.*

Table 5.1 Results of ANOVA for Overall Thallus Growth (transformed Ln (X+1), P<0.05)

Source	SS	df	MS	F	P	Error
Time	99.71	2	49.85	6.24	0.0342	Time x Bay
Bay	86.01	3	28.67	150.22	0.0000	Residual
Time x Bay	47.92	6	7.99	41.84	0.0000	Residual
Residual	16.03	84	0.19			
Total	249.67	95				

The mean % change in thallus length between deployment and retrieval was calculated for each cobble and averaged for each site (*Table 5.1*). After 12 months, *P.decipiens* at all of the translocation sites exhibited a mean loss in thallus length of between 79.6 and 96.8%, while over the same time period, thallus lengths at Sparkes Bay exhibited a mean increase of 31.6%. The mean percent change at OB1 was less than at the two Newcombe Bay sites (BB and MC). After 36 months, *P.decipiens* thalli lengths at the translocation sites decreased between 91.8 and 99.0% compared to initial deployment, while thallus lengths at Sparkes Bay exhibited a mean increase of 12.7% (*Table 5.2*).

Table 5.2   Mean % change in Palmaria decipiens thallus length after deployment times of 12 and 36 months, compared to initial thallus lengths at deployment (n=8).

	Brown Bay		McGrady Cove		O'Brien Bay 1		Sparkes Bay	
	mean	SE	mean	SE	mean	SE	mean	SE
12 months	-96.8	0.7	-92.4	2.5	-79.6	3.7	31.6	9.0
36 months	-99.0	0.4	-91.8	1.3	-97.6	0.8	12.7	15.4

Thallus growth within sediment treatments

Comparison of mean *P.decipiens* thallus lengths in each sediment treatment within sites (ANOVA) was undertaken separately for each time to satisfy the assumption of data independence.

At the time of deployment, differences in the mean length of thalli among sediment treatments and the three translocation sites (*Fig.5.3*) were not significant (*Table 5.3*). However, after 12 and 36 months, algae across all treatments at the three translocation sites had significantly shorter thalli than those replanted to Sparkes Bay.

Table 5.3 Results of ANOVA for Mean Thallus Length at Deployment (P<0.05)

Source	SS	df	MS	F	P	Error
Bay	1778.45	2	889.23	2.31	0.1075	Residual
Treatment	80.54	2	40.27	0.16	0.8595	Bay x T'ment
Bay x T'ment	1024.12	4	256.03	0.67	0.6183	Residual
Residual	24239.01	63	384.75			
Total	27122.12	71				

Comparison of mean thalli lengths after 12 months deployment within the sediment treatments at each of the translocation sites revealed a significant site x treatment interaction (*Table 5.4*), mainly as a result of significantly longer thalli in each treatment at O'Brien Bay 1 compared to Brown Bay and McGrady Cove (*Fig.5.3*). Mean thalli lengths were not significantly different between sediment treatments within each site.

Table 5.4 Results of ANOVA for Mean Thallus Length after 12 months (transformed Ln(X+1), P<0.05)

Source	SS	df	MS	F	P	Error
Bay	14.11	2	7.06	37.94	0.0000	Residual
Treatment	0.08	2	0.04	0.08	0.9270	Bay x T'ment
Bay x T'ment	2.01	4	0.50	2.71	0.0380	Residual
Residual	11.72	63	0.19			
Total	27.92	71				

After 36 months, mean thalli lengths exhibited a significant interaction between site and sediment treatment (*Table 5.5*), with longer thalli lengths within the 'natural sedimentation' treatment at McGrady Cove compared to 'natural sedimentation' treatments at Brown Bay and O'Brien Bay 1, and compared to thalli lengths in other treatments at McGrady Cove.

Table 5.5 Results of ANOVA for Mean Thallus Length after 36 months (P<0.05)

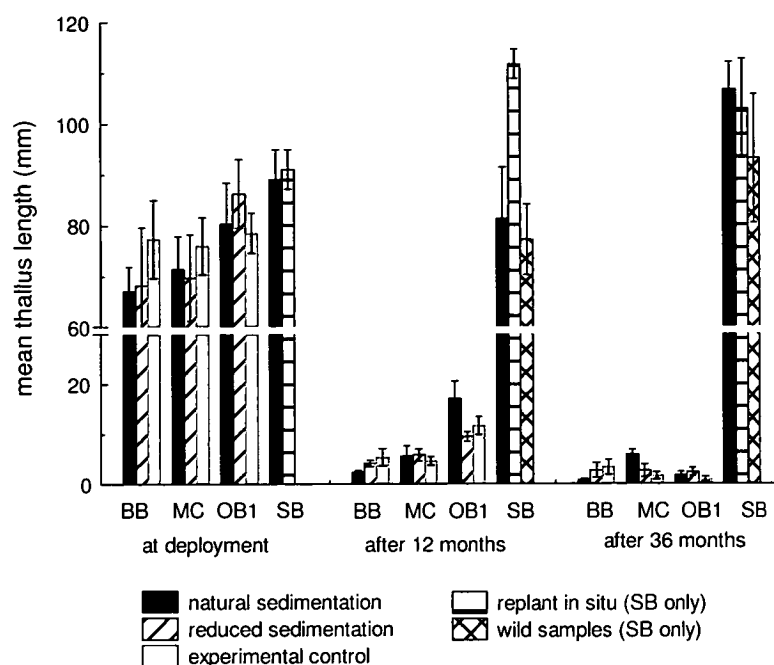| Source	SS	df	MS	F	P	Error
Bay	35.86	2	17.93	2.29	0.1099	Residual
Treatment	9.03	2	4.51	0.17	0.8530	Bay x T'ment
Bay x T'ment	109.14	4	27.28	3.48	0.0124	Residual
Residual	493.75	63	7.84			
Total	647.78	71				

Figure 5.3   Mean thallus lengths of Palmaria decipiens measured on translocated cobbles within sediment treatments at each bay at the time of deployment and at the two subsequent sampling times (±SE, n=8). BB=Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1, SB=Sparkes Bay

Sedimentation monitoring

Natural sedimentation (*Fig.5.4*) varied ~six-fold across the bays, with mean sedimentation rates between 0.6 and 4.0 $g.m^{-2}.day^{-1}$. Significant interaction between time and bay was evident (*Table 5.6*), with different sedimentation rates in each time period at McGrady Cove (Feb.04 – Jan.06 < Nov.03 – Feb.04 < Feb.03 – Nov.04), while at Sparkes Bay sedimentation was higher in the period Nov.03 – Feb.04 than either winter period.

