Fall 2015

Natural and Anthropogenic Disturbance in McMurdo Sound, Antarctica: Iceberg Scours, Human-Derived Pollutants, and their Effects on Benthic Communities

Clint Alan Collins
San Jose State University

Recommended Citation

Collins, Clint Alan, "Natural and Anthropogenic Disturbance in McMurdo Sound, Antarctica: Iceberg Scours, Human-Derived Pollutants, and their Effects on Benthic Communities" (2015). *Master's Theses*. 4629.
DOI: https://doi.org/10.31979/etd.bu3s-5bp7
https://scholarworks.sjsu.edu/etd_theses/4629

NATURAL AND ANTHROPOGENIC DISTURBANCE IN MCMURDO SOUND, ANTARCTICA: ICEBERG SCOURS, HUMAN-DERIVED POLLUTANTS, AND THEIR EFFECTS ON BENTHIC COMMUNITIES

A Thesis

Presented to

The Faculty of the Department of Marine Science

San Jose State University

In Partial Fulfillment

Of the Requirements for the Degree

Masters in

Marine Science

by

Clint Alan Collins

December 2015

The Designated Thesis Committee Approves the Thesis Titled

NATURAL AND ANTHROPOGENIC DISTURBANCE IN MCMURDO SOUND, ANTARCTICA: ICEBERG SCOURS, HUMAN-DERIVED POLLUTANTS, AND THEIR EFFECTS ON BENTHIC COMMUNITIES

by

Clint Alan Collins

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

SAN JOSÉ STATE UNIVERSITY

December 2015

Dr. Stacy Kim	Moss Landing Marine Laboratories
Dr. Ivano Aiello	Moss Landing Marine Laboratories
Dr. Scott Hamilton	Moss Landing Marine Laboratories

ABSTRACT

NATURAL AND ANTHROPOGENIC DISTURBANCE IN MCMURDO SOUND, ANTARCTICA: ICEBERG SCOURS, HUMAN-DERIVED POLLUTANTS, AND THEIR EFFECTS ON BENTHIC COMMUNITIES

By Clint Alan Collins

The purpose of this study was to explore the impact of icebergs on infaunal communities in McMurdo Sound, using cores taken from naturally occurring scours, experimental plots simulating iceberg disturbance, and undisturbed reference areas spanning a 24 year time period. Iceberg scours and experimental plots altered infaunal abundances, reduced diversity, and changed species compositions. Abundances were lower at inside scour locations, dominated by a suite of mobile crustaceans. Common sessile space-dominating species were higher at scour edges, suggesting that recolonization of scours occur inward from the edges. When compared to other samples from the McMurdo Sound exposed to varying degrees of anthropogenic disturbance and environmental conditions, iceberg scour samples had high levels of abundance and species richness, with reduced levels of diversity. These results suggest Antarctic benthic communities are resilient to episodic iceberg disturbance, yet lack the ability to cope with high levels of human-derived pollutants.

ACKNOWLEDGEMENTS

A special thanks is in order for everyone who has helped me progress as a scientist and a person throughout this program. First and foremost I would like to thank Stacy Kim, a wonderful advisor, teacher, den mother, and friend. Thank you for taking me to the end of the earth, and for bringing me back alive. I would like to thank my committee member, Ivano Aiello, for all of his guidance and compassion during the last three years, and for always being approachable no matter the problem. I would like to thank my committee member, Scott Hamilton, for making me a better scientist and writer, by always expecting my best work. I am indebted to Diana Steller, for her guidance, support, and passion for life and the outdoor world. I would like to thank many people that have helped me along the way: Laughlin Barker, Martin Hynes, and the rest of the SCINI team, Kamille Hammerstrom, John Oliver, Dorota Szuta, and the whole Benthic Ecology Lab, Alison Aceves for being an amazing intern, Grace Matteson & Charlotte Frank for all their help with sorting and identification, John Douglas, Jackson Winn, Stephen Loiacono, Scott Gabara, Angela Zepp, and everyone else around small boats, Devona Yates, Alex Olsen, Will Fennie, Catarina Pien, and everyone else at MLML, and last but not least Erin Funkhouser and my entire family for their endless support and encouragement.

This would not be possible without aid from these funding sources: National Science Foundation Award #0944747 and #0619622, the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust, the San Jose State University Harvey Fellowship, the Marine Technology Society Charles H. Bussman Graduate Scholarship, and the Coastal Conservation and Research Scholarship.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Introduction

A disturbance can been defined as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment (White & Pickett, 1985). Naturally occurring disturbances can be a significant factor in shaping the structure and function of marine and terrestrial ecosystems. Disturbances often reduce competitive pressures, increase access to resources such as space and food, and create habitat heterogeneity, which can help maintain and even improve species diversity within an ecosystem (Dayton & Hessler, 1972; Sousa, 1979, 2001; Paine & Levin, 1981). The intermediate disturbance hypothesis is an accepted explanation for these phenomena, suggesting that species diversity in a community peaks at intermediate levels of disturbance (Connell, 1978; Sousa, 1979; Dial & Roughgarden, 1998; Roxburgh *et al.*, 2004). At low disturbance levels, diversity is low as competitive dominants characteristic of late successional stage communities exclude inferior competitors. At high disturbance levels, diversity is also low as only fugitive species with high colonization potential are able to persist.

Natural disturbance regimes are a fundamental component of most ecosystems that can shape the composition and structure of communities over evolutionary time (Pickett & White, 2013). Disturbances are characterized by their spatial distribution, frequency, predictability, and magnitude (White, 1979; Pickett & White, 2013). Natural disturbances (e.g., fires, floods, hurricanes, storms, landslides) can perform critical functions, such as recycling nutrients, releasing propagules, reallocating space, and maintaining ecosystem structure by initiating successional processes and reducing competition (Pickett & White, 2013).

Native species and ecosystems adapt to natural disturbance events (Hanes, 1971; Lytle & Poff, 2004), yet due to increased human influence, ecosystems are now being exposed to new and more severe forms of perturbation (Villnäs *et al*., 2013). Anthropogenic disturbances often happen faster and at larger spatial scales than natural disturbance, tipping the threshold on ecosystem resilience and the functions ecosystems provide (Holling, 1973; Thrush *et al.*, 2009). Anthropogenic impacts can transform the predictability, frequency, and magnitude of natural disturbance regimes. Humans are altering fire regimes (Sousa, 1984; Uhl & Kauffman, 1990; Mack & D'Antonio 1998), creating biogeographic barriers (Uhl *et al.*, 1990; Allen *et al*., 2001; Waples *et al*., 2009), and removing resources on land (Swanson & Dyrness, 1979; Keenan & Kimmins, 1993) and sea (Dayton *et al.,* 1995; Watling & Norse, 1998). Global warming is increasing the rate of forest disturbance, due to an intensification of droughts, forest fires, windstorms, coastal flooding, and hurricanes (Overpeck *et al.,* 1990). In the world's oceans, rising atmospheric CO_2 and global climate change are changing the temperature, circulation, stratification, nutrient input, oxygen content, and acidification of the marine environment (Doney *et al.*, 2012).

Antarctica is not immune from global climate change, and may be especially sensitive to warming sea and air temperatures (Aronson *et al*., 2011). Subsurface waters in the Southern Ocean have warmed faster than any other part of the world's oceans (Robertson *et al.,* 2002), and have increased the calving rate of large tabular icebergs from ice shelves (Clarke *et al.,* 2007; Pritchard *et al.,* 2012). Yet as much of the Antarctic has been warming, certain regions, like the Ross Sea, have been experiencing an increase in sea ice extent and decline in sea surface temperatures (Comiso *et al.,* 2011), counter to what has been observed elsewhere. The increase in sea ice is thought to be influenced by an intensification and southward migration of westerly winds in the Southern Ocean, causing stronger dynamic isolation through a reduced poleward heat transport, and a subsequent atmospheric cooling of the Antarctic region (Thompson & Solomon 2002; Goosse *et al*., 2009). The International Panel on Climate Change (IPCC) models predict that the Ross Sea will be the last region on Earth to retain sea ice year round, with sea ice increasing over the next few decades, yet eventually declining (Solomon *et al*., 2007). Sea ice will still be present in the Ross Sea even after it has disappeared from the rest of the Southern Ocean, offering a reference area for comparisons with other regions of the Southern Ocean that are currently experiencing sea ice loss.

Though warming trends have not yet been observed in the Ross Sea region of Antarctica, large calving events from the Ross Ice Shelf have occurred in recent decades (Arrigo & van Dijken, 2003; Dinniman *et al.,* 2007; Martin *et al.,* 2007). Every summer in the Antarctic, as temperatures rise and seasonal ice along the ocean surface melts or drifts away, hundreds of thousands of icebergs ranging in size from 10^1 to 10^5 m^2 are freed from their previously corralled state and become subject to wind and ocean currents (Barnes *et al.,* 2007). There has been a significant increase in the number of icebergs in the last 15 years, originating from major calving events in the Weddell and Ross Seas (Ballantyne & Long, 2002; Arrigo & van Dijken, 2003; Dinniman *et al.,* 2007; Martin *et al.,* 2007), with over 200,000 icebergs total thought to be present in the Southern Ocean (Orheim, 1988 in Williams *et al.,* 1999). Icebergs can act as physical barriers, preventing sea ice production and dispersal, and altering the timing and extent of polynya development, sea surface circulation, and deep-water formation (Arrigo & van Dijken, 2003; Dinniman *et al.,* 2007; Martin *et al.,* 2007). Icebergs can also exert immense physical pressure on the benthos, by touching down and gouging the seafloor in a process known as iceberg scour. In zones where permanent ice shelves are not present, moving icebergs can touch down to depths of 600 m, altering the bathymetry and sediment composition (Barnes & Lien, 1988), and creating patches of disturbed and undisturbed areas in their wake (Gutt, 2001). Antarctic iceberg scours are so commonplace that they are estimated to scour each square meter of the Antarctic shelf every 340 years (Gutt, 2001; Gutt & Starmans, 2001), creating a natural disturbance with implications for the structure and function of the entire ecosystem.

