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SYMPOSIUM

Polar Ecosystem Dynamics: Recovery of Communities from Organic Enrichment in McMurdo Sound, Antarctica

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Synopsis Community structure and diversity are influenced by patterns of disturbance and input of food. In Antarctica, the marine ecosystem undergoes highly seasonal changes in availability of light and in primary production. Near research stations, organic input from human activities can disturb the regular productivity regime with a consistent input of sewage. McMurdo Sound has both high-productivity and low-productivity habitats, thereby providing an ideal test bed for community recovery dynamics under polar conditions. We used experimental manipulations of the subtidal communities to test the hypotheses that (1) benthic communities respond differently to disturbance from organic enrichment versus burial and (2) community response also varies in areas with different natural patterns of food supply. Both in low- and high-food habitats, the strongest community response was to organic enrichment and resulted in dominance of typical organic-enrichment specialists. In habitats with highly seasonal productivity, community response was predictable and recovery was rapid. In habitats with low productivity, community variability was high and caging treatments suggested that inconsistencies were due to patchy impacts by scavengers. In areas normally subject to regular organic enrichment, either from primary production or from further up the food web (defecation by marine mammals), recovery of benthic communities takes only years even in a polar system. However, a low-productivity regime is as common in near shore habitats around the continent; under these conditions, recovery of benthic communities from disturbance is likely to be much slower and follow a variable ecological trajectory.

Introduction

Accepted ecological theories point out the influence of disturbance and food availability on community diversity. Pearson and Rosenberg (1978) summarized the patterns of recovery of communities from disturbance that can be predicted from work in temperate marine systems. Following cessation of organic input, the community consisting of a few opportunistic species expanded to a diverse community. Recovery was most vigorous in the most polluted areas, but was initiated first in the areas furthest from contamination. This pattern has been supported by subsequent studies, with initial changes detectable within a year (Hunter and Evans 1995; Roberts et al. 1998; Bellan et al. 1999). The intermediate-disturbance hypothesis suggests that diversity is highest when there is a moderate intensity or frequency of disturbance and a patchwork of communities in varying stages of recovery (Connell 1978). Repeated disturbance on a time-scale much shorter than the time it takes a community to recover results in a limited array of opportunistic species. Communities are evolutionarily adapted to certain levels of disturbance (Barnes and Conlan 2007); human alteration of disturbance regimes results in unstable ecosystems with reduced diversity (e.g., over-control of chaparral fires and overgrazing on plains) (Shugart 1998).

Remote areas are historically less disturbed by human activities; the Antarctic thus exemplifies a relatively "undisturbed" environment. Despite the global-scale human-induced threats to Antarctica

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from climatic change, acidification of the ocean and depletion of ozone (Mayewski et al. 2009; Turner et al. 2009), local (point-source) impacts by humans are more limited in Antarctica than in highly populated or exploited areas. Ironically, as research is conducted, the very system under study is invariably altered. Nevertheless, the disturbances introduced are minimal relative to those encountered in more populated areas. The Antarctic represents a shrinking opportunity to learn the ecosystem mechanics of an evolutionarily adapted (as opposed to anthropogenically disturbed) community.

The current and past conditions that differentiate Antarctica from other environments have been well described (Knox 1970; Arnaud 1977; Hempel 1985; Dayton et al. 1994; Arntz et al. 1994; Clarke 1996). The seasonal pulse of particulate organic material (POM) from melting of the sea ice, advection of productivity from open water areas, and local biological production generally lasts <3 months of the year in McMurdo Sound. Locally variable environmental factors, such as duration and thickness of ice cover, and oceanographic flow patterns, impact productivity and cause marked differences in composition of the benthic community. The east (Ross Island) side of McMurdo Sound is eutrophic, relative to the west (continental) side, and supports a benthic assemblage that is more abundant by an order of magnitude (Dayton and Oliver 1977).