Table 5.6 Results of ANOVA for Sedimentation (untransformed,($P<0.01$)

Source	SS	df	MS	F	P	Error
Time	7.20	2	3.60	0.92	0.4492	Time x Bay
Bay	53.04	3	17.68	76.79	0.0000	Residual
Time x Bay	23.55	6	3.93	17.05	0.0000	Residual
Residual	8.29	36	0.23			
Total	92.08	47				

During the period Feb.03 – Nov.04 (first winter) (*Fig.5.4*), the sedimentation rate

was significantly higher at McGrady Cove than at all other bays, and higher at Brown Bay

than at O'Brien Bay 1 and Sparkes Bay. During the period Nov.03 – Feb.04, Brown Bay,

McGrady Cove and Sparkes Bay had similar sedimentation rates which were significantly

higher than at O'Brien Bay 1. During the period Feb.04 – Jan.06, sedimentation rates were

higher at Brown Bay than at all other bays, and higher at McGrady Cove than at O'Brien
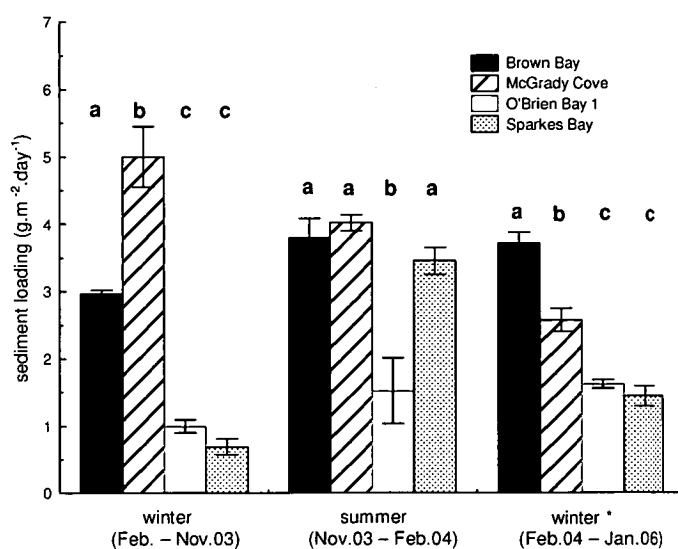
Bay 1 and Sparkes Bay.

Figure 5.4   Natural sedimentation rates at each of the bays where macroalgae was translocated
*(±SE, n=4). Within each time period, letters above bars refer to groupings determined by Tukey
HSD test results, bars with similar letters are not significantly different. * time period includes two
winters and two summers*

Comparison of sedimentation rates within sediment treatments at Brown Bay,

McGrady Cove and O'Brien Bay 1 for each time period revealed a three-way interaction

(*Table 5.7*). As would be expected where all experimental units were without Perspex

shielding, sedimentation rates during the first winter period were not significantly different

between treatments within each site (*Fig.5.5*).

Table 5.7 Results of ANOVA for Sedimentation Rates within Treatments (P<0.05)

Source	SS	df	MS	F	P	Error
Time	8.18	2	4.09	21.46	0.0000	Residual
Bay	130.68	32	65.34	342.71	0.0000	Residual
Treatment	12.36	2	6.18	32.42	0.0000	Residual
Time x Bay	28.29	64	7.07	37.09	0.0000	Residual
Time x T'ment	2.43	4	0.61	3.19	0.0174	Residual
Bay x T'ment	5.57	4	1.39	7.31	0.0000	Residual
Time x Bay x T'ment	6.65	8	0.83	4.36	0.0002	Residual
Residual	15.44	81	0.19			
Total	209.62	107				

However, during the summer period, *P.decipiens* within the 'reduced sedimentation' treatments at Brown Bay and McGrady Cove received significantly less sediment than algae within the open and control treatments at each site, whereas for the same time period at O'Brien Bay 1 algae within all treatments were exposed to similar rates of sedimentation.

During the second winter period, sedimentation rates within the 'reduced sedimentation' treatment were significantly lower than in the open and control treatments at Brown Bay but similar across all treatments at the other bays.
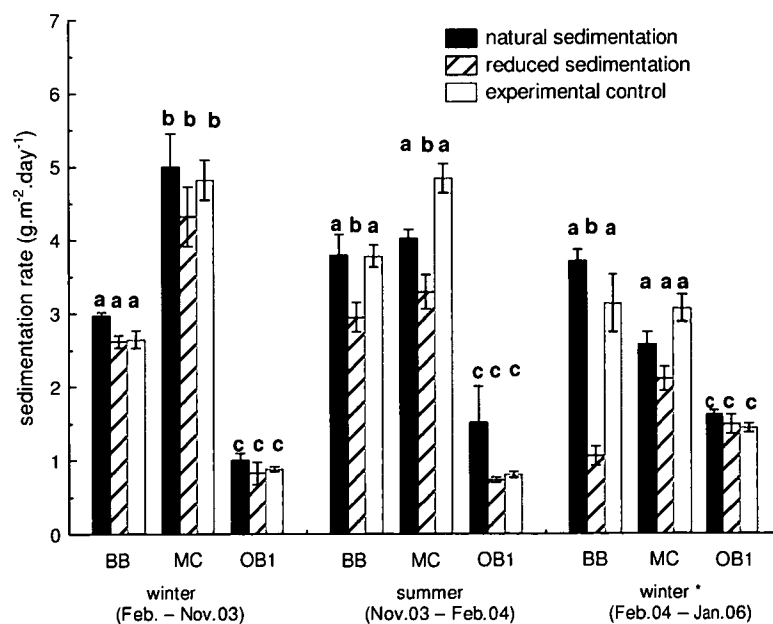

Figure 5.5   Sedimentation rates within treatments at each site across the three time periods ($\pm SE$, n=4) BB= Brown Bay, MC=McGrady Cove, OB1=O'Brien Bay 1. Within each time period, letters above bars refer to groupings determined by Tukey HSD test results, bars with similar letters are not significantly different. * time period includes two winters (2004 and 2005) and two summers (2004/05 and 2005/06)

Irradiance regimes at sites

The natural irradiance regimes differ at each site due to factors such as the snow and ice thickness, and the annual persistence of sea ice within the bays. Average sea ice thickness does not vary greatly between sites; however, the thickness of snow accumulating on top of the sea ice is different due to local topography and wind conditions (*Table 5.2*). The mean incident irradiance levels in air 300 mm above the snow surface at solar noon on a sunny, cloudless day in midsummer was measured as 2400 ±120 μmol photons.$m^{-2}.sec^{-1}$, while the mean levels of light simultaneously reaching the benthos at 6 m depth were 0.03±0.01, 1.79±0.01, 1.32±0.00, and 7.75±0.07 μmol photons.$m^{-2}.sec^{-1}$ for Brown Bay, McGrady Cove, O'Brien Bay 1 and Sparkes Bay, respectively.