Antarctic benthic communities are functionally diverse, and at depths greater than 30 meters many species have circumpolar distributions (Koltun, 1969; 1970; Sara *et al.,* 1992). Antarctic communities have remained isolated and relatively unchanged over long time periods due to spatial and oceanographic constraints on dispersal across the Antarctic Circumpolar Current, preventing any influx of invasive species (Barnes, 2002; Tavares & De Melo, 2004; Clarke *et al.,* 2005). As a result, benthic community composition remains similar to descriptions of Paleozoic ones (Thayer, 1979). Though similar suites of species are found around the continent, at small spatial scales benthic communities exhibit a considerable degree of patchiness in species composition (Gutt & Starmans, 1998). This patchiness has been attributed to variation in sediment type and benthic food supply, which depend on primary production and sedimentation, current regimes, hydrographic factors, and sea-ice cover (Grebmeier & Barry, 1991; Starmans & Gutt, 2002). Yet the main driver of benthic community heterogeneity appears to be the movement and scour impacts from millions of icebergs during the austral summer (Barnes *et al.,* 2007).

Iceberg scours are extreme and localized disturbances that result in immediate and catastrophic reductions in abundances of benthic species (Gutt *et al.,* 1996; Gerdes *et al.,* 2003; Smale & Barnes, 2008). Following a scour, organisms recolonize these perturbed areas of the Antarctic seafloor in a process known as succession. A suite of opportunistic and motile invertebrates with relatively high rates of reproduction dominate early successional, and highly physically disturbed communities (Lenihan & Oliver, 1995). Late successional communities replace early successional communities, with assemblages composed of long-lived species that are better competitors, dominated by suspension-feeders (Gallardo *et al.,* 1977; Oliver & Slattery, 1985; Gallardo, 1987; Lenihan *et al.,* 1990). The erratic and widespread movement of icebergs results in a patchwork of disturbed and undisturbed zones in the Antarctic benthos, creating a mosaic of different successional stages and community assemblages along the seafloor (Gutt, 2001; Gutt & Piepenburg, 2003; Conlan & Kvitek, 2005**)**.

Soft sediment habitats of McMurdo Sound, Antarctica harbor dense populations of infaunal invertebrates (Dayton & Oliver, 1977; Oliver & Slattery, 1985; Conlan *et al.,* 2004; 2010). These communities are dominated by polychaetes, crustaceans, cnidarians, and bivalves (Lenihan & Oliver, 1995; Fabiano & Donavaro, 1999). Antarctic benthic suspension feeders, such as the widely distributed bivalve *Laternula elliptica,* might be able to influence ecosystem processes due to their abundance and filtration capabilities (Gili & Coma, 1998). Abundant filter feeders are able to regulate primary production through phytoplankton capture, and are thought to be responsible for a large share of the energy flow from the pelagic to the benthic system (Jorgensen, 1990; Kimmerer *et al.,* 1994). The activity of suspension feeders is important in the trophic web, breaking down organic matter (Nedwell *et al*., 1993), resuspending nutrient-rich superficial sediments, and providing food for other benthic fauna through biodeposition, particularly in phytoplankton-impoverished waters (Ahn, 1993).

Polar invertebrate species tend to have slower growth rates when compared to species of similar size and ecology in other regions of the world (Clarke, 1980, 1983; Luxmoore, 1982; Arntz *et al*., 1994). Currently, it is unclear whether this generalization is accurate or a result of undersampling. Many species exhibit episodic or seasonal recruitment and growth (Quetin & Ross, 2003; Dayton *et al*., 2013), which can easily be overlooked in a harsh setting that only allows for sampling during small portions of the year. The majority of Antarctic studies on epibenthic communities have demonstrated slow and relatively unpredictable patterns of recovery following iceberg disturbance (Gutt & Starmans, 2001; Teixido *et al.,* 2004). This is most likely due to the classification of late successional communities using hexactinellid sponges, which experience erratic settlement and growth periods (Dayton *et al.,* 2013). Studies on infaunal communities have revealed much faster recolonization rates (Lenihan & Oliver, 1995; Lee *et al.,* 2002; Brown *et al.,* 2004; Gerdes *et al.,* 2008), with some studies finding scour samples comparable to undisturbed zones in under a year's time (Lee *et al.,* 2001; Smale *et al.,* 2008). Life history traits determine the speed of succession, with development rates (Oliver & Slattery, 1985), recruitment and settlement rates (Dayton, 1989), and the frequency and range of dispersal (Bolker & Pacala, 1999) implicated as the most important factors.

The recruitment of benthic marine invertebrates is dependent upon the supply of new individuals to an area and the availability of space for colonization upon arrival. For sessile and sedentary organisms, the larval stage is the only opportunity for dispersal. There is considerable variability regarding energetic strategies and durations of larvae, from direct development (hatching as juveniles) to lecithotrophy (nonfeeding, swimming) to planktotrophy (feeding, swimming) (Thorson, 1950). Interactions between larvae and established residents can influence the settlement choices of larvae (Meadows & Campbell 1972; Scheltema 1974; Burke 1983; Crisp 1984; Woodin 1986; Pawlik 1992), with conspecifics often indicating habitat suitability for recruiting larvae (Gabbott & Larman 1987; Raimondi 1988). The edges of disturbed habitats are also extremely important for the closure of patches, with sequential recruitment (Raimondi, 1990) and the encroachment of species often occurring from the perimeter of the patch inwards (Paine & Levin, 1981).

Increases in iceberg scour may be selecting for specific ecological traits in benthic communities. Relative abundances of sessile organisms increase with depth and are inversely related to scour frequency (Barnes & Brockington, 2003; Smale, 2008). Mobile organisms are capable of avoiding iceberg scour, and are able to quickly recolonize disturbed zones (Conlan *et al.,* 1998). Iceberg scours generate a great deal of detritus as they plough and till the seafloor, freeing up food for an abundant guild of secondary consumers (Slattery & Oliver, 1986; Smale, 2008). Perhaps most important is the interaction between iceberg scour and the reproductive modes of organisms in this community. Processes acting over evolutionary timescales have selected for a disproportionate number of brooding species in Antarctica compared to other areas of the world, whereas increases in iceberg scouring are acting on ecological timescales, potentially selecting for species with faster and farther-reaching dispersal abilities (Poulin *et al.,* 2002).

The slow rates of population growth in these communities requires multi-year, and even multi-decadal intervals between observations to measure the persistence of benthic assemblages, and any potential resilience to disturbances such as iceberg scouring. To date, there are numerous studies on the impact of icebergs on infaunal communities (Lenihan & Oliver 1995; Lee *et al.,* 2002; Brown *et al.,* 2004; Gerdes *et al.,* 2008; Smale *et al.*, 2008), which universally find drastic reductions (often 90-95%) in density and biomass following iceberg scour. Yet most studies on this subject span only one year, with the longest monitoring effort to date being three years. These time frames are likely too short to determine any patterns of community recovery, due to the variability and seasonality of settlement and recruitment in Antarctic benthic communities (Pearse *et al.*, 1991; Bowden, 2005; Dayton *et al.,* 2013) coupled with the varied timing of iceberg scours (Smale *et al.*, 2008) and variable sea ice conditions in some areas, such as the Ross Sea (Martin *et al.*, 2007; Comiso *et al.*, 2011).

Here, I explore the impact of icebergs on infaunal communities at one site within McMurdo Sound, with multiple scour and undisturbed reference samples taken over a 24 year time period. Specifically I asked the following questions: (1) How does iceberg scour change community composition and diversity compared to undisturbed areas? (2) What species are driving these changes in community composition? (3) Is the recolonization sequence consistent between years? (4) What is the mechanism for recolonization following iceberg disturbance? (5) Is iceberg disturbance selecting for specific ecological traits? (6) How similar are communities regularly exposed to icebergs when compared to other communities in the McMurdo Sound?

Materials and Methods

Study Area and Study System

Sampling took place during October or November at Cinder Cones (Fig. 1, Appendix A, B), located in eastern McMurdo Sound, at the western extension of the Ross Sea. Sea ice at Cinder Cones is generally seasonal, exposing this area to scour from