Organic input from sewage or other human sources in Antarctica is a disturbance to the regular regime of seasonal productivity. Although the history of Antarctic exploration is short, the consequences of human occupation of the continent are not fully known. There are 64 major facilities south of 60° with peak populations approaching 4000 annually (www.comnap.aq/operations/facilities/). McMurdo Station is the largest base on the continent, and its sewage outfall has contributed to the establishment of a unique habitat characterized by excessive organic input to the benthic community. Such enriched conditions are not found in the Antarctic except near research bases, whale falls, and other biotic depositions. Ecological assessment and monitoring in the nearshore McMurdo area have scrupulously characterized the epifaunal and infaunal communities, and the impact that the outfall, as well as other contaminants, have had on the benthos (Dayton and Robilliard 1971; Dayton et al. 1974; Dayton and Oliver 1977; Oliver 1980; Lenihan et al. 1990; Lenihan 1992; Lenihan and Oliver 1995; Conlan et al. 2004, 2010). The present conditions at McMurdo are more severe than at other, smaller stations in Antarctica (Conlan et al. 2004), but all coastal stations have some impact on the nearby benthos if they discharge their waste into the ocean.

McMurdo Sound can provide a model for understanding the processes of community recovery from organic enrichment under polar conditions and under various productivity regimes. The McMurdo Station outfall alters the habitat in two ways, by dramatically increasing the organic loading and by direct burial of the substrate. In this work, we examined impacts of these two factors on benthic communities. Despite the physiological and biochemical limitations of individual species, rates of community recovery from natural disturbances in the Antarctic (Dayton et al. 1969, 1970; Gutt et al. 1996; Bockus 1999) are comparable with those from organic disturbances in temperate and tropical regions (Hunter and Evans 1995; Roberts et al. 1998; Bellan et al. 1999). Similar patterns of zonation of the fauna along gradients of pollution and natural disturbance have been observed in McMurdo Sound (Lenihan and Oliver 1995; Bockus 1999). The time scale of years observed for recovery from natural disturbances (i.e., anchor ice) was expected to also apply to disturbances arising from organic enrichment.

We further hypothesized that the west-coast community was adapted to an environment with low productivity and hence would respond differently to organic enrichment than would the east-coast community. The prediction was that, because of the organically depleted conditions on the west coast caused by circulation under the Ross Ice Shelf, the west-coast community would lack fauna that are organic-enrichment opportunists. Therefore, the west-coast community would respond negatively to organic enrichment and would be slow to colonize unoccupied, enriched sediments. On the east coast, where availability of food is generally greater, a portion of the community consists of organic-enrichment opportunists (i.e., the polychaetes *Capitella perarmata* and *Ophryotrocha notialis*), and these species respond positively to organic enrichment (Lenihan et al. 2003). A consistent differential response will facilitate predictions of the benthic response to organic contamination by humans in other parts of Antarctica. The results inform efforts to minimize environmental impacts in Antarctica through broad applicability to the number of research stations that discharge sewage on the Antarctic coast and to the increased activity from tourism.

Materials and methods

The hypothesis that benthic communities respond differently to type of disturbance (enrichment and burial) depending on the natural pattern of food supply (location) was tested by deploying containers of treated sediment in low and high food environments and determining patterns of colonization under the different treatments in the different locations. The experimental design was fully orthogonal, with collections after 1 and 2 years, and six replicates per treatment.

Replicate experimental-substrates were placed at a depth of 18 m at four undisturbed sites: Cinder Cones, Turtle Rock (east coast, high food), Explorers Cove, and Cape Bernacchi (west coast, low food) (Fig. 1). Substrates were sediments collected from the immediate area by divers and returned to the laboratory where they were kept at room temperature for at least three days to kill existing polar fauna, and then sieved over coarse nitex screen to remove large bodies such as bivalves. Sediments were loaded into marked PVC rings (12 cm high) and returned to the field, where they were pushed into the substrate so that they were flush with surrounding sediments, to minimize hydrodynamic disruption. Rings were open at the bottom, allowing vertical porewater circulation, although lateral porewater circulation was limited by the PVC walls.

Organic enrichment treatments were defaunated sediments enriched with macerated food to approximate the C:H:N ratios of sewage (*sensu* the experimental design of C.H. Peterson, Lenihan et al. 2003). Burial treatments contained defaunated sediment alone. Controls were empty PVC rings pushed into the sediment, surrounding the existing infaunal community. Six replicates of each of the three treatments (organic, burial, and control) were regularly distributed in a rough circle; the variability in depth was <2 m.

Previous experience indicated that organically enriched treatments would be targeted by scavenging *Odontaster validus* and *Parborlasia corrugatus*, but that for short time frames these organisms could be removed and kept at bay by a fence on the sea floor. Hence, we set up duplicate treatments within a nitex mesh fence that surrounded the entire area. By using this setup, as well as arranging treatments in a circle, hydrodynamic concerns that must be addressed in studies involving cages were minimized. As scavenging organisms are natural components of the ecosystem, the question of what happens when these species are not excluded was addressed by the uncaged treatments.

