

Antarctic patterns of shallow subtidal habitat and inhabitants in Wilke's Land

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Abstract Studies of east Antarctic marine assemblages on hard substrata are rare. In relation to sea-ice breakout, we assessed benthic patterns of habitat and inhabitants between islands and bays at each of two depths (6 and 12 m) across the Windmill Islands coast. Island sites experience sea-ice breakout in the austral spring, while bay sites typically retain sea-ice cover into the summer and in some places the cover is virtually permanent. Composition of assemblages differed between sheltered bays and exposed islands. Islands were dominated by macroalgae, which also varied with depth. Immediately below the ice-foot zone at 6 m, substratum space were monopolised by foliose red (*Palmaria decipiens*) and foliose brown (*Desmarestia* sp.) algae, whereas at 12 m large canopies of *Himantothallus grandifolius* was abundant. The understory consisted of a mixture of turfs and encrusting red algae at 6 m, and coralline algae at 12 m. Sheltered bays had

large areas of sediment/algal complex and no canopy-forming macroalgae. We found more sponges and hydroids in bays, and more brittle stars around islands. Experiments testing factors that covary with exposure and depth in Antarctica, such as light, sedimentation and ice scour are necessary to determine processes that maintain these striking patterns.

Keywords Rocky-coast · Macroalgae · Invertebrates · Ice-cover · Antarctica · community structure · Ice-sheets

Introduction

The quantitative description of pattern forms the basis of ecological research and it is useful to establish predictions of pattern based on some key and easily quantifiable variables (Underwood et al. 2000; Quinn and Keough 2002). Physical variables are often correlated and single factors are therefore unlikely to fully explain patterns, but they may still act as useful predictors. Ice cover is one of the most dynamic physical variables to influence Antarctica's continually cold and nutrient-rich waters (Drew and Hastings 1992; Gomez et al. 1997). Ice plays a major role in the ecology of shallow Antarctic marine systems. The detachment or movement of ice in close proximity to hard-substrata is a major source of physical disturbance (Clarke and Leakey 1996; Gutt 2001), while the presence of sea-ice greatly reduces light penetration to the waters beneath (Buckley and Trodahl 1987; Dummermuth and Wiencke 2003).

A striking feature of the coast of Wilkes Land, east Antarctica, is the extensive nature of islands and bays, which are likely to provide quite different physical

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conditions that may affect the distribution of habitat forming organisms. Bays are generally protected areas subject to prolonged ice-cover and islands represent exposed areas experiencing ice-breakout earlier in the season. We therefore predict that canopy-forming algae that rely on light will predominate in exposed areas where ice breaks out first, whereas invertebrates that are sometimes more abundant in the absence of light (Glasby 1999) will predominate in more protected ice-bound areas where they are not outcompeted by algae. We also predict a stronger effect of depth at islands where light may be attenuated.

Past studies in Antarctica have described patterns in invertebrate and algal distribution, although they are largely confined to west Antarctica, particularly the Antarctic peninsula (Amsler et al. 1995; Barnes 1995b; Brouwer et al. 1995; Kloser et al. 1996). Furthermore, due to the extreme conditions of fieldwork at latitudes higher than 60° south, the majority of near-shore coastal studies have been undertaken at a limited number of sites (e.g. one transect at one site, Miller and Pearse 1991; Barnes and Brockington 2003). Larger scale surveys have been conducted remotely (using grab samples and photosampling) at greater depths off the continental shelf (Clarke et al. 2003; Teixido et al. 2004).

The primary aim of this study was to test for an association between habitat-type (bays and islands) and inhabitants in relation to water depth and exposure. This study provides a direct comparison of the flora and fauna in communities subject to different durations of ice-cover, which was used to represent a suite of environmental conditions (e.g. light intensity, sedimentation, and ice scour) that are likely to be strong drivers of Antarctic rocky coast ecology (Martin Riddle, personal communication). While such influences superficially appear to be unique to ice-covered coasts, many of the actual mechanisms involved may be common to temperate coasts (Connell 2006). Such tests may provide insight into which patterns are likely to represent the outcome of special events (i.e. unique to eastern Antarctica) and which patterns may be susceptible to future tests about the existence of broader phenomena (i.e. regional–biogeographic–global).