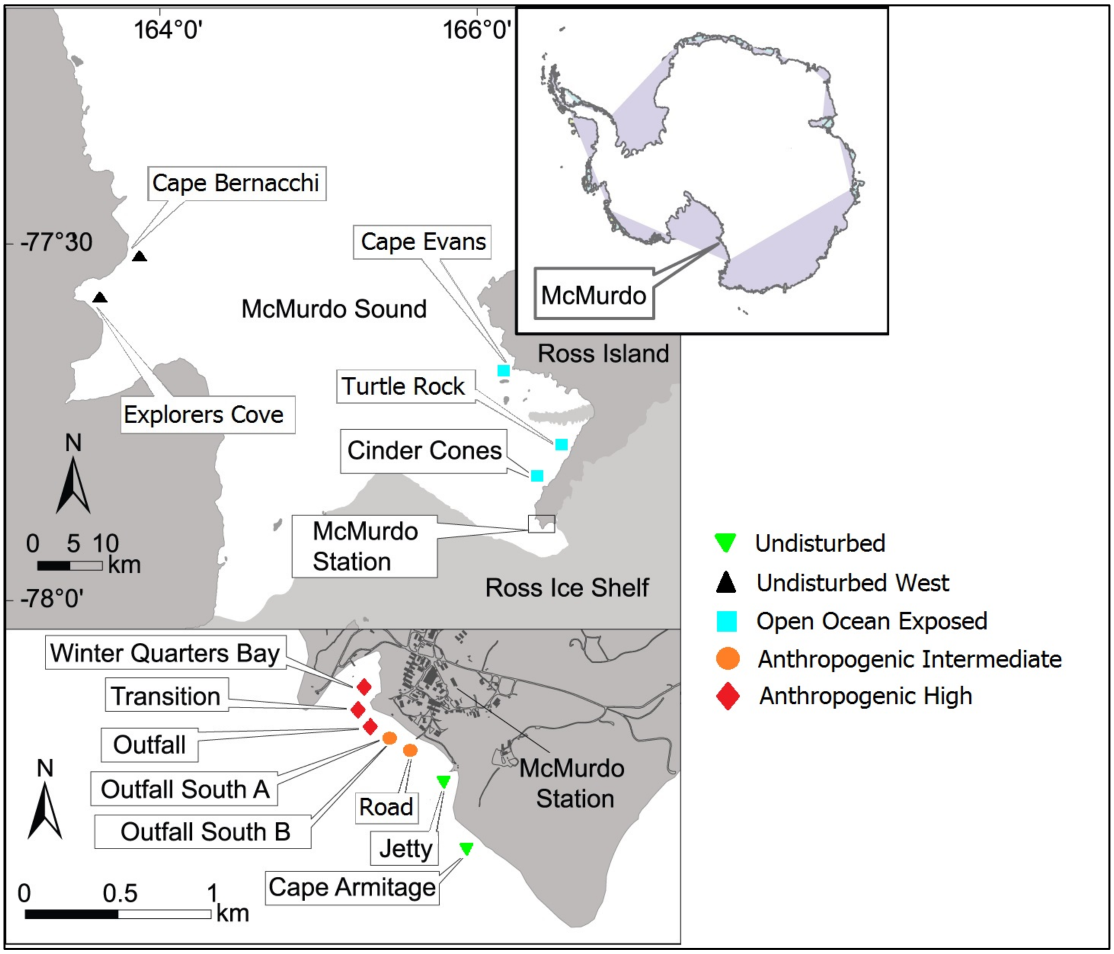

Figure 1. Map of Cinder Cones and other sites in McMurdo Sound with corresponding disturbance regimes. Map insert shows sites close to McMurdo Station.

floating icebergs. Cinder Cones is a highly sloping area characterized by coarse pebble to cobble sized volcanic basalt sediments. Depths at Cinder Cones quickly descend from 5 m to greater than 100 m. Infaunal communities at Cinder Cones are dominated in biomass by the suspension feeding bivalve *Laternula elliptica* and predatory burrowing anemones of the genus *Edwardsia,* and in abundance by the burrowing polychaete *Spiophanes tcherniai* and omnivorous tanaid *Nototanais dimorphus.*

Ecological community data used from areas outside of ice scour (i.e., reference samples) at Cinder Cones and for McMurdo Sound comparisons came from a 24-year period of biological sampling dating from 1988 to 2012 (Lenihan & Oliver, 1995; Stark *et al.,* 2014). A total of 108 samples were used for the Cinder Cones site (Table 1), and a total of 597 samples were used for the comparison study in the McMurdo Sound (Appendix A, B). Sample depth ranged from 18 m – 24 m, with the majority of samples taken from a depth of 18 m. Current patterns are responsible for the variation in productivity in McMurdo Sound (Dayton & Oliver, 1977). Southward advection from the Ross Sea brings nutrient-rich waters to the eastern Sound. This water circulates under the Ross Ice Shelf and arrives at the western Sound in a relatively oligotrophic state (Dayton & Oliver, 1977; Barry & Dayton, 1988). Sites in McMurdo Sound also experience a range of disturbances, both natural and anthropogenic. McMurdo is unique in terms of Antarctic stations, with a relatively large population (~1500 people) circulating through every austral summer. It has a varied history of anthropogenic impacts, from its beginnings as a military base to its current state as a research facility. In certain locations,

Table 1

Summary of samples taken at Cinder Cones that were used for comparisons in this study. Samples are separated based upon natural disturbance, experimental disturbance, and site reference. n = total number of samples taken during each year.

	Natural Disturbance			Experimental Disturbance			Reference	Samples
				1 m Disturbance		10 cm Disturbance		
Sampling Year	**Scour Year**	**Inside Scour**	**Scour Edge**	**Inside**	**Edge**	**Scour**	**Site Reference**	**n**
1988							6	6
1997	1995/96	6					12	18
1998							6	6
2002	2000/01	6					6	12
2003				3	3	3	6	15
2004				3	3	3	6	15
2007							6	6
2012	2010/11	8	8				14	30

the benthos is as polluted as industrial harbors in other parts of the world as a result of these activities (Risebrough *et al.*, 1990; Hale *et al.,* 2008; Kennicutt *et al.*, 2010).

Infaunal Sampling in Iceberg Scour and Reference Zones

Infaunal taxa in the soft sediment habitats of Cinder Cones and McMurdo Sound were sampled by divers using 10 cm diameter hand-held cores, inserted into the sediment to a depth of 10 cm, with six replicate cores per location and some locations sampled at several water depths. Only infaunal species were sampled, with any noticeable mobile epifaunal species removed prior to core insertion. Samples were sieved alive over a 500 μm sieve, placed into jars containing MgCl for relaxation of the organisms, then preserved with 10% buffered formalin in seawater. Samples were transferred into 90% ethanol two days later for storage. All samples were collected with the same methodology, with each sample having a volume of approximately 785.4 cm^3. Densities were calculated as the total number of individuals per sample. All individuals were identified to the lowest taxonomic level possible, and listed as morphospecies where identifications were uncertain or could not reliably be made (see Appendix C for a complete list of species). All analyses were performed at species level unless specified otherwise.

To examine the impact of naturally occurring iceberg scour on infaunal communities, cores were taken from iceberg scours ranging from 18 – 21 m depth in 1997, 2002, and 2012. Scours were identified by a depression in bathymetry generally 1 m or less, as well as recognizable changes in community composition. Scours at Cinder Cones ranged from 2 – 5 m wide, and 3 – 10 m long. In 1997, six samples were taken inside an iceberg scour that occurred in 1995 or 96, with samples taken outside the disturbed area for reference during each of these years. In 2002, six samples were taken from inside a scour that occurred in 2000 or 2001. In 2012, samples were taken from the inside and edge of two scours separated by 10 m, which scoured the seafloor in either 2010 or 2011. Divers visit Cinder Cones on average every other year, preventing precise timelines to be established for each scour.

Experimental Manipulations Simulating Iceberg Scour Disturbance

From 2002 to 2004, an *in-situ* experiment simulating aspects of iceberg disturbance was conducted at Cinder Cones, to test how resettlement processes vary based upon disturbance size and patch location (inside versus edge). In 2002, six 1 m diameter plots, and six 10 cm diameter plots were created using defaunated sediment taken from Cinder Cones. Sediment was defaunated by warming to room temperature to kill all animals and sieving over coarse (2 mm) mesh, while also manually removing any visible animals smaller than the mesh size. For small plots, 10 cm diameter cores were put in place, and then filled with defaunated sediment to a depth of 10 cm. For larger plots, large cores with a diameter of 1 m were inserted into the sediment to a depth of 10 cm, and were then filled with defaunated sediment. All cores were open at the bottom, potentially allowing organisms to move in from underneath, as well as from the surface of the seafloor. In 2003, half of these plots were sampled; three from the inside and edge of the 1 m diameter plots and three from the 10 cm diameter plots. In 2004, the remaining plots were sampled in the same fashion.

Diversity Calculations

To examine differences between communities at different scour locations, a variety of indices were used to describe species diversity and evenness. Species richness (S) is a measure of the total number of species per sample, and gives as much weight to species that have very few individuals as to those that have many. To examine the relative abundance of the different species making up the richness of an area, Shannon-Wiener's diversity index: ($H = -\Sigma P_i * \ln[P_i]$), where P_i is the proportional abundance of species i, was calculated. In addition, Evenness ($E = H/\ln(S)$), where H = Shannon-Wiener's index and S = species richness, was calculated to evaluate the how evenly species were distributed among species at each sampling location. To test for differences in diversity across sample locations, univariate ANOVA tests were conducted. Species accumulation curves were used to compare species richness between scour sampling locations. Species accumulation curves were created by plotting the cumulative number of species resulting from an increase in sampling effort, generated by PERMANOVA (Clarke & Gorley, 2001).

Ecological Characteristics

Ice disturbance is a common and long-established disturbance in Antarctic shelf communities, and is potentially selecting for specific ecological characteristics. Each species was categorized by its mobility, feeding strategy, and dispersal potential, as outlined in Table 2 (adapted from Smale, 2008; see Appendix D for complete list). Some taxa were classified as unknown or variable due to having unknown traits for certain ecological characteristics, or because they could only be identified to genus level within a genus that had variability regarding that trait. There is a lack of extensive knowledge on life history characteristics in Antarctic organisms (Poulin *et al.*, 2002). Therefore a broad dichotomous classification was used for simplification of the diverse array of life history strategies. Though this simplification can be limiting, it should demonstrate general patterns in ecological traits that may be selected for by iceberg scours. To test for differences between ecological groups, PERMANOVA tests were performed on data at inside, edge, and outside sampling locations (Clarke & Gorley, 2001). Data are the proportion of the total number of individuals, not species, within each ecological category.

Table 2

Categories of ecological traits applied to each organism sampled at Cinder Cones scours.

Trait	Category	Description
Mobility	1	Low mobility. Taxa are completely or largely immobile. Includes sedentary, burrowing, and tube-dwelling worms, bivalves and all sessile taxa.
	2	High mobility. Includes mobile worms, most crustaceans, gastropods, and various other taxa.
Feeding	0	Unknown or Varies. Either no information for that species or specimen identified only to genus level, with high plasticity within that genus
	1	Primary consumers. Taxa that primarily feed on algae and plankton-derived matter, including all suspension feeders, herbivores, deposit feeders and detritivores.
	2	Secondary consumers. Includes carnivores, omnivores, & scavengers. Principally scavenging amphipods & predatory worms.
Dispersal	0	Unknown or Varies. Either no information for that species or specimen identified only to genus level, with high plasticity within that genus
	1	Low dispersal potential. Includes all brooders and taxa with benthic egg masses or short-lived, non-feeding pelagic stages (1–2 days).
	2	High dispersal potential. Taxa with medium to long lived pelagic larvae (more than 2 days in the water column), either planktotrophic or lecithotrophic.