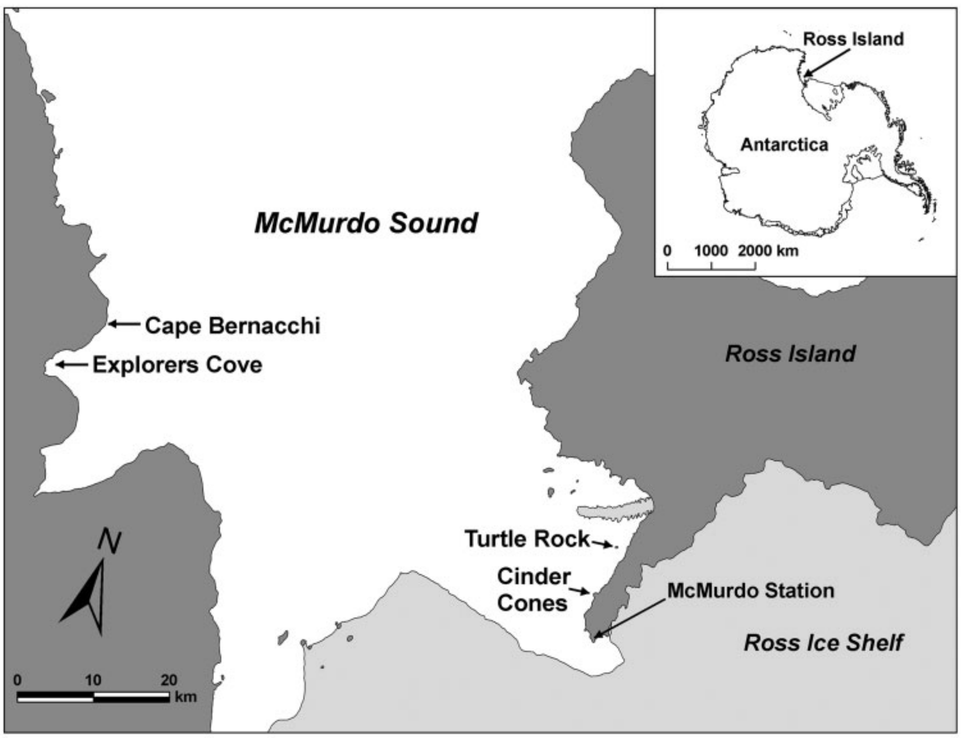

Fig. 1 Map of the study area in McMurdo Sound, Antarctica.

One set of cores (145 samples total) was recovered after 1 year, and the second (120 more samples, fewer because of lost replicates) after 2 years. Treatments were collected by divers capping the top and bottom ends of the PVC rings *in situ* and returning the whole sample to the surface, and then to the laboratory in seawater in coolers that prevented them from freezing.

In the laboratory, samples were sieved over 500 μm mesh, relaxed in 3% magnesium chloride, preserved in 5% buffered formaldehyde, shipped to the United States and stored in 70% ethanol. Sorting was done under a dissecting scope, and individuals were counted and identified to the lowest possible taxon, usually species.

All multivariate analyses were conducted on Bray–Curtis dissimilarity matrices calculated using fourth-root transformed data, which allows common, intermediate and rare species to contribute to measures of sample similarity. We used nonmetric multidimensional scaling (MDS) ordination to examine broad patterns in assemblage differences between sides of McMurdo Sound, between sites on each side of the sound, and between treatment and caging factors (Clarke and Warwick 2001). MDS uses rank order from the sample dissimilarity matrix to map relative similarities as distances between samples in space and is a visualization tool, not a statistical analysis. Each MDS has an associated stress value, which indicates how much distortion there is in achieving a two-dimensional representation of the high-dimensional community similarities (i.e., stress <2 is a good representation) (Clarke and Warwick 2001).