Table 5.2   Site specific sea ice and snow thicknesses (±SE, n=4), and mean incident irradiance levels underwater 30 mm below the sea ice, and 300 mm above the sea bed at 6 m depth, presented as percentage of mean incident irradiance (2400 ±120 μmol photons.$m^{-2}.sec^{-1}$) on a sunny cloudless day in midsummer.

site	Sea ice (m)	Snow (m)	Mean irradiance levels (% of surface)	
			below ice	sea bed
Brown Bay	1.32 ±0.01	1.01 ±0.04	0.002	0.001
McGrady Cove	1.35 ±0.01	0.29 ±0.01	0.195	0.073
O'Brien Bay 1	1.32 ±0.01	0.24 ±0.01	0.077	0.030
Sparkes Bay	1.31 ±0.01	0.15 ±0.01	0.442	0.323

Brown Bay typically has thick snow cover of ~1 m or more which reduces the light reaching the benthos to near the detection limit of the sensor. McGrady Cove and O'Brien Bay 1 have 0.2 - 0.3 m of snow cover that reduces light availability at 6 m depth to <0.1% of surface irradiance, while Sparkes Bay has thin snow cover and therefore higher irradiance levels reaching the benthos.

Sea ice persistence varies between sites: Brown Bay and McGrady Cove are free of sea ice for ~4 wks during January and February, O'Brien Bay is generally ice free for

<4 wks in February, and Sparkes Bay is ice free for 8 - 10 wks from the middle of December.

Growth under varying irradiance levels (aquarium experiment)

The mean ambient irradiance level from the fluorescent light banks above the aquaria was measured as 85.97 μmol photons.m^{-2}.sec^{-1}. The mean irradiance levels within the five experiment irradiance treatments were measured as 0.1, 5, 11, 22, and 40 μmol photons.m^{-2}.sec^{-1}. The lowest irradiance roughly equates to the benthic light level at Brown Bay and ~10% of benthic irradiance at McGrady Cove and O'Brien Bay 1 on a sunny midsummer day. The second lowest irradiance level is 3 - 4 times the benthic irradiance at McGrady Cove and O'Brien Bay 1 and 60% of the benthic irradiance at Sparkes Bay. The third lowest irradiance level is equal to 6 - 8 times the benthic irradiance at McGrady Cove and O'Brien Bay 1 and 40% higher than the benthic irradiance at Sparkes Bay.

Comparisons between mean growth of thalli in replicate aquaria within the five irradiance treatments using ANOVA found highly significant differences among irradiance treatments ($F_{4,20}=2232.24$, $P<0.0001$). There were no significant differences between the replicate aquaria within each irradiance treatment ($F_{5,20}=0.12$, $P=0.9862$).

Mean lengths of thalli under all irradiance treatments increased, suggesting a close relationship between available irradiance and the mean increase in thallus length (*Fig.5.6*).

Significant increases in thalli length were apparent with each increase in irradiance level ($P<0.01$ for all increases except for the increase under 11 and 22 μmol photons.m^{-2}.sec^{-1} irradiances that only had a significance level of $P<0.05$).
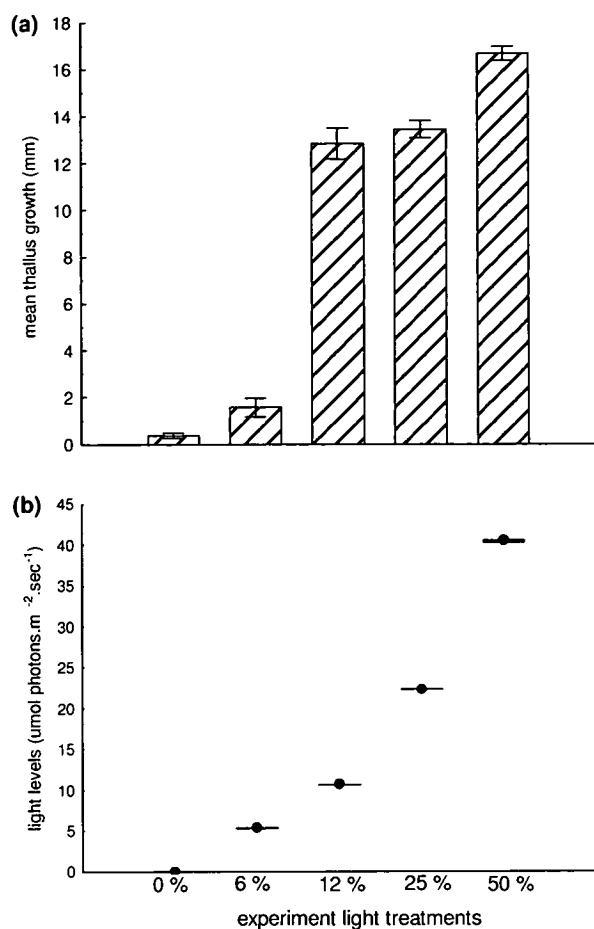
Figure 5.6   (a) Mean P.decipiens thallus growth in response to (b) the five experiment irradiance treatments in aquaria (±SE). Mean growth (n=6); irradiance levels (n=12).

Discussion:

Translocation of individuals of 'wild' *Palmaria decipiens* to similar depths at locations where these macroalgae are not found naturally results in significantly lower growth of thalli over 12 and 36 month periods compared to algae relocated back to the collection site. Except at the collection site, growth of thalli did not occur and thalli decreased in size by more than 90% after a 36 month deployment period. These results clearly suggest that conditions within the translocation bays are unsuitable for algal growth.

The impact of location on growth of algae could be due to factors such as sedimentation rates and irradiance levels.

Sedimentation impacts on macroalgal growth

While sedimentation rates are shown to vary between the different treatments and the three translocation sites, sedimentation rates do not explain patterns of algal growth. Moreover, peak sedimentation rates during summer at the collection site (Sparkes Bay) where the algae thrived were equal to those at the translocation sites.

Reduction of sedimentation rates at the three translocation sites did not significantly affect the measured growth rates of algal thalli, suggesting that sedimentation rates at these bays are insufficient to negatively affect the growth of *P.decipiens* thalli under the irradiances experienced at each location. Elevated sedimentation has been shown to alter abundances and growth of crustose coralline algae (Fabricius & De'ath 2001) and *Sargassum* (Umar *et al.* 1998), but these studies were undertaken within tropical waters. In Antarctic locations, where sedimentation rates are naturally low and irradiances are very low for most of the year, the effect of sedimentation rates on the growth of established algae appears to be negligible, even in areas where human activities may be artificially increasing sediment runoff.