McMurdo Sound Disturbance Regimes

Sites in McMurdo Sound are exposed to a variety of environmental conditions and physical and chemical disturbances. Each site was nominally classified based upon its regional location and predominant disturbance type experienced at each site (Fig. 1). Sites around McMurdo Station have been exposed to various degrees of environmental contamination in the form of trace metals, hydrocarbons, and organic enrichments (see Stark *et al.*, 2014). Sites are classified into groups that are broadly representative of their contamination status: undisturbed (uncontaminated background levels), anthropogenic intermediate (moderate local contamination in comparison to undisturbed or anthropogenic high) or anthropogenic high (highest levels of contamination). Due to known differences in communities between east and west regions of McMurdo Sound (Dayton & Oliver, 1977; Dayton *et al.*, 1986; Barry & Dayton, 1988), sites from the west region are classified as undisturbed west region. Sites north of McMurdo Station, such as Cinder Cones, are regularly exposed to open ocean conditions and physical disturbances from icebergs. These sites are classified as open ocean exposed. Finally, Cinder Cones scour samples from inside locations have been classified as iceberg scour. See Appendix B for a full list of sites, locations, and disturbance regime classifications.

Multivariate Statistical Analysis

To test hypotheses regarding differences between infaunal communities from scour samples at Cinder Cones and other McMurdo Sound sites, a range of multivariate methods were used. PERMANOVA tests were employed to compare the variation in species abundance and composition among sampling units (Beta diversity). If any significant differences were found, pairwise tests were used to evaluate the factors or sampling units responsible for these differences. PERMANOVA is a permutation based analogue of traditional ANOVA and gives equivalent results, but caters to unbalanced designs by offering a choice for the type of sums of squares used for partitioning, and there are no assumptions regarding the distribution of variables (Anderson *et al.,* 2005). Analysis of similarities (ANOSIM) was calculated to test for variation of Beta diversity. The ANOSIM statistic compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. An R-value close to "1.0" suggests dissimilarity between groups while an R-value close to "0" suggests an even distribution of high and low ranks within and between groups. R-values below "0" suggest that dissimilarities are greater within groups than between groups (Clarke & Gorley, 2001). Similarity percentage analysis (SIMPER) was used to identify which taxa most contributed to these differences. Multi-dimensional scaling ordinations (MDS) were used to visually represent differences in communities. In certain MDS plots, cluster analysis was included to demonstrate similarity between groups. For community analysis of Cinder Cones and greater McMurdo Sound samples, principal component analysis (PCA) was performed on the distance between group centroids in each disturbance regime. Principal component analysis models the variation in a set of variables in terms of a smaller number of independent linear combinations (the principal components) of those variables (Clarke & Gorley, 2001). Principal component analysis is a way to describe the structure of the data as completely as possible by using as few variables as possible. Organism counts were 4th root transformed to reduce the influence of abundant taxa on community analysis (Clarke & Green, 1988; O'Hara & Kotze, 2010). Distributions of taxa failed the Shapiro-Wilk normality test (Srivastava & Hui, 1987), therefore resemblance matrices were created based upon Bray-Curtis dissimilarities (McCune *et al.,* 2002). All multivariate calculations were performed in PRIMER v6.0 (Clarke, 1993; Clarke & Gorley, 2001; Clarke & Warwick, 2001). ANOVA and Tukey HSD tests were performed in JMP v12.0.

Results

Abundance and Community Structure Following Iceberg Scour

Samples from natural iceberg scours and reference areas at Cinder Cones were compared to evaluate differences in species abundance and benthic assemblage composition. The impact of iceberg scours resulted in different assemblages as shown by differences in the total number of individuals per sample and differences in abundance of most taxa (Fig. 2; Table 3). ANOVA tests revealed total individuals per sample was significantly different across sampling locations ($F_{2,89} = 4.27$, $p = 0.017$). Abundances were lower at locations inside scour zones and were higher at locations on the edge of scours relative to samples outside scour zones. Bivalves were more abundant at edge and inside locations, driven by a higher abundance of small-sized *Laternula elliptica.* The cnidarian *Edwardsia meridionalis* had higher abundances at edge locations, and lower abundances at inside locations. Overall, the relative contribution of polychaetes to total

Table 3
Summary table of mean number of taxa and standard error at each sampling location. Samples pooled in each location (n = number of samples averaged).

Taxa	Outside (n = 62)	Edge (n = 8)	Inside (n = 20)
Total Individuals	794.7 ± 48.9	1100 ± 171.7	606.7 ± 101.3
Crustacea	433.8 ± 28.1	535.9 ± 109.5	466.1 ± 74.3
Chelicerata	6.7 ± 1.5	22.8 ± 3.5	21.1 ± 6.6
Amphipoda	37.8 ± 2.6	22.8 ± 3.5	32.0 ± 4.6
Ostracoda	101.5 ± 9.2	120.1 ± 31.2	55.5 ± 14.5
Cumacea	38.9 ± 6.3	9.8 ± 3.6	20.4 ± 5.7
Isopoda	59.5 ± 4.9	35.5 ± 7.8	70.2 ± 11.0
Tanaidacea	189.4 ± 22.9	331.5 ± 94.7	267.0 ± 54.2
Polychaeta	248.1 ± 22.4	398.1 ± 132.2	96.9 ± 42.8
Capitellidae	1.2 ± 0.4	4.0 ± 1.0	2.8 ± 0.8
Maldanidae	12.9 ± 1.8	34.0 ± 11.3	6.0 ± 1.8
Cirratulidae	1.1 ± 0.2	0.8 ± 0.5	0.9 ± 0.4
Spionidae	190 ± 21.8	349.1 ± 134.5	79.6 ± 42.0
Other Polychaeta	40.9 ± 3.4	8.5 ± 2.9	6.8 ± 1.7
Mollusca	11.1 ± 1.6	27.0 ± 7.9	25.5 ± 7.7
Bivalvia	5.2 ± 1.5	24.5 ± 8.2	20.0 ± 6.2
Gastropoda	5.9 ± 1.0	2.5 ± 0.7	5.5 ± 1.8
Cnidaria	82.9 ± 9.2	115.8 ± 38.7	11.1 ± 3.8
Echinodermata	0.4 ± 0.1	0.1 ± 0.1	0.4 ± 0.2
Oligochaeta	2.7 ± 0.6	6.3 ± 1.8	3.2 ± 0.7
Other	14.7 ± 2.2	16.9 ± 5.5	4.7 ± 1.3

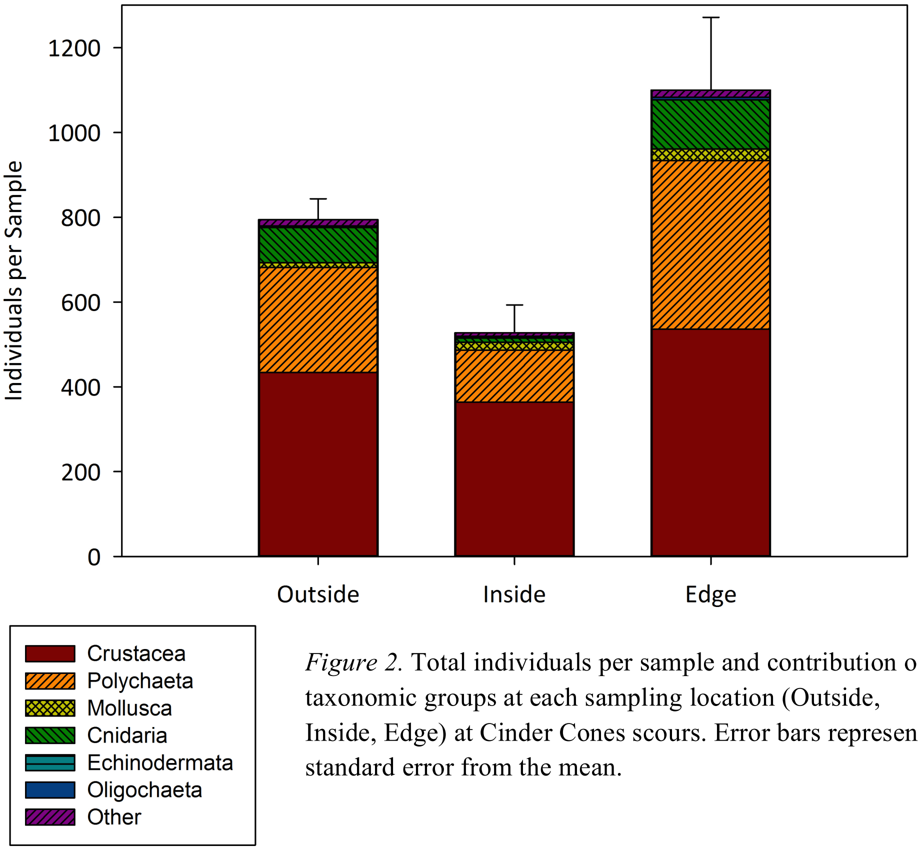

Figure 2. Total individuals per sample and contribution of taxonomic groups at each sampling location (Outside, Inside, Edge) at Cinder Cones scours. Error bars represent standard error from the mean.

community abundance was higher at sampling locations on the edge of scours, and noticeably lower inside scour locations. Crustacean abundance was proportionally higher inside scour locations, and lower at edge locations.

Samples collected from iceberg scours were compared to outside reference areas at Cinder Cones and visualized using a MDS plot at species-level taxonomic resolution (Fig. 3). PERMANOVA tests revealed significant differences between samples taken from inside and the edge of scours when compared to outside samples ($Pseudo\text{-}F_{2,89}$ = 8.42, $p = 0.001$), which can be visualized by the distinct clustering of these samples on the MDS plots. Differences in community composition across sampling locations were evaluated using SIMPER analysis (Appendix E). The common space-dominating polychate *S. tcherniai* and late successional species of cnidarian *E. meridionalis* were the main contributor to differences between sampling locations. Both of these species had higher abundances at scour edges and lower abundances at inside scour locations. Higher abundance of the tanaid *N. dimorphus* at edge and inside locations was another driver of the differences observed among disturbance locations. Inside scour locations were dominated by a suite of crustaceans, with high contributions to the community assemblage by the isopod *Austrosignum glaciale*, the amphipod *Heterophoxus videns*, and the cumacean *Eudorella splendida*. Grouping of samples taken from locations inside and on the edge of iceberg scours were much less distinct, potentially due to limited sample sizes from a single year for comparision. Pairwise PERMANOVA and ANOSIM tests revealed differences between all sample locations except pairwise ANOSIM tests between inside and edge samples (Table 4). This suggests that samples taken from the edge of scours are more similar to samples taken from inside the scour, as demonstrated visually in the MDS ordination.