Materials and methods

Study sites

We sampled shallow rocky coast assemblages from the Windmill Islands coast of east Antarctica during the austral summer of 2004. We avoided areas of severe and direct ice abrasion, which occurs as an “ice-foot” zone

by sampling assemblages below 5 m (Barnes 1995a; Brouwer et al. 1995). Four sites (two bays and two islands) in close proximity to Casey Station, Antarctica (66°S 110°E) were sampled for invertebrates and algae (Fig. 1). Sites were selected according to exposure (presence or absence of ice-cover), presence of rocky coast, and accessibility by boat. Benthic communities at Windmill island sites are exposed to long days (up to 24 h) and little sea-ice cover for much of November through to February each year (Riddle, personal communication). Bay sites may experience sea-ice breakout for only brief periods (several days) often in January or February (Allison 2005). The ice covering the exterior coast of our island sites had broken up and disappeared by October of 2003, whereas bays retained ice-cover throughout the survey period (January and February 2004).

Sampling protocol

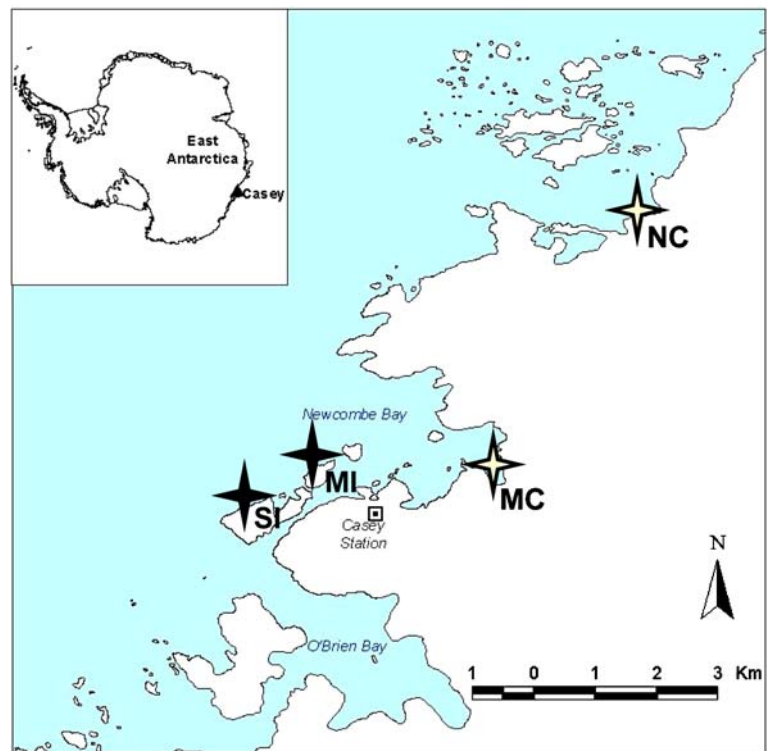
The distribution and extent of habitats were quantified using transects (see Goodsell et al. 2004) that were laid along the 6 and 12 m depth contours ($n = 4/\text{depth}$). Each transect was 30 m long and separated by at least 10 m. Finer scale sampling involved quadrats (400 cm² and 1 m², $n = 8$) at both 6 and 12 m depths. Quadrats were haphazardly sampled at each depth and site and replicates were separated by at least 5 m. All sampling was done in situ.

Major habitat types consisted of macroalgae (*Himantothallus grandifolius*, *Palmaria decipiens* and *Desmarestia* sp.) and sediment/algal complex (fine sediment and diatom film combined with varying densities of filamentous green algae). Fine sediments were generally less than 5 mm thick overlying a rock substrate. Habitat types were quantified using the transect method described above. Understorey assemblages (turf-forming algae, coralline and non-coralline encrusting algae) and encrusting invertebrates were quantified in 400 cm² quadrats by recording the identity of all organisms under each point in a 25 point grid (Drummond and Connell 2005). This provided an estimate of percent cover of the rocky substrate. The smallest organisms counted using the point grid method in 400 cm² quadrats were spirorbids (~2 mm diameter). All macro-invertebrates were counted in 1 m² quadrats and included ophiuroids, asteroids, holothurians, gastropods, sponges, hydroids, anemones and sabellid polychaetes. The smallest organisms counted in 1 m² quadrats were gastropods (>5 mm).