We used a permutational analysis of variance (PERMANOVA) routine to test for the response of a species assemblage to multiple factors on the basis of the Bray–Curtis dissimilarity matrix (Anderson 2001; McArdle and Anderson 2001; Anderson and ter Braak 2003; Anderson et al. 2008). In particular, we tested for significant year, caging, and treatment effects within each site. If a factor was significant in the main model, we then ran additional PERMANOVA routines to do pair-wise comparisons on that factor (Anderson et al. 2008). In some cases, tests of homogeneity of dispersions (PERMDISP) were used to examine the variability in species assemblages within sites and between years as an indicator of stress in the infaunal community (Warwick and Clarke 1993; Anderson et al. 2008). The PERMDISP routine compares distances from observations to a group centroid using the ANOVA *F*-statistic and is a dissimilarity-based multivariate extension of Levene's test (Anderson 2006).

To test for differences in diversity on the eastern and western sides of the sound as affected by caging and treatment factors, we conducted a three-way analysis of variance (ANOVA) on ES(100) values after confirming normality of the data and homogeneity of variance. We used ES(100) as a measure of diversity as it has few underlying assumptions and allows comparison with other studies that may have used different replication of samples (Sanders 1968; Gotelli and Colwell 2001).

Results

The communities in controls were diverse both taxonomically and ecologically (Table 1). At the eastern sites, the polychaete *Spiophanes tcherniai* formed a dense tube mat (see also Conlan et al. 2004). At the western sites, *Galathowenia wilsoni*, a polychaete that utilizes a diversity of feeding modes, dominated.

Ordination by nonmetric MDS summarizes patterns in species composition. The resulting map of community differences incorporates all the data on all the species, not just a select few. In the two-dimensional representation in Fig. 2, the further apart the symbols are, the more different the communities they represent.

The major pattern is that communities at sites on the eastern side of McMurdo Sound are separated from those on the western side. This is expected *a priori* in controls, from known differences in the natural communities. Communities in organic treatments are more different from their corresponding controls at sites on the western side than on the eastern side. To further determine if oceanographic regime had an impact on response to treatments, we performed an ANOVA on diversity ES(100). Diversity is known to be lower on the western side (Dayton and Oliver 1977); the proportional decrease in diversity following organic enrichment is also greater on the western side, as we predicted (Table 2).

The other strong pattern in the MDS is that communities with organic treatments are very different from those with burial treatments or from controls. This pattern holds regardless of location or of caging. Organic enrichment has the largest impact, but in addition, there is a more subtle pattern: communities at the two sites within each side are different. The within-site differences between treatments are minimal at Turtle Rock, moderate at Cinder Cones, and rather large at Cape Bernacchi and Explorers Cove. The variability in species composition is greatest in communities with organic enrichment, and this indicates that the differences due to organic

Table 1 Indicator species of benthic communities in McMurdo Sound

Location	Feeding style
Eastern side	
Cinder Cones	
Spiophanes tcherniai	Selective deposit feeder
Protodriloides symbioticus	Surface deposit feeder, interface grazer, facultative suspension feeder
Edwardsia meridionalis	Omnivore, predator, scavenger
Nototanais dimorphus	Grazer, predator
Philomedes sp.	Surface deposit feeder, interface grazer, facultative suspension feeder
Turtle Rock	
Spiophanes tcherniai	Selective deposit feeder
Nototanais dimorphus	Grazer, predator
Austrosignum grande	Grazer, scavenger
Philomedes sp.	Surface deposit feeder, interface grazer, facultative suspension feeder
Oligochaeta	Subsurface deposit feeder
Western side	
Explorers Cove	
Galathowenia wilsoni	Surface deposit feeder, interface grazer, facultative suspension feeder
Fabricia sp.	Surface deposit feeder
Aedicira belgicae	Subsurface deposit feeder
Eudorella splendida	Surface deposit feeder, interface grazer, facultative suspension feeder
Edwardsia meridionalis	Omnivore, predator, scavenger
Cape Bernacchi	
Galathowenia wilsoni	Surface deposit feeder, interface grazer, facultative suspension feeder
Protodriloides symbioticus	Surface deposit feeder, interface grazer, facultative suspension feeder
Aedicira belgicae	Subsurface deposit feeder
Edwardsia meridionalis	Omnivore, predator, scavenger
Capitella spp.	Deposit feeder, subsurface, surface, detritus feeder, grazer, carnivore

Feeding style listed from World Register of Marine Species (http://www.marinespecies.org/index.php) and personal observations.