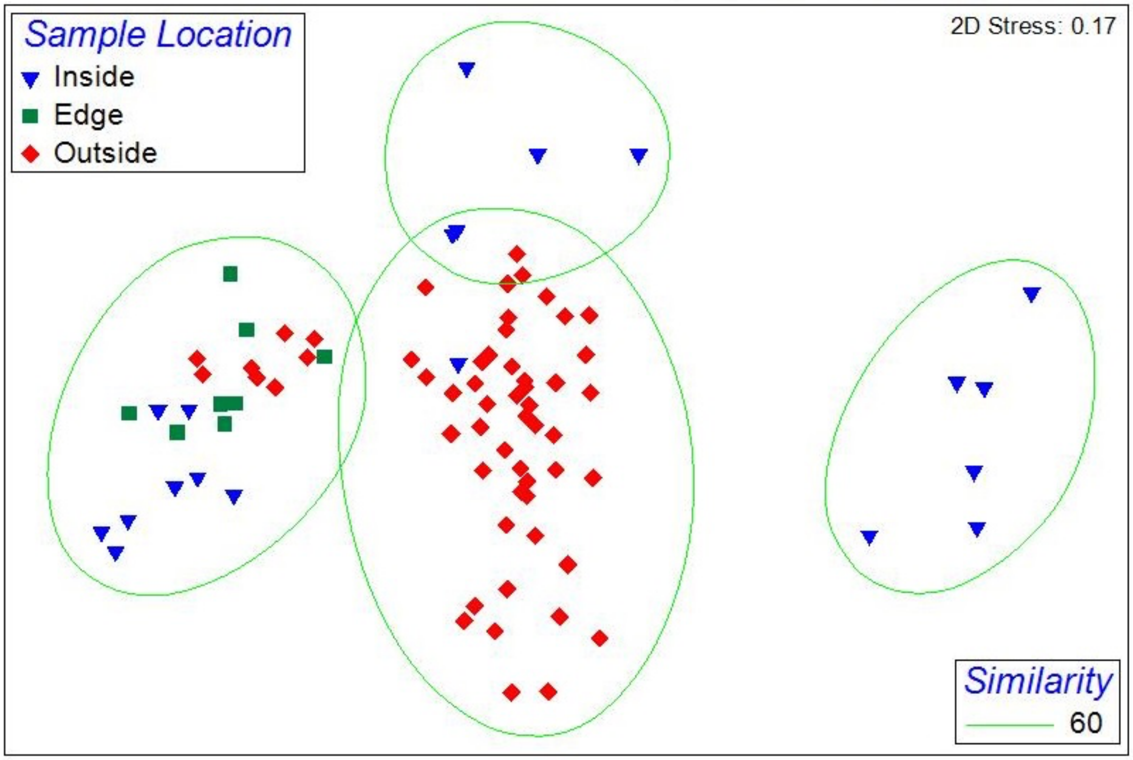

Figure 3. MDS ordination of Cinder Cones samples classified by sampling location (Inside, Edge, Outside). Based upon 4th root transformed abundances and Bray-Curtis similarities. Similarity based upon cluster analysis showing level of similarity between groups.

Table 4

Tests for differences between sampling location at Cinder Cones. Based upon 4th root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences in both PERMANOVA and ANOSIM tests.

	PERMANOVA Tests				ANOSIM Test	
Sample Location	**t**	**P (perm)**	**Average Similarity Between Groups**	**Distance Between Group Centroids**	**R**	**P**
Outside vs Inside*	3.15	0.001	49.23	24.07	0.62	0.001
Outside vs Edge*	3.17	0.001	55.34	30.75	0.53	0.001
Inside vs Edge	1.73	0.028	51.87	25.67	0.04	0.642

Biodiversity Responses to Iceberg Scour

Impacts of iceberg scour on species diversity were assessed using a suite of diversity indices. Species richness (S) was not significantly different among sampling locations ($F_{2,89} = 2.50$, $p = 0.087$). However, evaluation of other diversity indices revealed a drop in diversity at locations inside and on the edge of scours compared to samples outside of scour zones (Fig. 4). Significant differences were found for both Shannon-Wiener diversity index ($F_{2,89} = 4.32$, $p = 0.016$) and Evenness ($F_{2,89} = 6.76$, $p = 0.002$). The drop in diversity on the edge and inside of scours was driven by the extreme

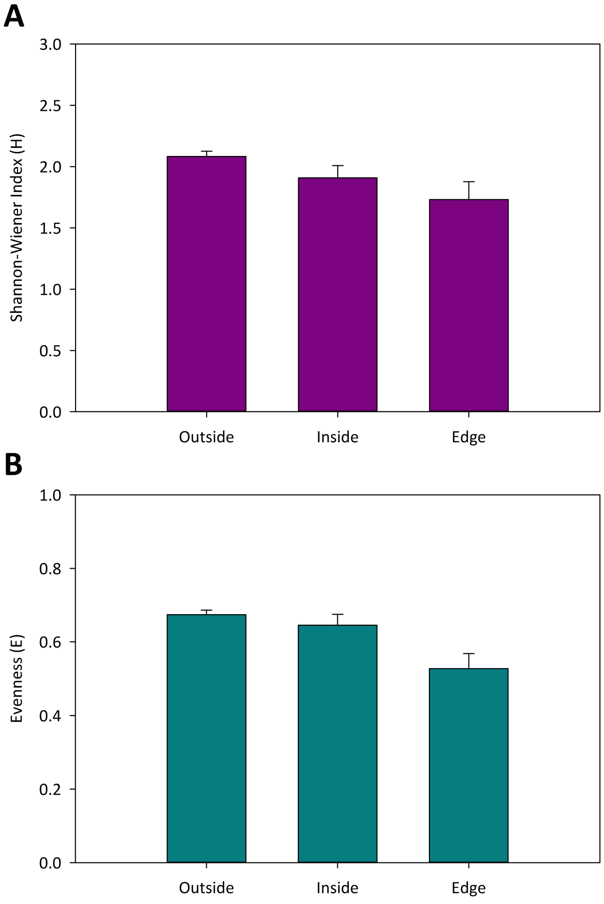

Figure 4. Diversity measures for A) Shannon-Wiener Diversity Index (H) and B) evenness (E) at each sampling location (Outside, Inside, Edge) at Cinder Cones scours. Error bars represent standard error from the mean.

abundance of a handful of species that dominated the assemblage in zones of highest disturbance. Species accumulation curves revealed that inside scour locations supported a higher number of species than outside and edge sampling locations (Fig. 5). Edge locations supported the lowest number of taxa, when compared to outside and inside sampling locations.

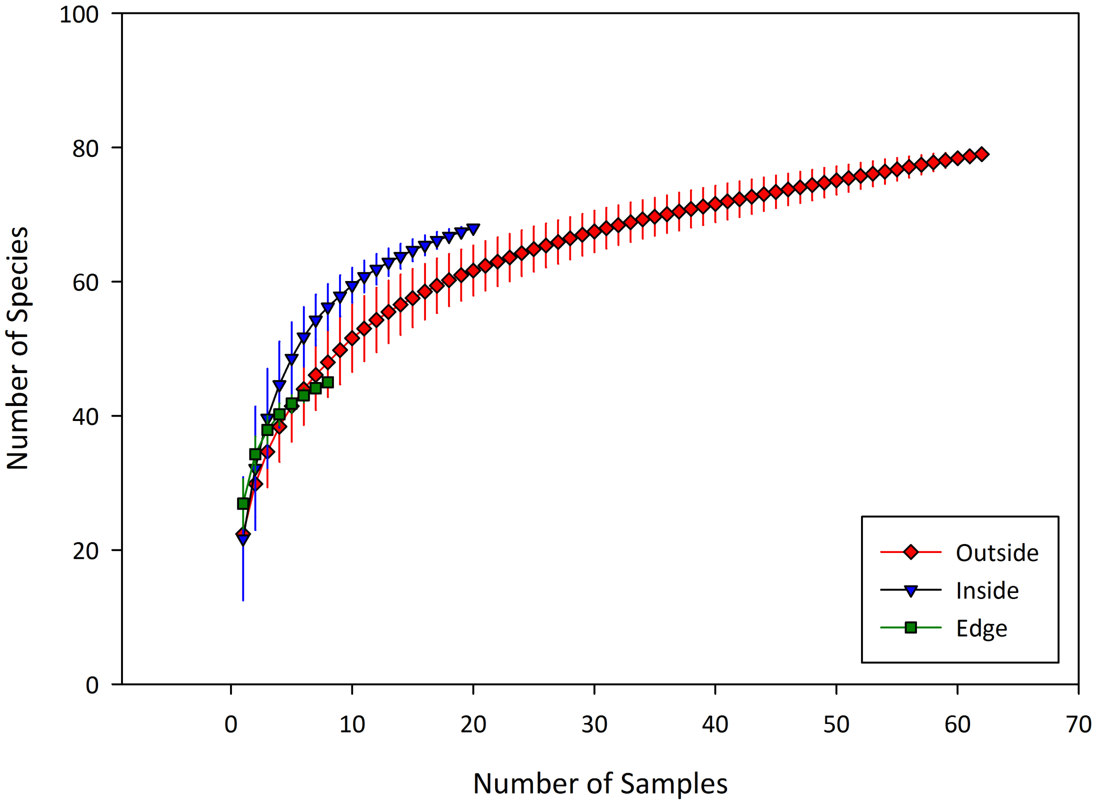

Figure 5. Species accumulation curves for samples at Cinder Cones scour locations (Outside, Inside, Edge). Curve based upon cumulative number of species resulting from an increase in sampling effort. Error bars represent one standard deviation from each observation.