Statistical analyses

To test for a difference between assemblages across all sites and depths, a three-factor multivariate analysis of

Fig. 1 Map of sites at which sampling was done. Open stars represent sheltered bay sites and filled stars represent exposed island sites. Casey Station and the major sites are labeled. *NC* North Corner, *MC* McGrady Cove, *MI* McMullin Island, *SI* Shirley Island



variance (PERMANOVA, Anderson 2001) was done on the fourth-root-transformed Bray–Curtis transect and quadrat data. Exposure (islands or bays) and depth (6 or 12 m) were treated as fixed factors while site was random and nested within exposure. The permutation of raw data was unrestricted and used correct permutable units (Anderson 2001) with a total of 4,999 permutations used. Pairwise tests among the levels of the factors of site and depth were done separately to examine the site(exposure) \times depth interaction term. To visualise multivariate differences, a non-metric multi-dimensional scaling (nMDS) ordination was constructed from the Bray–Curtis similarity matrices using the SYSTAT statistical package.

Univariate analyses were used to test for a difference in the abundance of individual taxa. Individual taxa were subject to univariate analyses if they were sampled with a mean of $>5\%$ cover in at least one depth-site combination (in transects and 400 cm^2 quadrats) or with a mean density >1 (in 1 m^2 quadrats). Organisms that did not meet this criteria were: anemones, urchins, scallops, fish and sabellid polychaetes. These organisms also had a low frequency of occurrence in quadrats ($<17\%$). When organisms occurred in both bays and islands they were subject to three-factor univariate analysis of variance, treating factors as described above. When organisms were completely absent from either bays or islands the fixed factor of Exposure (ie. bays or islands) was removed from the analysis and a two-factor ANOVA was done using depth

(fixed) and site (random) on the reduced data set. When an interaction term was non-significant at $P > 0.25$, the term was removed and a reduced model was run. When an organism occurred at only one site or depth a single-factor ANOVA was done. When an organism occurred in only one site by depth combination, no analyses were done. Analyses of variance were done using SYSTAT Version 10 (SPSS Inc.). The assumptions of normality and heterogeneity of variance were tested for each variable by examining residual histograms and scatterplots of estimates versus residuals, respectively (Quinn and Keough 2002). When necessary, data were square root transformed to satisfy the assumptions of ANOVA. In certain cases (for spirorbids, hydroids, sponges, brittle stars and bryozoans) homogeneity of variance could not be achieved because the organism was absent from at least one site-depth combination. ANOVA are robust to breaches of this assumption but we are nevertheless cautious in interpreting tests for these taxa.

Results

Benthic assemblages

Assemblages of benthos at islands differed from bays (Table 1; Fig. 2). There was also a significant site within exposure \times depth interaction (Table 1). Pairwise tests showed that island assemblages differed with depth but

Table 1 Multivariate analyses of variance (PERMANOVA) comparing assemblages between exposure (E = islands or bays), depths (De = 6 or 12 m) and sites within islands or bays

Source	df	MS	F	P(MC)
Exposure	1	59211.0248	42.4400	0.0018
Site(E)	2	1395.1715	5.0636	0.0042
Depth	1	6716.2591	7.5988	0.0420
ExDe	1	2623.0715	2.9677	0.1546
Si(E)xDe	2	883.8630	3.2079	0.0330
Residual	24	275.5298		
Total	31			

Analyses were based on Bray Curtis dissimilarities, using 4,999 permutations of the raw data. Monte–Carlo *P* values are presented. Significant probability values at $P < 0.05$ are highlighted in bold