Irradiance impacts on macroalgal growth

Aquarium results suggest that there is a strong correlation between irradiance levels and thallus growth in the absence of sedimentation. Even at irradiance levels as low as 10 μmol photons.m^{-2}.sec^{-1}; thallus growth of more than 13 mm is evident over an eight week period. The 'solar noon' benthic irradiance at 6 m depth at the macroalgal dominated location of Sparkes Bay was measured as approximately 8 μmol photons.m^{-2}.sec^{-1} during the period of sea ice cover in mid summer. Clearly, if sea ice was retained in Sparkes Bay for the duration of summer the *P.decipiens* growth would be expected to be ~6 mm per month, a growth rate that would be insufficient to allow algae to attain the lengths of 200 mm or more observed in Sparkes Bay during the summer months. This illustrates the importance of a long ice-free period to support significant algal growth.

Benthic irradiance levels (at 6 m depth) even on a cloud-free, midsummer day at Brown Bay, McGrady Cove and O'Brien Bay 1 are insufficient to allow *P.decipiens* to grow. In fact, the benthic irradiance levels measured at these locations are equivalent to less than half of the irradiance within the 6% aquarium treatment. Within that treatment the mean thallus growth was <2 mm over eight weeks, so it could be expected that rates of thallus growth at Brown Bay, McGrady Cove and O'Brien Bay would be equivalent to or less than this value during the period of highest irradiance in summer. Irradiance levels would be significantly higher at each location during times when the sea ice was absent; however, at all the translocation sites, the ice free period is <4 weeks, and occurs late in the summer (February) when the sun's elevation is lower, and therefore overall photon flux through the summer period is low.

The main determinant of macroalgal distribution in Antarctica is recognised as the benthic irradiance levels and overall irradiance dose throughout the year (Wiencke 1996, Schwarz *et al.* 2003, 2005). At Cape Evans in the Ross Sea, sea ice of up to 2.5 m thickness is present for at least 10 months of the year, and the branched red alga *Phyllophora antarctica* is heavily dependant on ice-free periods to achieve most production (Schwarz *et al.* 2003). In contrast, non-geniculate coralline algae that have overlapping depth distributions with *P.antarctica*, maintain a high photosynthetic capacity despite *in situ* irradiance of less than 2 μmol photons.m^{-2}.sec^{-1} (Schwarz *et al.* 2005).

Results from the present study support the view that the irradiance environment is the primary determinant of growth (and health) of *P.decipiens* within small bays of the Windmill Islands region of Eastern Antarctica. Interestingly, *P.decipiens* can sustain life for at least three years in areas with low irradiance that is clearly unsuitable for growth of thalli. This ability may be an important survival strategy in areas where the persistence of sea ice varies from year to year. However, algae this close to the limits of survival and at the extreme margin of its distribution is unlikely to be reproductively viable.

Macroalgae in Brown Bay

The physical environment of Brown Bay currently precludes the natural occurrence of *P.decipiens*, and given the benthic irradiance regime, it is unlikely that the macroalgae have been a natural resident of the innermost reaches of Brown Bay, or the other translocation sites, in the recent past. Therefore, it is unlikely that the absence of *P.decipiens* at Brown Bay can be attributed to the elevated sedimentation rates evident within the bay. Despite the higher sediment loads in Brown Bay, the low levels of benthic irradiance due to thick snow cover and the long-term cover of sea ice throughout the year prevent the successful growth of thalli and reproductive ability. This study illustrates the importance of sufficient benthic irradiance for the successful growth of macroalgae, and infers that in areas where sea ice is persistent for most of the year, irradiance levels for algal growth are marginal at best.

The potential for human activities to alter the natural irradiance levels within bays close to research stations is apparent. Construction of buildings or fences, placement of cargo, or modification of the natural landscape can and does alter snow accumulation patterns. If persistent snow thicknesses on sea ice are increased due to anthropogenic activity, there is the potential for benthic irradiances to be reduced below critical levels for macroalgal survival. Similarly, if meltwater runoff from station areas increases turbidity levels (ie. reduces benthic irradiance) and/ or sedimentation rates in coastal waters the distribution of macroalgae could be affected.

Conversely, if the predicted climate change trends associated with greenhouse gases occur (Anisimov *et al.* 2007), there is a distinct possibility that sea ice thickness and/or persistence and snow cover will decrease, causing an increase in benthic light irradiances that may allow expansion of macroalgal distribution ranges into areas that are currently unsuitable.

Conclusions:

The distribution of the macroalga, *Palmaria decipiens*, is strongly determined by the irradiance levels available for growth. In some shallow bays supporting hard substrata, sea ice and snow cover reduce benthic irradiance levels by more than 99% of incident light. All locations in the Windmill Islands are covered by sea ice for part of the year, yet abundant macroalgae is only found in areas where the ice free period is more than four weeks during summer. The lack of macroalgae in bays adjacent to Casey Station cannot be attributed to elevated sediment, but is more likely due to the low irradiance dose as a result of heavy snow cover on sea ice, and the presence of sea ice for almost 11 months each year. This study has shown that established *P.decipiens* are able to tolerate marginal increases in sediment loads, at least in the short to medium term, as long as irradiance levels are sufficient, and growing season of suitable length.

However, the distribution of Antarctic marine macroalgae could be negatively affected on a local scale by station activities that inadvertently increase the depth of snow cover overlying sea ice (thereby reducing benthic light levels), or be positively affected on a continent-wide scale, by the predicted decrease in extent and persistence of sea ice, and snow cover under climate change scenarios (Anisimov *et al.* 2007).

Chapter 6
General Conclusions

Overview

Research described in this thesis examined the potential impacts of sedimentation and benthic irradiance on shallow rocky reef assemblages in Antarctica. The research focused on Brown Bay in the Windmill Islands where turbid surface plumes occur each summer due to meltwater runoff from Australia's Casey Station. Observations made during previous studies indicated a paucity of reef species in Brown Bay compared to other bays nearby, and differences were attributed to two possible factors: 1) elevated sedimentation rates resulting from human activities, and 2) lower benthic irradiance caused by thicker snow cover overlying sea ice.

The Brown Bay catchment includes Casey Station and local activities undertaken here such as snow clearing, road maintenance and vehicular traffic that increase the sediment flux entering Brown Bay. Despite having the smallest catchment of the five bays within this study, Brown Bay received more than three times the sediment load as the other bays during the peak mid-summer meltwater period between December and February.