Temporal Variability in Scouring Events

The year-to-year variability of recolonization was examined using samples taken from inside scour locations (Fig. 6). Species assemblages from each scour event show distinct clustering and separation along MDS axis 1, while temporal variation in the community composition of reference samples collected outside of ice scours was much lower and primarily varied along MDS axis 2 (Fig. 6A). MDS analysis demonstrated that recolonization of scours was highly variable from year to year, despite similar elapsed time from the estimated timing of the disturbance event to sampling (Fig. 6B). PERMANOVA tests revealed significant differences between samples taken inside scours from 1997, 2002, and 2012 ($Pseudo\text{-}F_{2,19} = 25.54$, $p = 0.001$). Pairwise PERMANOVA and ANOSIM tests revealed strong differences between all years (Table 5). Average total abundances at inside scour locations varied widely among different scouring events in 1997 (Avg. = 192.7 ± 150.6), 2002 (Avg. = 398.7 ± 137.8), and 2012 (Avg. = 1086.6 ± 393.2). These differences could have been caused by scours of different ages, differences in successional sequences, as well as environmental factors affecting communities at Cinder Cones. Examination of abundances in outside reference samples across each sampling year demonstrated a link between inside scour and outside reference abundances (Fig. 7). SIMPER analysis was performed to determine the species contributing to differences between scour years (Appendix F). *Nototanais dimorphus* was the number one contributor in all years. Interestingly, *S. tcherniai,* a common and dominant member in inside samples from 1997 and 2012 as well as outside reference samples, was not present in 2002. The other species contributing to temporal differences

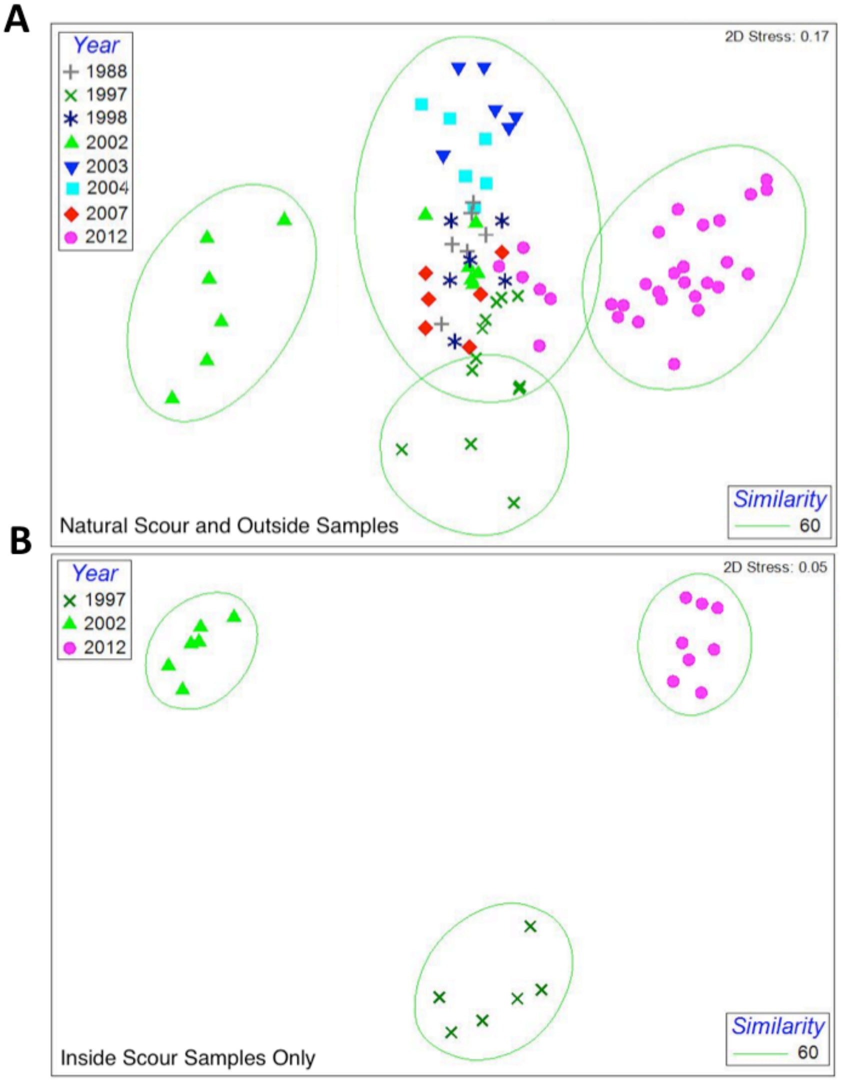

Figure 6. MDS ordination of Cinder Cones samples classified by sampling year. A) All sampling locations (Outside, Edge, Inside) are classified by sampling year. B) Inside sampling location classified by sampling year. Based upon 4th root transformed abundances and Bray-Curtis similarities. Similarity based upon cluster analysis showing level of similarity between groups.

Table 5

Tests for differences between sample years at inside scour locations. Based upon 4th root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences in both PERMANOVA and ANOSIM tests.

	PERMANOVA Tests				ANOSIM Test	
Sample Year	**t**	**P (perm)**	**Average Similarity Between Groups**	**Distance Between Group Centroids**	**R**	**P**
1997 vs 2002*	4.72	0.003	37.29	56.80	1.00	0.002
1997 vs 2012*	6.25	0.002	44.53	48.14	1.00	0.001
2002 vs 2012*	4.14	0.003	29.96	65.50	0.99	0.001

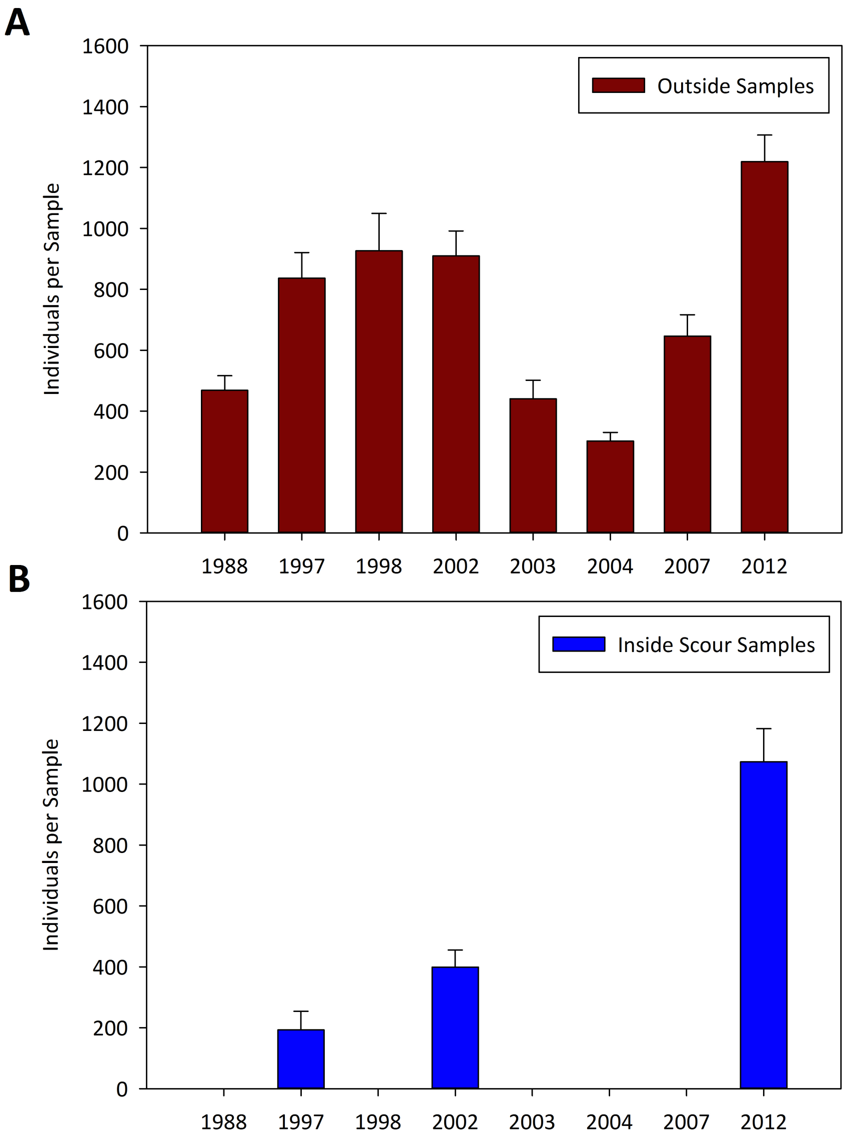

Figure 7. Total individuals per sample at A) outside and B) inside scour sampling locations. Error bars represent standard error from the mean.

are common members of this community, but exhibited varying average abundances from year-to-year.

Experimental Manipulations Simulating Iceberg Scour Disturbance

Differences in sample locations (inside, edge), disturbance size (1 m, 10 cm), and scour age (1, 2) were tested within the experimental plots. PERMANOVA analysis did not reveal any significant differences in assemblage composition as a function of scour ages (*Pseudo*-$F_{1,17} = 1.61$, $p = 0.112$) or sampling location (*Pseudo*-$F_{2,17} = 1.33$, $p = 0.148$). Total infaunal abundance was higher in the 1 m edge and 10 cm plots compared to the 1 m inside plots and in the reference samples collected outside from the same years (Fig. 8). SIMPER tests were performed to determine the species responsible for differences at each sample location (Appendix G), and revealed that *S. tcherniai* was the most dominant member and responsible for differences between disturbance treatments. Other sessile and burrowing species also had higher abundances in the 1 m edge and 10 cm plots compared to 1 m inside, including the cnidarian *E. meridionalis*, the polychaete *Capitella* sp. A, and the polychaete *Axiothella* sp..