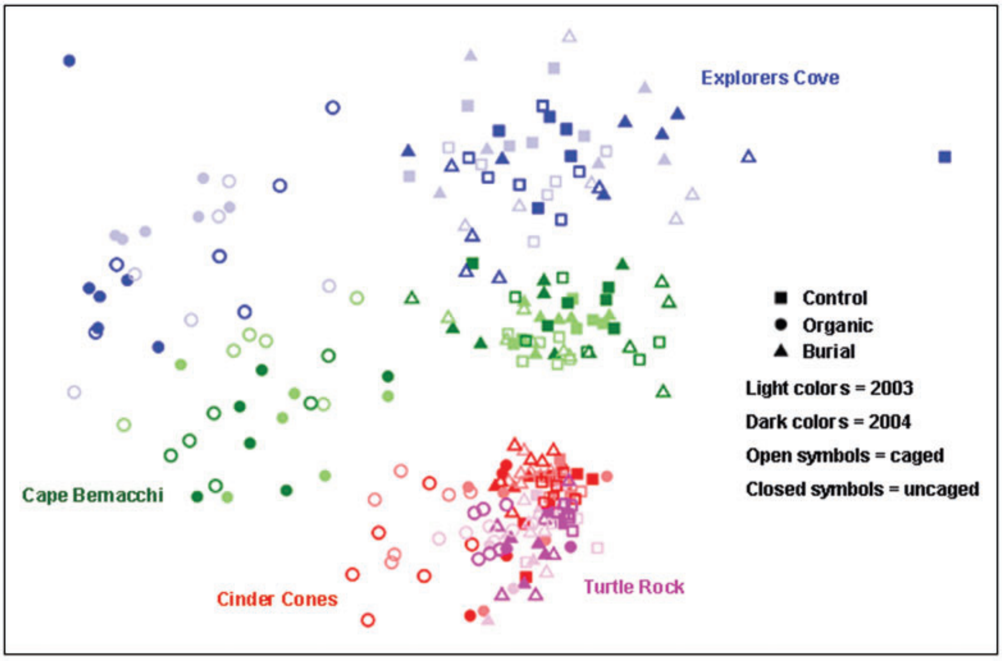

Fig. 2 Multi-Dimensional Scaling analysis of benthic communities in McMurdo Sound. Analyses were conducted on fourth-root-transformed Bray–Curtis similarity matrices of data on species abundance. Stress value is 0.17.

enrichment are subtle at Turtle Rock, and more definitive at sites on the western side. It is also evident that the communities of the western sound are in general more variable than those on the eastern side.

To look more closely at the patterns we used PERMANOVA. Because the differences in variability between sites could obscure differences in other factors, we separated sites for these analyses. We did not use parametric statistical tests because no transformation could be found that made the data meet the required assumptions of normality and homogeneity, and low and unequal replication in Year 2 due to lost treatments contributed to low overall power were an ANOVA attempted. Results of PERMANOVA for treatment, year, and caging gave the significant terms summarized in Table 3.

At Cinder Cones, treatment, year, and the interaction term between them were significant. We then separated years and combined caging for further analysis with higher power; in 2003, all treatments were different from each other, but in 2004, only enrichment and burial were different from each other. A further test of the variability of the assemblages, PERMDISP, demonstrated statistically that in both years organic enrichment resulted in more variability than in other treatments (Table 4).

Communities at Turtle Rock showed significant differences due to treatment and year in PERMANOVA tests (Table 3). All treatments were different from each other, and variability was significantly higher in organic treatments than in controls in 2003, although replication was too low in 2004 to run PERMDISP (Table 4).

On the other side of the sound at Cape Bernacchi, treatment, year and the interaction term were significant (Table 3). In PERMANOVAs on combined caging, within each year, all treatments were different from each other ($P = 0.001$). In both years variability in organic treatments was greater than in controls, and in 2004 variability in organic treatments was also greater than in burial treatments (Table 4).

The results were more complex at Explorers Cove. Along with treatment and year and their interaction, the caging × year interaction was significant (Table 3). Because there was no interaction between treatment × caging or treatment × caging × year, we separately looked within year at treatment effect, and within year at caging effect (Table 5). In both years, all treatments were different from each other (all $P = 0.002$). In 2003, caging did not have an effect, but in 2004 it did (Table 5). Because of the interaction terms in the initial PERMANOVA we cannot perform PERMDISP to statistically confirm the visual assessment of higher variability in organic treatments at this site.