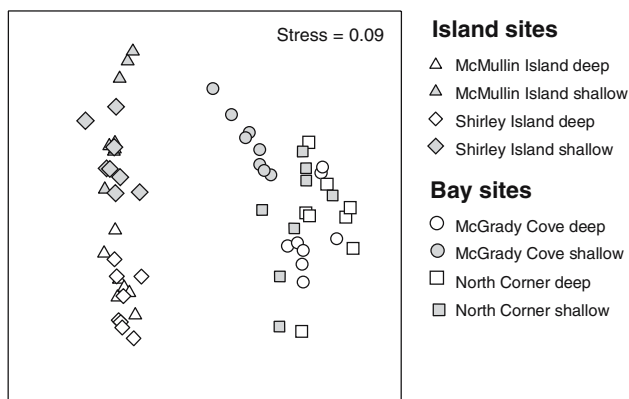


Fig. 2 nMDS ordination of transect and quadrat data from two depths (6 and 12 m) at four sites (two island sites and two bay sites)

showed no significant difference between sites at either depth. In contrast, for bays, significant differences were found between sites and there were also significant differences between depths within each site (Table 1; Fig. 2). This difference was more pronounced at North Corner.

Patterns of habitat: transect data

Macroalgae were only observed at island sites. *Himantothallus grandifolius* (brown macroalga) was most extensive at a depth of 12 m at both islands (~80% cover). It did not occur at McMullin Island at 6 m but covered ~20% at this depth at Shirley Island (ANOVA, site by depth interaction $P = 0.001$, Fig. 3a). *Palmaria decipiens* (foliose red) and *Desmarestia* sp. (foliose brown) were most extensive at 6 m depth together comprising 80–90% of macroalgal cover. They occurred to a lesser extent at a depth of 12 m (ANOVA, depth $P = 0.001$, Fig. 3b, c). There was no effect of site for either *P. decipiens* or *Desmarestia* sp. (ANOVA, $P > 0.2$, Fig. 3b, c). A fine layer of sediment

(sediment/algal complex) covered the majority (~80%) of hard-substrata in bays, but did not differ between sites or depths (ANOVA, $P > 0.7$, Fig. 3d).

Understorey assemblages: 400 cm² quadrat data

Turf-forming algae (defined as filamentous, branching or foliose algae less than 5 cm high) predominantly occurred at 6 m (60% cover). They comprised ~5% cover at 12 m at McMullin Island but were almost entirely absent at 12 m from Shirley Island (ANOVA, depth by site interaction $P = 0.037$, Fig. 4a). The percent cover of coralline algae showed the reverse pattern covering approximately 75% at 12 m and less than 10% at 6 m (ANOVA, depth $P = 0.033$, Fig. 4b). There was slightly greater coralline cover at Shirley Island than McMullin Island (ANOVA site = 0.036, Fig. 4b). Non-coralline encrusting algae, showed no strong patterns with depth or site (ANOVA, $P > 0.3$, Fig. 4c).

Sediment/algal complex generally dominated space in bays (>90% cover) but was slightly lower (~80%) at 6 m at McGrady Cove (ANOVA, depth by site interaction $P = 0.042$, Fig. 4d). Spirorbid polychaetes and the bryozoan *Inversiula nutrix* occurred at both island and bay sites. Spirorbids occurred in high densities at both depths at islands but in reduced numbers at a single bay site (McGrady Cove) at 6 m (ANOVA, depth × site(exposure) interaction $P = 0.017$, Fig. 4e). *Inversiula nutrix* distribution was patchy, only occurring at 12 m at McMullin Island and at 6 m in McGrady cove (ANOVA, site $P = 0.106$, Fig. 4f). Hydroids were only recorded from quadrats at 12 m bay sites and then only in >5% cover at North Corner (ANOVA, depth $P = 0.004$, Fig. 4g).

Macroinvertebrate assemblages: 1 m² quadrat data

Ophiuroids, asteroids and sponges were recorded from 1 m² quadrats at both islands and bays. Ophiuroids (predominantly the brittle star *Ophiura crassa*), occurred in the highest densities at deeper island sites. McMullin Island had ~10 m⁻² while Shirley Island had ~30 m⁻², at 12 m. They occurred in densities <1 m⁻² at all other sites and depths (ANOVA, depth × site(exposure) interaction $P = 0.001$, Fig. 5a). Asteroids occurred in generally low densities (<1 m⁻²) at all depths and sites (ANOVA, $P > 0.1$, Fig. 5b). Sponge cover was greater in bays than islands (ANOVA, exposure = 0.036, Fig. 5c). Hydroids were only recorded in bays and there was no effect of depth or site (ANOVA, $P > 0.1$, Fig. 5d). Small herbivorous gastropods occurred in quadrats at 12 m at McMullin Island only (Fig. 5e). Filter feeding holothurians