The potential impact of elevated sedimentation rates on nearshore reef assemblages in Antarctica was unknown before this study. Through systematic surveys of the benthos, assessment of physical characteristics of survey locations and the application of *in situ* manipulative experiments in association with aquarium-based studies, it is now known that terrestrially-derived sediments can and do have a significant negative influence on Antarctic reef assemblages. In addition, the level of benthic irradiation was confirmed as an important factor influencing post-settlement growth of two endemic species of macroalgae.

Diversity of Antarctic Benthic Assemblages

The diversity of benthic marine assemblages on hard substrata at the innermost reaches of five shallow, low energy bays in the Windmill Islands (i.e. Brown Bay plus four 'control' bays) was assessed through analysis of video quadrats. Benthic assemblages at 6 m depth were dominated by sessile filter-feeding invertebrates such as sponges, tube-dwelling polychaetes, bryozoans and hydroids. A total of 40 fauna and five flora taxa were found in a combined survey area of 67.5 m^2 yet diversity was highly variable between bays with the highest diversity at O'Brien Bay 1 (23 taxa per 2.25 m^2) and the lowest at Brown Bay (5 taxa). Diversity values, particularly those for Brown Bay, were considered low in comparison to results from other Antarctic surveys undertaken on hard substrata at similar depths - e.g. 13 – 20 species per m^2 in Terra Nova Bay, Ross Sea (Gambi *et al.* 1994); >75 species in 2.75 m^2 at Adelaide Island off the Antarctic Peninsula (Barnes & Brockington 2003).

The subtidal zonation patterns described by Dayton *et al.* (1970) for southern McMurdo Sound are skewed towards shallow depths at the bays surveyed in the Windmill Islands, with a narrower 'bare zone' (at 0 - 4 m water depth *c.f.* 0 - 15 m at McMurdo) and a shallower upper margin of the 'coelenterate-hydroid zone' (at 4 m water depth *c.f.* 15 m). Ice disturbance to benthos was less severe within the protected environments of the five bays studied because ice scouring was only apparent to a depth of approximately 4 m (ie. Dayton's 'bare zone') and there was no evidence of anchor ice. In addition, the geographical shape and position of the five bays and the shallow bathymetry adjacent to survey locations, provided significant protection from icebergs that are known to scour benthic habitats elsewhere in polar regions (Gutt 2001). These factors, together with sea ice cover for >10 months per year, resulted in a low incidence of ice scour and a consequent increase in the cover of sessile invertebrates on hard substrata in shallow depths (~6 m). The upper sub-littoral zonation described here is suggested to be more typical of environments that are exposed to low wave and current energy, and low incidence and magnitude of ice scour activity because of stable sea ice cover for much of the year. Barnes

et al. (2006) observed similar patterns in a *"uniquely protected"* location (Moraine Fjord on South Georgia Island) where disturbance from ice, waves and currents was largely absent.

Gambi *et al.* (1994) discuss two patterns of benthic community organisation in the Ross Sea: 1) highly diverse, structurally complex assemblages largely controlled by biological factors with slow growing, long-lived species deemed highly sensitive to physical disturbance (e.g. Dayton *et al.* 1974, Battershill 1990), and 2) oligospecific, poorly structured assemblages controlled by high levels of physical disturbance from ice (e.g. Dayton *et al.* 1970), and they concluded that a third pattern, typical of shallow hard substrata in the Ross Sea, is composed of few species at relatively high densities that are positively correlated with macroalgal cover. A further benthic assemblage was described by Barnes *et al.* (2006) who recognised a rich and diverse community in shallow depths within Moraine Fjord on South Georgia Island. They concluded that the assemblage was a good example of how a Southern Ocean benthic community can develop in the absence of disturbance from ice, waves and currents.

Clearly, the low diversity, low density assemblages apparent in the five bays studied for this thesis do not fit neatly into any of these previously described benthic assemblage patterns from elsewhere in the Antarctic. The combination of low ice disturbance, low energy water flow, and persistent sea ice (and snow) cover for >10 months of the year creates a stable low light environment where macroalgae are rarely seen, and a low number of sessile invertebrate taxa dominate in shallow water. This newly described benthic assemblage pattern is attributed to the specific environmental conditions of bays which have low ice scour and low irradiance levels. Understandably, the vast coastline of Antarctica has a myriad of unique environmental conditions that influence benthic community organisation and as further benthic surveys are undertaken the range of assemblage patterns is likely to expand further.

Low diversity is not suggested as indicative of the entire range of habitats in the Windmill Islands region but is attributed to the low energy, protected bays targeted for this research. Indeed, more diverse, algal dominated assemblages are known to occur at

exposed locations nearby (author's unpublished data). In the protected bays of the Windmill Islands, the benthic communities are less likely to experience the high levels of physical disturbance that are often attributed to promoting higher diversity (e.g. Gutt 2000, Barnes & Conlan 2007), and are subjected to long periods of sea ice and snow cover that significantly reduces the annual benthic irradiance budget that strongly influences macroalgal distribution (Wiencke 1990a,b). According to Gambi *et al.* (1994), benthic diversity and abundance on the shallow rocky reefs of Terra Nova Bay in the Ross Sea is positively correlated with the presence of well developed macroalgal communities that provide micro-habitats. In the five Windmill Island bays discussed here, macroalgae is largely absent and the benthic assemblages are potentially less diverse due to the reduced number of micro-habitats available in the absence of macroalgae.

Shallow Reef Assemblages in Brown Bay

Assemblages on hard substrata at Brown Bay were significantly different to those at control bays. Some taxa found at all control bays were absent from Brown Bay (e.g. *Gellius* sp., *Potamilla antarctica*, *Sterechinus neumayeri*, and several species of encrusting bryozoa), while the benthic assemblage in Brown Bay was depauperate in terms of total sponge taxa. In contrast, two taxa (*Ophiura crassa* and *Homaxinella balfourensis*) were significantly more common at Brown Bay than at any of the control bays.

Sessile filter-feeding invertebrates are known to be affected by increased sediment loads due to clogging of their feeding apparatus and smothering (Moore 1977, Ellis *et al.* 2002). In the Western Mediterranean, Maldonado *et al.* (2008) showed that sponge recruits protected from siltation lived longer than those exposed to siltation, and concluded that sediment loads are a major mortality factor among small sponge individuals in sublittoral rocky communities. The absence of sponges, encrusting bryozoa and *P.antarctica* in Brown Bay is attributed to the elevated sedimentation rates evident in the bay. The urchin, *S.neumayeri*, is less likely to be directly affected by sedimentation although elevated sediments (and low light levels) might be responsible for the low diatom and encrusting algae cover found at Brown Bay, and therefore limit food availability for the urchin. The

reason for the higher numbers of the ophiuroid, *O.crassa*, and higher cover of the sponge, *H.balfourensis*, at Brown Bay is less clear. However, these species might simply be more tolerant of the elevated sediments (and low light levels), and therefore more able to capitalise on the lower abundance of competitors (and/or predators) and increased availability of space. Interestingly, both *O.crassa* and *H.balfourensis* are dominant species observed in the low energy environments beneath persistent sea ice cover at New Harbour on the western shores of McMurdo Sound (Dayton 1990, Dayton *et al.*1970, 1974).