Table 2 ANOVA testing effect of organic enrichment, caging, and side of the sound on diversity as measured using ES(100)

Source	DF	*F*-value	*P*-value
Treatment	2	51.92	**<0.0001**
Side	1	44.84	**<0.0001**
Caging	1	0.64	0.4241
Side × treatment	2	42.37	**<0.0001**
Caging × treatment	2	0.10	0.9031
Side × caging	1	0.99	0.3221
Side × caging × treatment	2	0.09	0.9160

Bold values indicate significant results.

Table 3 *P*-values of PERMANOVA results for individual sites

Source	Cinder Cones	Turtle Rock	Cape Bernacchi	Explorers Cove
Treatment	**0.001**	**0.001**	**0.001**	**0.001**
Year	**0.001**	**0.001**	**0.001**	**0.001**
Caging	0.450	0.072	0.108	0.767
Treatment × year	**0.001**	0.168	**0.001**	**0.001**
Year × caging	0.750	0.288	0.252	**0.008**
Treatment × caging	0.913	0.472	0.279	0.901
Treatment × year × caging	0.955	0.486	0.456	0.155

Bold values indicate significant results.

Table 4 *P*-values from PERMDISP pairwise comparisons of variability within different treatments

Cinder Cones				Turtle Rock				Cape Bernacchi			
2003		2004		2003		2004		2003		2004	
B = C	0.319	B = C	0.155	B = C	0.123	[a]		B = C	0.072	B = C	0.974
O > B	**0.001**	**O > B**	**0.001**	O = B	0.100	[a]		O = B	0.417	**O > B**	**0.010**
O > C	**0.001**	**O > C**	**0.001**	**O > C**	**0.003**	[a]		**O > C**	**0.006**	**O > C**	**0.021**

[a]Indicates too few replicates to perform the test.
Bold values indicate significant results.
B = burial treatment, O = organic treatment, C = control.

Table 5 *P*-values of Explorers Cove PERMANOVA for each year separately

Source	2003	2004
Caging	0.482	**0.020**
Treatment	**0.001**	**0.001**
Caging × treatment	0.387	0.667

Bold values indicate significant results.

Discussion

Sequences of colonization in the shallow benthic community in McMurdo Sound change in response to organic enrichment, as well as to burial. The dominant colonists indicative of organic treatments were *Capitella* spp. and *Ophryotrocha notialis*; both genera are known enrichment opportunists (Conlan et al. 2004). Their presence in controls and increased abundance in organic treatments suggests that these components of the community are well poised to take advantage of periodic organic input. Under enrichment and disturbance, there is a synergistic effect that results in a community dominated by a subset of the normal species pool. The best-known paradigm of Antarctic communities is the krill-based ice-edge system, subsisting in intensely seasonal habitat rich in food (Bargagli 2005; Knox 2006). Our study supports the hypothesis that in these Antarctic habitats the climax communities are adapted to the disturbance of seasonally high productivity.

In contrast to the food-rich but highly seasonal ice-edge ecosystem, the deep benthic community is supplied with a consistent food source from a bank of material built up from seasonal input of dead and dying plankton, which is too great to be immediately utilized (Mincks et al. 2005; Smith et al. 2006, 2008). From the experiment reported here, the Antarctic nearshore benthic ecosystem is different from both ice-edge and deep-benthic communities, being both highly seasonal and highly food limited.

On the eastern side of McMurdo Sound, where the seasonal bloom is a consistent pattern, community colonization was well advanced by 2 years. Lenihan and Oliver (1995) reported that the community takes 3–6 years to recover from defaunation. The plankton bloom is a less regular occurrence in the western Sound, where colonization of the benthic community did not proceed as quickly. Over an evolutionary timescale, regularly repeating natural inputs of organic matter from pelagic and benthic primary production leads to a community that is well adapted to take advantage of seasonal enrichment but can also persist during periods of low input of food. The environment and community of eastern McMurdo Sound exemplifies this, and responds quickly to additional enrichment.