The effect of time on scour recolonization was examined using experimental scour plots from 2003 and 2004. There were no distinct differences between samples that were collected 1 or 2 years post-scour disturbance (*Pseudo*-$F_{1,17} = 1.45$, $p = 0.131$) (Fig. 9). The lack of differences between experimental plots of ages 1 and 2 years provides justification for pooling natural scour samples with poorly defined times (< 2 years) for recolonization.

Tests were performed to determine if experimental plots of defaunated sediment and naturally occurring scours could be pooled for analyses. Inside scour samples and inside experimental manipulations of large (1 m) and small sizes (10 cm) were compared to outside reference samples. PERMANOVA tests revealed significant differences

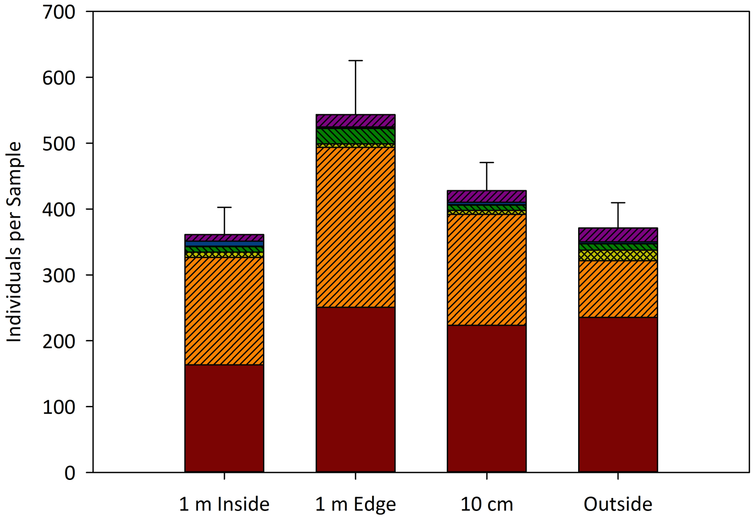

Figure 8. Total individuals per sample and contribution of taxonomic groups at experimental sampling plots (Outside, 1 m Inside, 1 m Edge, 10 cm) at Cinder Cones from 2003 and 2004. Error bars represent standard error from the mean.

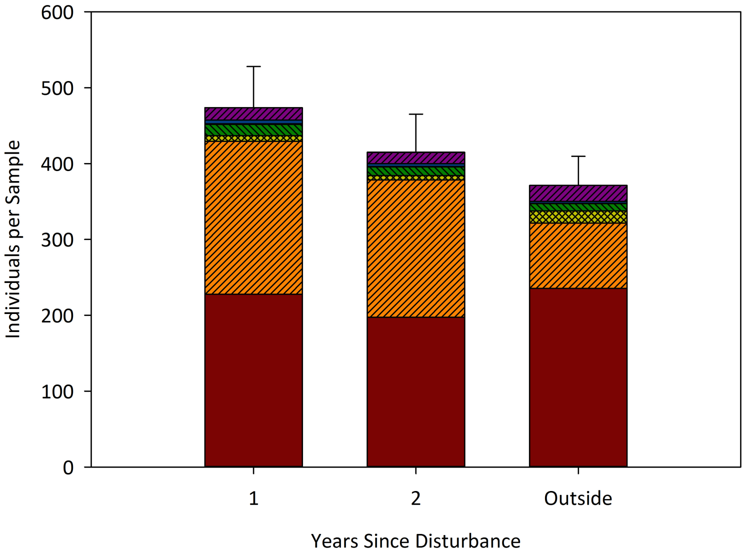

Figure 9. Total individuals per sample and contribution of taxonomic groups for each scour age (1 year, 2 years) at Cinder Cones experimental plots compared to outside samples from 2003 and 2004. Error bars represent standard error from the mean.

between experimental and natural scours ($Pseudo\text{-}F_{1,31} = 5.08$, $p = 0.002$). The experimental plots did not mimic the physical and environmental conditions that could influence natural scour recolonization, with differences reaffirmed through statistical analysis, and therefore were excluded from community-wide analyses.

Ecological Traits of Communities Characteristic of Scour Recolonization

To determine if iceberg scours select for certain suites of ecological traits in the colonizing Antarctic infauna, species were classified into functional groups based upon their dispersal potential, feeding mode, and mobility (Table 2). PERMANOVA tests revealed differences across all ecological traits based upon sampling location ($Pseudo\text{-}F_{2,89} = 11.13$, $p = 0.001$). Pair-wise tests revealed significant differences for each ecological trait between samples from sites inside and outside of scour locations, with no differences between edge and outside sampling locations (Table 6). The abundances of secondary consumers with high mobility and low dispersal were proportionally higher at inside scour locations (Fig. 10), corresponding to higher numbers of crustaceans in these sampling locations. Although there were no significant differences between edge and outside sampling areas, there were higher abundances of low mobility organisms observed on the edge of iceberg scours (Fig 10C), driven by high abundances of *S. tcherniai* and *E. meridionalis*. The other ecological traits (dispersal, feeding) also did not indicate any significant differences between outside and edge sampling locations (Fig 10A & B, Table 6). Despite low statistical power, differences in ecological traits were detected at sampling locations disturbed by iceberg scour. This is interesting because of the small spatial scales between samples, demonstrating how iceberg scours can create a

Table 6

Tests for differences between ecological traits at sampling locations. Totals refers to pooled totals of all ecological traits tested at each sampling location. Based upon one-way PERMANOVA and ANOSIM with 4th root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences in both PERMANOVA and ANOSIM tests.

	PERMANOVA Tests				ANOSIM Test	
Totals	**t**	**P (perm)**	**Average Similarity Between Groups**	**Distance Between Group Centroids**	**R**	**P**
Outside vs Edge	1.25	0.209	87.94	4.13	0.09	0.139
Outside vs Inside*	3.55	0.001	81.45	9.93	0.45	0.001
Inside vs Edge	2.18	0.006	79.70	13.32	0.05	0.203
Mobility						
Outside vs Edge	1.30	0.180	89.47	3.81	0.12	0.114
Outside vs Inside*	3.97	0.001	83.84	9.62	0.45	0.001
Inside vs Edge	2.54	0.005	81.39	13.45	0.11	0.093
Feeding						
Outside vs Edge	1.46	0.125	86.05	5.39	0.16	0.028
Outside vs Inside*	2.16	0.014	84.42	6.00	0.19	0.004
Inside vs Edge	1.58	0.103	82.55	8.83	0.06	0.199
Dispersal						
Outside vs Edge	1.03	0.363	88.28	3.69	0.01	0.509
Outside vs Inside*	4.43	0.001	75.29	15.73	0.45	0.001
Inside vs Edge	2.22	0.016	74.41	18.43	0.00	0.394

mosaic of communities containing organisms with varying ecological traits.

McMurdo Sound Disturbance Regimes

Cinder Cones inside scour and outside reference samples were compared to samples from the greater McMurdo Sound region to evaluate how communities from sites commonly disturbed by icebergs compare to sites disturbed by anthropogenic influences as well as undisturbed locales from the east and west regions (Fig. 2, Appendix B). MDS plots revealed a clear separation between different disturbance regimes, with gradual changes in communities corresponding to differing disturbance

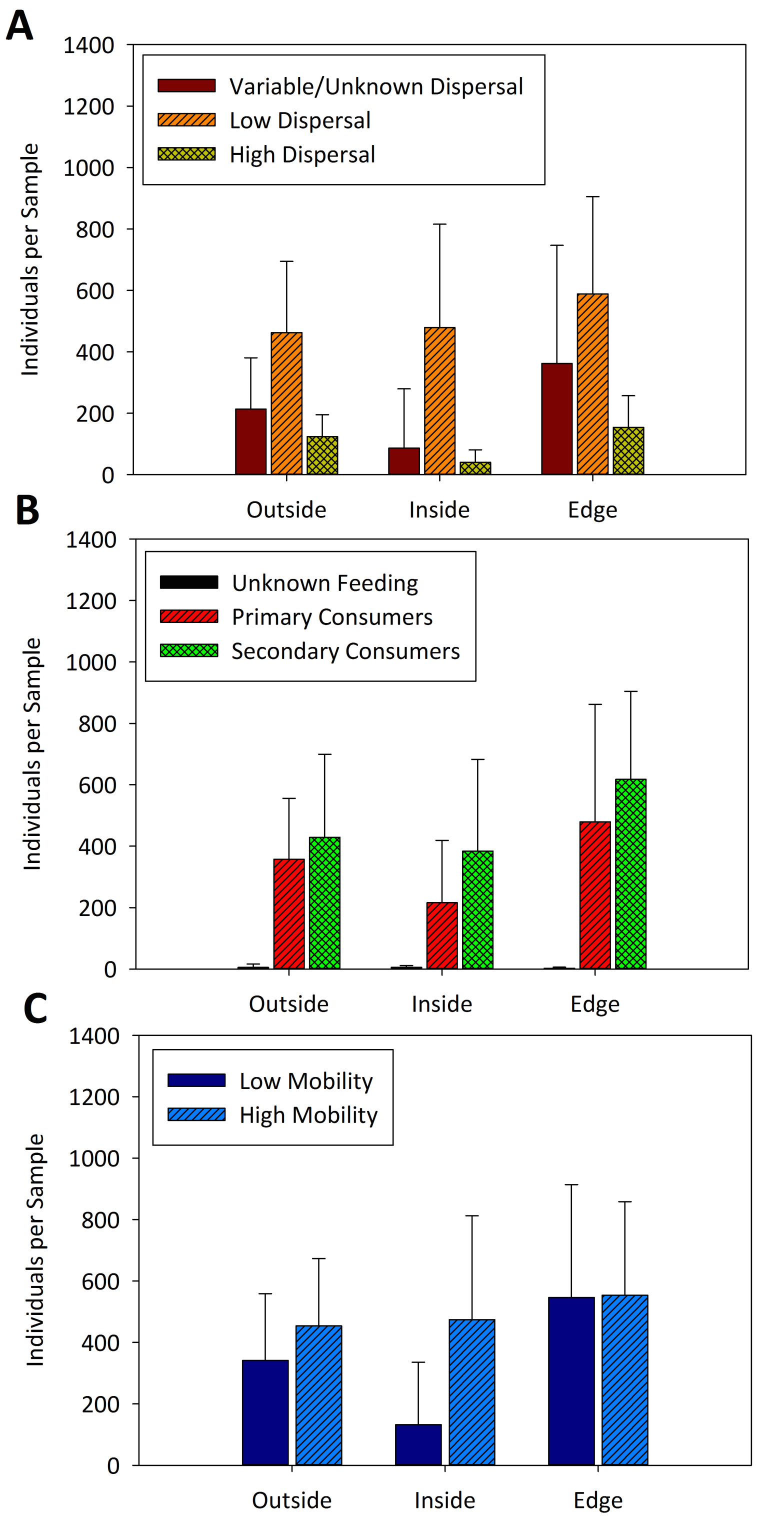

Figure 10. Total individuals per sample at each sampling location (Outside, Inside, Edge) based upon ecological traits A) Dispersal B) Feeding and C) Mobility at Cinder Cones scours. Error bars represent standard error from the mean.