High physical disturbance by ice has been implicated in the loss of benthic biomass, and changes to biodiversity and community structure (Gutt 2001, Brown *et al.* 2004, Barnes & Conlan 2007), however, the low diversity and low cover of benthos identified for the shallow, low scour environments in the five bays studied must be determined by factors other than physical disturbance by ice. Brown Bay had the lowest benthic irradiance levels of all of the survey bays presumably because of the thick layer of snow overlying the sea ice. This feature, along with sedimentation rates that are more than three times the rate at control bays, indicates that the differences in benthic assemblages in Brown Bay are potentially related to the sedimentation and irradiance regimes.

Sedimentation Impacts

Recruitment to hard substrata

Recruitment rates of sessile invertebrates to artificial hard substrata were low at all bays studied, with only 5 - 20% of available tile surfaces colonised after 37 months. Recruiting assemblages were numerically dominated by spirorbid polychaetes and encrusting bryozoan species, suggesting they are opportunistic recruiters in Antarctic coastal waters. These patterns are similar to findings from other studies also utilising artificial substrata elsewhere in the Antarctic (Dayton 1989, Pearse & Pearse 1991, Bowden 2005b, Webster *et al.* 2006).

The sessile assemblage recruiting to artificial hard substrata in Brown Bay was depauperate compared to control bays, with fewer total species, and fewer bryozoan species recruited after 13 months. Only the most common taxa (e.g. spirorbid polychaetes,

Celleporella antarctica, Inversiula nutrix), were found on tiles from Brown Bay. Recruitment rates in Brown Bay were slower than at the other bays, where it took 37 months for the number of recruiting individuals to attain the numbers that recruited after 13 months in control bays. Sedimentation rates on the tiles were significantly reduced at all bays by installing Plexiglas shields, yet significant increases in total diversity associated with this treatment were only apparent at Brown Bay. This suggests that a reduction in sediment loading in Brown Bay could potentially allow more species to recruit to available hard substrata than currently recruit under 'natural' sediment loads, and sediment loads at control bays are insufficient to reduce diversity of recruitment to hard substrata. Despite the inherent natural variability between recruiting assemblages in the study bays, sediment caused a measurable negative effect on recruitment to hard substrata in Brown Bay but not at control bays. This result suggests that the anthropogenic activities at Casey Station are artificially elevating sedimentation rates in Brown Bay and causing detectable negative impacts on benthic communities in the bay.

No other published studies have focused on sedimentation impacts on recruitment to reefs in Antarctica; however, in lower latitudes sediment deposition is well recognised as a factor structuring marine subtidal communities on hard substrata (Irving & Connell 2002, Airoldi 2003, *et al.* 2004, 2006a,b), and the early development stages of benthic taxa are considered most susceptible to sediment impacts (Santelices 1990, Coelho *et al.* 2000, Maldonado *et al.* 2008). Reduced larval or spore settlement success rates under sustained levels of increased sedimentation can have a long-lasting influence on community structure and may even affect the genetic structure of populations (Maldonado *et al.* 2008). In coral reef environments, sedimentation strongly inhibits coral settlement and recruit survival, and has been implicated in decreased juvenile coral densities on reefs (Fabricius 2005). As a result of this research in the Windmill Islands, it is now known that recruitment to hard substrata in polar environments is also susceptible to the effects of sedimentation, particularly in areas where human activities are artificially increasing sediment loads to coastal environments above natural levels.

Recruitment of macroalgae

Sedimentation had a significant negative impact on *Himantothallus grandifolius* spore settlement and subsequent early gametophyte growth. The presence of a 0.5 mm layer of sediment effectively precluded the ability of spores from successfully attaching to substrata. In addition, post-settlement smothering of attached early stage gametophytes by a thin layer of sediment significantly reduced the growth rate of germ tubes. Sediment inhibition of *H.grandifolius* spore settlement is believed to be due to physical effects rather than chemical characteristics of the sediments since a layer of sediment, whether 'clean' or 'contaminated', equally prevented spore settlement, with no additional effects apparent when using sediments contaminated with heavy metals and hydrocarbons.

During aquarium experiments small scale disturbances to sediment layers provided opportunities for successful spore settlement and subsequent growth. Sea ice covers the inner most reaches of bays in the Windmill islands for up to ten months each year effectively reducing wind and wave action, and allowing fine sediment layers to form on hard substrata. Consequently, the presence of small scale substratum surface irregularities and faunal disturbance (e.g. caused by echinoderm grazing) are likely to be important in disturbing sediment layers and facilitating spore settlement. Similarly, the thalli of large macroalgae species such as *H.grandifolius* may assist in clearing sediment from patches on the substratum by sweeping during tidal movement.

Sedimentation effects on spore settlement have been reported for temperate and tropical macroalgae species. Small amounts of fine sediment *"sufficient to occlude the substrate surface"* were sufficient to prevent attachment of *Macrocystis pyrifera* spores (Devinny & Volse 1978), and they concluded that *"conditions which allow sediment layer formation may be a natural disaster for algae reproduction"*. More recently, sediment was confirmed as an important constraint on the colonisation and development of a macroalgal community along the rocky shores of the Swedish Baltic (Eriksson & Johansson 2005) where the effect of sediment deposition was species-specific and tolerance to sediment deposition was correlated with reproductive strategies and water depth. In shallow waters of the Baltic (~8 m), those algal species producing spores over long periods of the year

were considered less prone to impacts from sedimentation than species with short reproductive periods since sediment deposition was highly seasonal and periods of storm activity cleared substrata of sediment. Antarctica macroalgae typically have short reproductive cycles with spore release occurring prior to or just after sea ice break-out (Drew & Hastings 1992, Wiencke & Clayton 2002). If Antarctic species are affected by sedimentation in accordance with the findings from the Swedish Baltic, then the short reproductive periods would make them highly susceptible to sediment deposition.