Fig. 3 Transect data. **a–c** Percent cover of macroalgae from two depths and four sites. **d** Percent cover of sediment/algal complex from line transects at four sites. Island sites were *MI* = McMullin Island, *SI* = Shirley Island. Sheltered bay sites were *Mc* = McGrady Cove, *N* = North Corner. Shown are mean ± 1 standard error

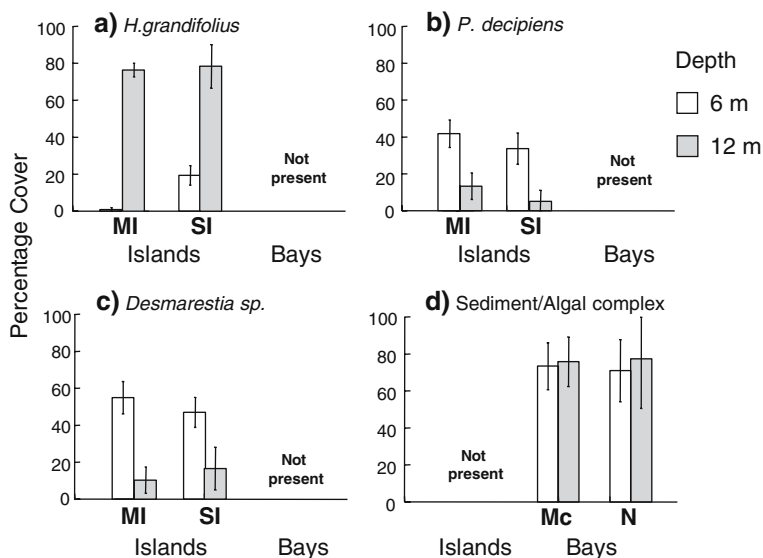
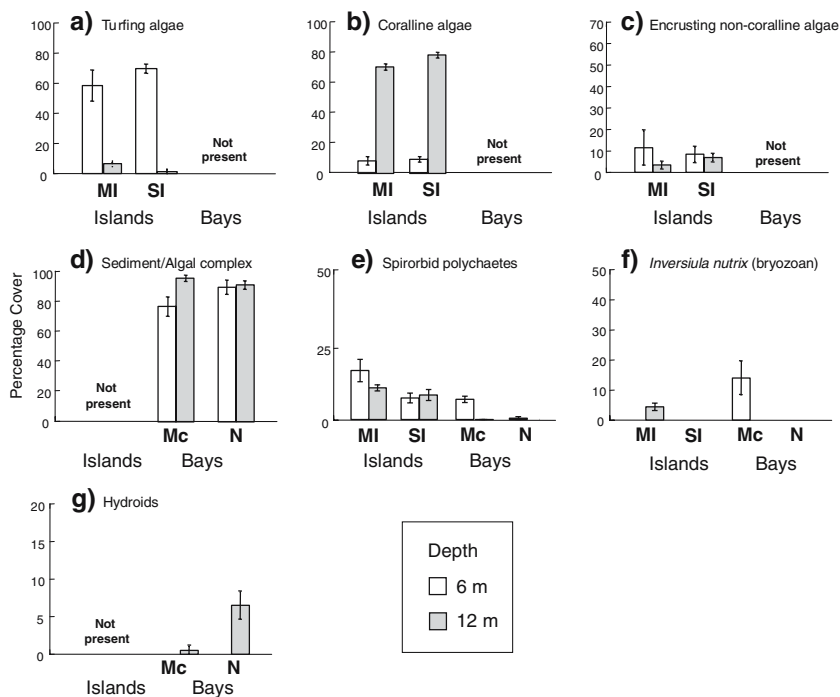