Response to organic treatment differed not only by side of the sound, but also by site within side. The amount of organic material that settles from primary productivity does not reach the level of enrichment provided by this experiment, which was designed to mimic input of sewage. A natural input of equivalent intensity comes from Weddell seals (*Leptonychotes weddellii*), which deposit fecal material on the seafloor in discrete piles. Weddell seals congregate during the austral summer at pupping and haulout areas; Turtle Rock generally hosts a local population of several hundred seals, and Cinder Cones an order of magnitude fewer (R.A. Garrott and G.E. Stauffer, personal communication). One or two seals are seen at Cape Bernacchi each year, and none at Explorers Cove (S. Kim, K.E. Conlan, and A.R. Thurber, personal observation). The consistent localized annual input of feces may influence the benthic communities and their recovery by maintaining a local species-pool of colonists tolerant of organic disturbances. At Turtle Rock, the control communities dominated by the polychaete *Spiophanes tchernai* contained a substantial number of *Capitella* spp.; under conditions of organic enrichment *Capitella* spp. bloomed. At Cinder Cones, *Spiophanes tchernai* control communities included many *Protodriloides symbioticus*, and although *Capitella* spp. was not such a significant member of control communities it still was abundant in treatments with organic enrichment. On the western side, the community dominated by *Galathowenia wilsoni* was replaced by one dominated by *Ophyrotrocha notialis* under organic enrichment, despite the presence of *Capitella* spp. at Cape Bernacchi. *Capitella* spp. was the organic-enrichment dominant on the eastern side, *Ophyryotrocha notialis* on the western side. Although both genera are enrichment opportunists, the abundance of *Capitella* spp. in the control community appears to correlate with the abundance of Weddell seals, and may influence recruitment of this species into treatments with organic enrichment.

At sites along the West Sound, there was more variability in species composition between replicates. The western sites had lower abundance and species richness, so that the effect of a single individual was magnified in comparison with communities with more individuals and species. Sampling a larger area in these sparser communities would likely bring the variability down. There is little visual or documented variability in microhabitat in this area

(Dayton and Oliver 1977), so although patchy settling and recruitment may play a role in the patterns, a more parsimonious explanation is simple statistics.

Many Antarctic species are omnivores or scavengers, or switch between different feeding methods to take advantage of any available source of food (Peck et al. 2005; Kim and Thurber 2007). Due to this rapid and intense response to organic material, we expected that excluding megafaunal scavengers would have a substantial impact on colonization. However, the lack of a caging effect suggests that the immediate scavenging of organic material does not always affect settlement and recruitment of macrofauna. The experiments were emplaced in October; most macrofaunal settlement occurs late in the austral winter, at least on hard substrates (Stanwell-Smith and Barnes 1997; Bowden 2005); no seasonal studies on soft substrates in shallow water have been carried out. The response of scavengers to enrichment may have decreased sufficiently in the interim so that no general effect was seen. The only exception to this was at Explorers Cove after 2 years, where the caging effect was significant. Detailed examination of the data showed that this was due to two uncaged samples containing only one or two individuals rather than the usual tens of individuals; most likely these replicates had been fed upon by scavengers. Scavenging megafauna on the western side of the sound are much lower in abundance and are different species than on the eastern side. The *Odontaster validus* from the eastern side are very responsive to food falls (Kim et al. 2007); *Notasterias armata* from the western side may not be as efficient at locating organic material, although they are just as efficient at decimating infauna once they have found a food source. The outliers on the western side are likely a result of the sparser distribution of consumers there.

The fauna that colonized burial treatments was significantly different from the undisturbed communities at all four locations. The species indicative of burial were all subsurface deposit feeders, although the species were different at each site. At Cinder Cones, *Axiothella antarctica* joined the *Spiophanes tchernai* and *Protodriloides symbioticus* assemblage and was distinctive in burial treatments. At Cape Bernacchi, *Protodriloides symbioticus* dominated communities; in burial treatments *Capitella* spp. replaced the *Galathowenia wilsoni* that was abundant in controls. At Explorers Cove, the control assemblage of *Galathowenia wilsoni* and *Fabricia* sp. was replaced by one dominated by *Aediciria belgicae* in burial treatments. At the western sound sites, the species that were indicative of burial were also abundant in controls. Recruitment from local populations may drive community composition in the western sound because of isolation by oceanographic circulation patterns (Dayton and Oliver 1977).

At other locations around the Antarctic continent, recovery from organic enrichment, including sewage outfalls, is not likely to be as rapid as observed near McMurdo Station. The eastern side of McMurdo Sound experiences regular inputs of organic matter that lead the communities to recover quickly from enrichment. On the western side of the Sound, where organic inputs are less common, a community colonized as quickly but did not match the composition of the control as quickly, with substantial differences remaining after 2 years. This pattern is likely to be more typical of other locations around the Antarctic (Drewry 1983; e.g., Stark et al. 2004). The normal pattern of disturbance over evolutionary time influences the rapidity of community recovery and of response to different types of disturbance.

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