Furthermore, Eriksson & Johansson (2005) indicated that sedimentation impacts were more apparent for algal species in deeper water (15 m) where species are operating at the lower part of the light response curve and any small reduction in available light due to a thin layer of sediment was critical to reproductive success. This observed pattern is of particular relevance to the sheltered Windmill Island bays, where sediment deposition could significantly constrain the successful settlement of macroalgal spores and subsequent gametophyte growth due to the naturally low levels of benthic irradiation throughout most of the year (due to overlying sea ice and snow), and fine sediment layers are persistent due to low water movement. Indeed, the results of aquarium experiments conducted for this research at Casey Station confirmed that post-settlement growth of sporeling germ tubes was significantly reduced when sediment smothering occurred at low irradiances.

Growth of macroalgae

The potential effect of sedimentation on the annual growth of macroalgae was investigated in five bays within the Windmill Islands to assess whether anthropogenically elevated sedimentation rates could impact established macroalgal communities on shallow reefs. Significant reduction in thallus growth over 12 and 36 months was identified in individuals of *Palmaria decipiens* (Rhodophyta) that were translocated to three bays in the Windmill Islands where this species is not naturally found. While sedimentation rates were shown to vary between bays, there was no evidence of a significant correlation between sedimentation and thallus growth. Reduction of sedimentation rates (using Plexiglas shields) did not significantly alter the measured growth rates of *P.decipiens* thalli,

suggesting that sedimentation, at least at the rates measured in each bay, was not sufficient to negatively affect thallus growth of established individuals.

Impacts of Benthic Irradiance

Sea ice and snow cover are known to significantly reduce benthic light levels (McMinn *et al.* 1999) and therefore are strong determinants of macroalgal distribution (Wiencke 1996). The Windmill Island survey locations all had long-term sea ice and variable but persistent amounts of snow cover, factors that are likely to underpin the low cover of macroalgae evident in the survey. Indeed, variance components for diatoms and encrusting algae were largely attributed to differences in bays (rather than quadrats) suggesting that large scale (bay-wide) factors such as sea ice and snow cover rather than small scale factors such as ice scour are responsible for the observed differences in their cover.

Spore settlement and growth

Not surprisingly, irradiance has a strong influence on the success of spore settlement and subsequent growth of gametophytes (Santelices 1990, Miller & Pearse 1991). In aquarium experiments at Casey Station, fewer *H.grandifolius* spores settled successfully at irradiances of 0.04 μmol photons.m^{-2}.sec^{-1} than at all higher irradiance treatments. However, even at these extreme low light levels *H.grandifolius* spores are able to settle and successfully attach to available hard substrata, although subsequent growth of early stage gametophytes was shown to be more highly light dependent.

Experimental results indicated that an irradiance level of >7.12 μmol photons.m^{-2}.sec^{-1} is required to provide for growth of *H.grandifolius* spores, while a distinct increase in the growth of gametophyte germ tubes was indicated when irradiance levels reached 12.04 μmol photons.m^{-2}.sec^{-1}. Interestingly, the mean benthic irradiance level at 6 m depth under sea ice in mid-summer in four Windmill Island bays was measured as 0.007, 1.894, 1.385, and 8.974 μmol photons.m^{-2}.sec^{-1} (author's unpublished data), and the only location that supported abundant benthic macroalgal species, including *H.grandifolius*, was the bay with the highest irradiance level (Sparkes Bay). These results provide evidence that the

irradiance regime at Windmill Islands bays where macroalgae are not typically found is below the critical levels required for successful post-settlement growth of sporelings; with low irradiance attributable to persistent sea ice and snow cover for most of the year.

No other published studies have investigated spore settlement and early gametophyte growth in relation to benthic irradiance levels for Antarctic algae, but spore settlement and post-settlement growth in macroalgae at lower latitudes is known to be affected by irradiance levels. Santelices *et al.* (2002) assessed spore germination and growth under low light regimes for 17 green, brown and red algal species found in tide pools along the central Chilean coast. They found that propagules from eight species (47%) germinated under total darkness and the remaining species could do so under irradiances as low as 2 - 5 μmol m^{-2}.s^{-1}. Furthermore, once germinated the microscopic forms of 13 species were able to survive in total darkness for periods between 60 and 500 days. Inter-specific variability was apparent for growth at low irradiances and short photoperiods. Both low and high irradiances restricted growth indicating an optimal range for most species tested, for example the germlings of *Chaetomorpha firma* (Chlorophyta) grew best under irradiances between 2 and 25 μmol m^{-2}.s^{-1} and could tolerate up to 50 μmol m^{-2}.s^{-1} only when incubated under short day regimes.

The implications for Antarctic macroalgae are that successful spore settlement is possible under the low irradiances apparent under sea ice and thick snow cover, and that germlings can possibly survive long periods of low irradiance during periods of extended sea ice persistence. This is an important strategy for species distributed in areas along the Antarctic coast where sea ice and snow cover varies inter-annually.

Growth of macroalgae

Significant reduction in thallus growth over 12 and 36 months was identified in individuals of the rhodophyte *Palmaria decipiens* that were translocated to three bays where this species is not naturally found. While sedimentation rates did not correlate with reduced thalli lengths during *in situ* experiments, experiments in aquaria indicated that in the absence of sedimentation there is a strong correlation between irradiance levels and

thallus growth. At irradiance levels as low as 10 µmol photons.m^{-2}.sec^{-1} thallus growth of more than 13 mm was evident over an eight week period. The benthic irradiance at 6 m depth at the macroalgal dominated location of Sparkes Bay was measured as approximately 9 µmol photons.m^{-2}.sec^{-1} during the period of sea ice cover in mid-summer. Therefore, if sea ice was retained in Sparkes Bay for the duration of summer, growth of approximately 6 mm per month could be expected for *P.decipiens*. That growth rate would not be sufficient to allow algae to attain within a single summer, the lengths of 200 mm or more observed in Sparkes Bay, and illustrates the importance of sea ice-free periods where higher benthic irradiance facilitates increased thallus growth.

Under-ice benthic irradiance levels (at 6 m depth) at Brown Bay, McGrady Cove and O'Brien Bay 1, even on a cloud-free mid-summer day, are insufficient to allow *P.decipiens* to grow. Benthic irradiance levels measured at these bays are equivalent to less than half of the irradiance treatment that produced mean thalli growth <2 mm over eight weeks in aquaria. Optimal growth would therefore only occur at these bays during periods without sea ice, yet each of these bays has ice-free periods of less than four weeks each summer. Such short periods of irradiance suitable for growth are insufficient to sustain growth and therefore macroalgae are absent from those bays. The absence of *P.decipiens* (and most other macroalgae) at Brown Bay is most likely attributed to low benthic light levels rather than a negative effect of elevated sedimentation rates on adult algae.