Fig. 4 Four hundred centimeter square quadrat data. **a–c** Percent cover of turf-forming algae, coralline algae and an encrusting red alga at two depths. **d–g** percent cover of sediment/algal complex, spirorbid polychaetes, *Inversiula nutrix*, and hydroids at two depths. Island sites were *MI* = McMullin Island, *SI* = Shirley Island. Sheltered bay sites were *Mc* = McGrady Cove, *N* = North Corner. Shown are mean ± 1 standard error



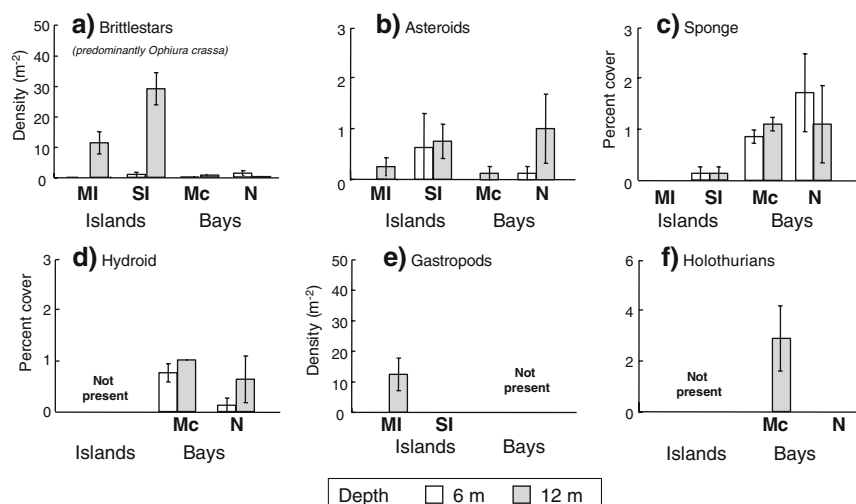
(predominantly *Psolus charcoti*) only occurred at McGrady Cove at 12 m depth (Fig. 5f).

Discussion

We assessed patterns of benthic assemblages in relation to the length of time that sea-ice breaks out (i.e. islands > bays). We recognise that physical variables are often correlated and that whilst such single factors are unlikely to fully explain patterns, they may act as powerful predictor variables (Peters 1991). Extensive

stands of canopy-forming algae were present at islands but conspicuously absent from sheltered bays. Bay sites were distinguished by a sediment/algal complex that consisted of very fine sediment, live and dead diatoms and filamentous green algae overlying a rock substrate. Invertebrate assemblages were also distinct between islands and bays. In sheltered bays there were fewer grazers and more filter feeders such as sponges, hydroids and filter feeding sea cucumbers. Differences with depth were more obvious at island sites, associated with differences in macroalgal canopies and their associated understory. The large brown alga

Fig. 5 One square meter quadrat data. **a–c** Density of ophiuroids, asteroids and sponges (m^{-2}) at two depths, **d–f** density of hydroids, gastropods, and filter feeding holothurians (m^{-2}) at two depths. Island sites were *MI* = McMullin Island, *SI* = Shirley Island. Sheltered bay sites were *Mc* = McGrady Cove, *N* = North Corner. Shown are mean \pm 1 standard error



Himantothallus grandifolius was strongly associated with a coralline algal understory at 12 m, whereas the canopy forming foliose red (*Palmaria decipiens*) and brown (*Desmarestia* sp.) algae were strongly associated with an understory of algal turf at 6 m.

No direct comparisons have previously been made between sheltered bay and exposed island sites in Antarctica, but surveys have been carried out at both locality types such as Signy Island (Barnes et al. 1996) and Ellis Fjord (Kirkwood and Burton 1988). At exposed locations, where ice breaks out early in the season, differences in macroalgal depth distribution have been attributed to the differential rates of recovery following disturbance from ice scour (Kloser et al. 1996; Dummermuth and Wiencke 2003). As reported in the current study, foliose brown algae (e.g. *Desmarestia* sp.) generally occur in shallower waters while the large brown alga *Himantothalus grandifolius* generally occurs at depths greater than 12–15 m (Amsler et al. 1995; Brouwer et al. 1995; Kloser et al. 1996). Antarctic macroalgae including, *Desmarestia anceps*, *Palmaria decipiens* and *Himantothalus grandifolius*, display similar light requirements, however, growth rates differ markedly with the larger *H. grandifolius* displaying lower photosynthetic light efficiencies at 10, 20 and 30 m (Gomez et al. 1997). *H. grandifolius* may therefore be able to recruit in the shallows but not exhibit fast enough growth to recover during the time between ice–scour disturbances (Kloser et al. 1996, Dummermuth and Wiencke 2003). Total irradiance in near-shore environments may be determining macroalgal canopy presence or absence (Dummermuth and Wiencke 2003), whereas processes related to ice–scour might influence depth distributions.