The main determinant of macroalgal distribution in Antarctica is recognised as the benthic irradiance levels and overall irradiance dose throughout the year (Wiencke 1996). At Cape Evans in the Ross Sea, sea ice of up to 2.5 m thickness is present for at least 10 months of the year, and the branched red alga *Phyllophora antarctica* is heavily dependant on ice-free periods to achieve most production (Schwarz *et al.* 2003). In contrast, non-geniculate coralline algae that have overlapping depth distributions with *P.antarctica*, maintain a high photosynthetic capacity despite *in situ* irradiance of less than 2 µmol photons.m^{-2}.sec^{-1} (Schwarz *et al.* 2005).

Results from the present study support the view that the irradiance environment is the primary determinant of growth (and health) of *P.decipiens* within small bays of the Windmill Islands. Interestingly, this research has shown that *P.decipiens* can sustain life for at least three years in areas with low irradiance that is clearly unsuitable for growth of thalli. This ability is an important survival strategy in areas where the persistence of sea ice varies from year to year. However, algae this close to the limits of survival and at the extreme margin of its distribution is unlikely to be reproductively viable during the long periods of low irradiance.

The annual benthic irradiance budget is critical for the sustained growth of macroalgae in Antarctic bays, whereby the length of the ice free period is particularly important. In the Windmill Islands, Sparkes Bay has an ice free period of more than two months (author's personal observations) whereas bays with limited or no macroalgae cover were ice free for one month or less each year. Schwarz *et al.* (2003) identified the two month ice-free period at Cape Evans, Antarctica as the only time when irradiance was sufficient to enable *Phyllophora antarctica* (Rhodophyta) to undertake measurable thallus growth. They concluded that low respiration rates enhanced the longevity of the *P.antarctica* thallus, enabling it to survive the winter darkness and take advantage of periods of higher irradiance. Antarctic macroalgae are able to successfully colonise suitable substrate only where the annual irradiance budget exceeds the critical threshold for the full range of lifecycle stages.

Anthropogenic Impacts on Antarctic Benthos

Sedimentation rates are significantly higher and benthic irradiance is significantly lower at Brown Bay than at the control bays in the Windmill Islands. Brown Bay benthic assemblages had the lowest cover, lowest number of individuals and lowest number of species compared to the control bays. *In situ* and aquarium experiments confirmed that sedimentation rates experienced in Brown Bay are capable of reducing the diversity of recruitment of most invertebrates to hard substrata, while benthic light levels are insufficient to support settlement and growth of macroalgae such as *H.grandifolius* and

P.decipiens. Overall, the recruitment of benthos and the development of benthic communities on nearshore hard substrata in Brown Bay is strongly influenced by sedimentation and irradiance.

Elevated sedimentation rates measured in Brown Bay are directly attributed to human activities on and around Casey Station. Disturbance of natural snow cover causing the exposure of bedrock and soil within the station limits and the establishment of crushed rock roads for the annual resupply of the station are contributing to increased sediment loads to the nearshore marine environment. The annual pulse of sediment-laden meltwater into Brown Bay at the height of summer (December – February) is sufficient to negatively influence the recruitment of benthic species to the shallow reefs. As a result, the reef assemblages in Brown Bay are considered to artificially depauperate compared to reefs in similar environments in the Windmill Islands.

Mitigation of elevated sedimentation rates in Brown Bay can most easily be addressed through the reduction of sediment loading in the snow melt discharged to the bay. Changing methods of road construction to reduce reliance on the mechanical removal of snow and the addition of crushed rock would significantly reduce the sediment loading of meltwater. Alternatively, establishing engineering controls for the downstream treatment of meltwater prior to discharge to the bay would also reduce sedimentation rates on shallow reefs. Meltwater treatment could include techniques such as construction of settlement ponds for the passive reduction of suspended solids, or channelling of meltwater through a variety of sediment screens prior to release into Brown Bay.

In comparison with sedimentation rates, benthic irradiance levels in Brown Bay are less likely to be directly affected by human activities at Casey Station and are more likely a direct result of the local geography influencing the natural distribution of both sea ice and snow cover. However, the removal (and disposal) of snow during snow clearing activities at Casey, and the alteration of natural snow deposition adjacent to artificial structures (e.g. snow drifts) could inadvertently increase snow thickness overlying sea ice, contributing to reduced benthic irradiance and negatively impacting benthic assemblages. Mitigation of

such impacts is best undertaken through the careful consideration of snow clearing and disposal areas, and judicial placement of structures to reduce the build-up of snow.

On a larger scale, climate change is predicted to affect the development and distribution of sea ice, rates of snow fall and snow melt (Anisimov *et al.* 2007). Although still uncertain, the increased temperatures and precipitation predicted for Antarctica could result in larger volumes of meltwater passing across areas of reduced snow cover and entrainment of sediment causing more widespread elevation of sedimentation rates above current levels. In addition, the continued shrinkage of glaciers (Anisimov *et al.* 2007) is likely to expose moraine fields to wind and water transport leading to higher sediment loading of meltwater. These scenarios could potentially increase the rates of sediment impacting nearshore marine environments in Antarctica and affect the distribution and recruitment of benthic assemblages on shallow reefs. Alternatively, any reduction in the extent and duration of sea ice along the Antarctic coast could result in higher benthic irradiance levels providing the opportunity for a widened distribution of macroalgal communities. Regardless of the mechanism, the distribution of benthos along the Antarctic coast is likely to be changed as a result of significant climate change.

Anthropogenic impacts to nearshore benthos are likely to occur in all areas where human activities are causing or have the potential to cause an increase in the levels of terrestrially-derived sediment entering the marine environment. To date, the assessment of potential impacts to marine environments in Antarctica has largely focussed on contaminants such as metals and hydrocarbons associated with abandoned rubbish dumps (e.g. Stark *et al.* 2005) and oil spills (e.g. Thompson *et al.* 2007). Results described in this thesis highlight the need to consider also the physical stressors such as sediment runoff and the potential negative impacts of artificially increased sedimentation rates on nearshore marine assemblages.

Negative impacts of anthropogenically elevated sedimentation rates on reef benthos in Brown Bay were identified during this research; however, it must be noted that pollutants are also known to have entered the bay prior to and during the research period.

Research described in this thesis has concentrated on the physical effects of sediment and irradiance on reef benthos, and the *in situ* experiments could not separate these factors from any potential chemical effects of polluted sediments and/or meltwater within the Brown Bay. Notably however, comparisons of 'clean' and 'contaminated' sediments in the spore settlement experiments partly explored the independent effects of pollutants and physical effects of sedimentation, and the results of these experiments and the *in situ* work at Brown Bay using sediment shields to manipulate sediment loads, illustrate an effect of sediment alone. The potential effects of contaminated sediments are largely beyond the scope of this thesis and are being addressed by other researchers in order to more fully understand the range of human impacts occurring in the region.

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