Macroalgal canopies were absent at bay sites and habitat instead consisted of a film of fine organic sediment

interspersed with filamentous green algae. Intense coastal phytoplankton blooms have been reported in many parts of Antarctica resulting in diatom sedimentation to the seabed (Clarke and Leakey 1996). Sediment accumulation, as indicated by percent cover of this sediment/algal complex, was much greater in bays than islands possibly due to reduced currents and proximity to glacial activity. Experiments that directly manipulate both light availability and sedimentation (e.g. Connell 2005) are needed to identify the relative contribution of these two factors to the patterns we observed. Whilst in temperate systems these factors are key to the assembly and maintenance of subtidal habitat heterogeneity at the scale of metres (e.g. Connell 2005), it is possible that the scale and intensity of influence of these factors is substantially greater in this Antarctic system.

Invertebrate assemblages were distinct between islands and bays. In sheltered areas, there were fewer grazers and more filter feeders such as sponges, hydroids and sea cucumbers. Kirkwood's (1988) survey of Ellis Fjord showed abundant filter feeders in an area subject to extensive ice cover while only one red macroalgae was recorded—*Phyllophora antarctica*. In McMurdo sound, 55% of the benthos beneath ice is covered by sponges with another 5% comprising bryozoans, actinians and hydroids (Dayton et al. 1974). Dayton worked at depths (30–60 m) that are unlikely to be affected by ice–scour, unlike our relatively shallow study. Even sponges at intermediate depths (15–30 m) undergo massive mortalities when subjected to unusually thick anchor ice (Dayton 1989). Our sites had substantially fewer invertebrates than either Kirkwood or Dayton report, yet a preliminary survey of a third bay site (O'Brien's Bay) did indicate a far greater cover of invertebrates than that sampled at North

Corner or McGrady cove. This difference emphasizes the need to be cautious in interpreting the results of this study and the desirability of further survey work to sample more sites of the east Antarctic coast.

We observed few large grazers (e.g. urchins), which differs from reports of Adelaide Island on the Antarctic Peninsula (Barnes and Brockington 2003; Bowden 2005) and neighboring austral coasts of temperate Australia (Andrew 1993). We did observe small grazing gastropods and brittle stars in association with macroalgae and this is possibly related to food supply through a detritus food chain. *Himantothallus grandifolius* blades decompose rapidly and the detritus is likely to support a diverse invertebrate fauna (Dieckmann et al. 1985; Miller and Pearse 1991). In temperate systems, such supply of detritus can sustain herbivores so that they have no measurable affect on assemblages of living macroalgae (Vanderklift and Kendrick 2004). Whilst untested, it appears that the capacity of herbivores to maintain space free from the overgrowth of erect algae is weak at our study sites, a phenomenon that characterizes the exposed south coast of Australia (Connell and Vanderklift 2006).

In summary, we observed marked differences in composition and abundance of benthic assemblages between exposed islands and sheltered bays of east Antarctica, as well as strong differences with depth. Such patterns are likely to be easily predicted by the duration of sea-ice cover, which appears to signal the influence of related physical processes (e.g. light penetration and sedimentation) and their direct influence (e.g. physical abrasion by ice). While such influences superficially appear to be unique to ice-covered coasts, the actual mechanisms involved may be common to temperate coasts (e.g. light regimes and sediment loads). Indeed, understanding how Antarctic systems relate to temperate, and even tropical coasts would be particularly instructive to assessments of the influence of biogeography and latitude in contemporary ecology. Frameworks that incorporate local scale research into regional scale phenomena (Connell and Irving 2006) could use Antarctic habitats to provide fresh opportunities for a more coherent understanding of communities at local through to global scales.

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