pressures (Fig. 11A). This pattern is clearly visualized in the PCA ordination based upon distance between group centroids (Fig. 11B). PERMANOVA analysis revealed significant differences between disturbance regimes ($Pseudo\text{-}F_{5,596} = 46.48$, $p = 0.001$). Two-way PERMANOVA analysis revealed that anthropogenic disturbances were driving differences more than iceberg disturbance, and explained a higher percentage of variation in community composition (Table 7). Pairwise ANOSIM and PERMANOVA tests revealed significant differences between all groups when compared to undisturbed samples (Table 8, see Appendix E for full list). The strongest differences (low average similarity between groups, large distance between groups centroids, high R-values) occurred between undisturbed west region samples and undisturbed samples. Within the east region of the McMurdo Sound, differences were greater in areas highly disturbed by anthropogenic influences than in samples exposed to iceberg scour. This demonstrates that persistent chemical exposure has a greater impact on benthic infaunal communities in the McMurdo Sound compared to episodic physical disturbance. Both open ocean exposed and anthropogenic intermediate samples demonstrated weak differences (high average similarity between groups, small distance between groups centroids, low R-values) with undisturbed samples.

To determine what was driving differences between disturbance regimes, abundances and diversity measures were compared at each regime. Total infaunal abundance differed significantly among disturbance regimes ($F_{5,596} = 50.31$, $p < 0.001$), with the highest abundances found at iceberg scour and open ocean exposed locations, and the lowest abundances at undisturbed west locations (Fig. 12). Both anthropogenic

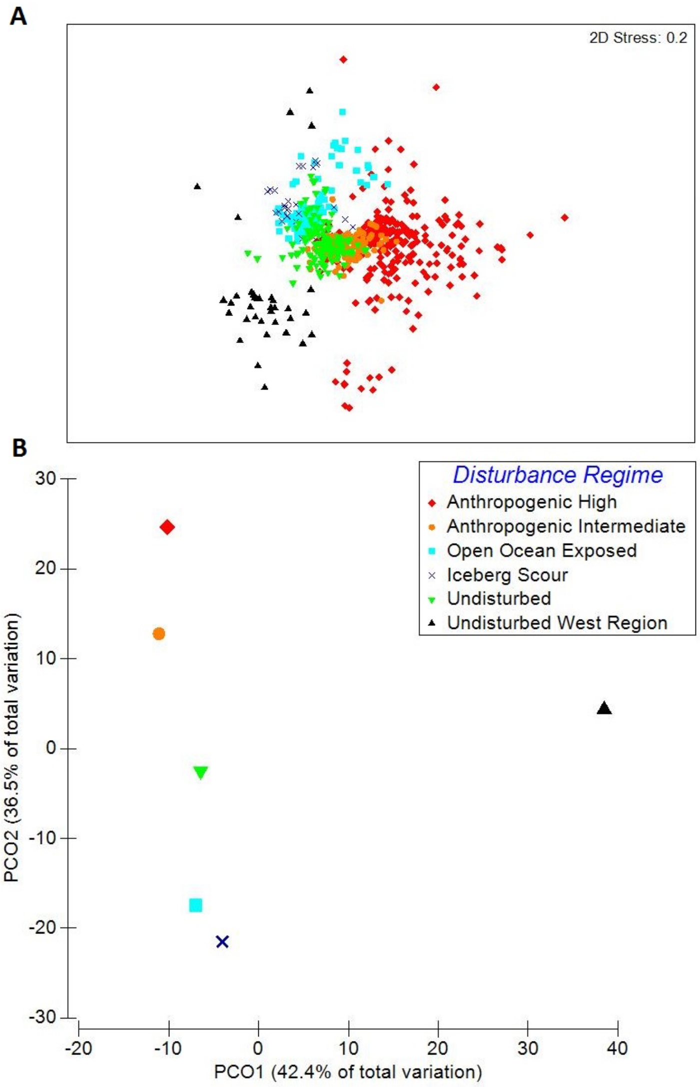

Figure 11. Visual classification of disturbance regimes in McMurdo Sound based upon A) MDS ordination and B) PCA ordination based upon distance between group centroids. Based upon 4th root transformed abundances and Bray-Curtis similarities.

Table 7

Two-way PERMANOVA analysis for differences in assemblages based upon anthropogenic and iceberg disturbance levels. Based upon 4th root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences.

PERMANOVA Tests						
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P**	**% Variance**
Anthropogenic Disturbance*	2	1.71 E5	85567	54.38	0.001	22.30
Iceberg Disturbance*	2	5.22 E4	26112	16.59	0.001	13.367
Residual	592	9.31 E5	1573.5			64.32
Total	596	1.21 E6				

Table 8

Tests for differences between disturbance regimes and undisturbed locations within the McMurdo Sound. Table sorted based upon average similarity between disturbance regimes. Based upon one-way PERMANOVA and ANOSIM with 4th root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences in both PERMANOVA and ANOSIM tests.

	PERMANOVA Tests				ANOSIM Tests	
Disturbance Regime Comparison to Undisturbed	**t**	**P (perm)**	**Average Similarity Between Groups**	**Distance Between Group Centroids**	**R**	**P**
Undisturbed West Region*	6.66	0.001	25.65	47.54	0.90	0.001
Anthropogenic High*	8.33	0.001	34.32	38.48	0.33	0.001
Iceberg Scour*	4.28	0.001	43.06	30.57	0.54	0.001
Open Ocean Exposed*	5.03	0.001	46.17	24.62	0.30	0.001
Anthropogenic Intermediate*	5.29	0.001	52.49	21.80	0.26	0.001

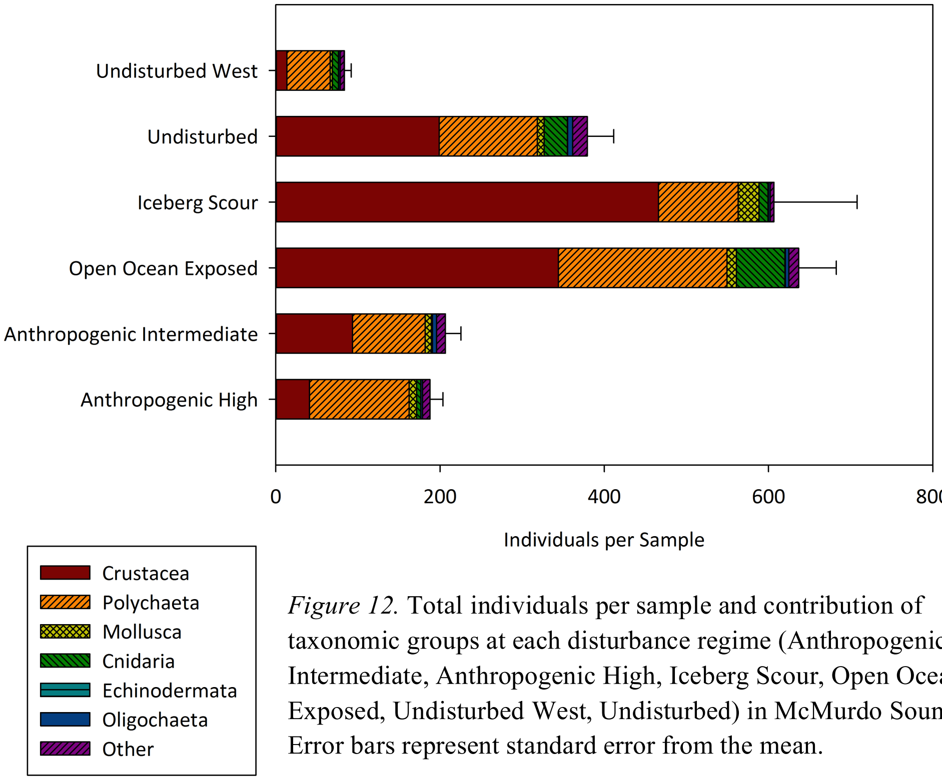

Figure 12. Total individuals per sample and contribution of taxonomic groups at each disturbance regime (Anthropogenic Intermediate, Anthropogenic High, Iceberg Scour, Open Ocean Exposed, Undisturbed West, Undisturbed) in McMurdo Sound. Error bars represent standard error from the mean.

high and intermediate disturbance locations exhibited lower infaunal abundances compared to undisturbed samples from the east region. Crustaceans outnumbered all other taxa at iceberg scour, ocean open exposed, and undisturbed areas, whereas polychaetes were the most abundant taxa at anthropogenically disturbed areas, as well as undisturbed areas in the west region. Species richness was significantly different across regimes ($F_{5,596} = 57.02$, $p < 0.001$), with the lowest values of richness found at sites exposed to high levels of anthropogenic disturbance, followed by undisturbed sites in the west region (Fig. 13). Shannon-Wiener diversity index ($F_{5,596} = 16.59$, $p < 0.001$) and Evenness ($F_{5,596} = 5.55$, $p < 0.001$) also differed significantly across disturbance regimes, with the lowest values found at anthropogenic high sites and iceberg scour sites, respectively (Fig. 14).

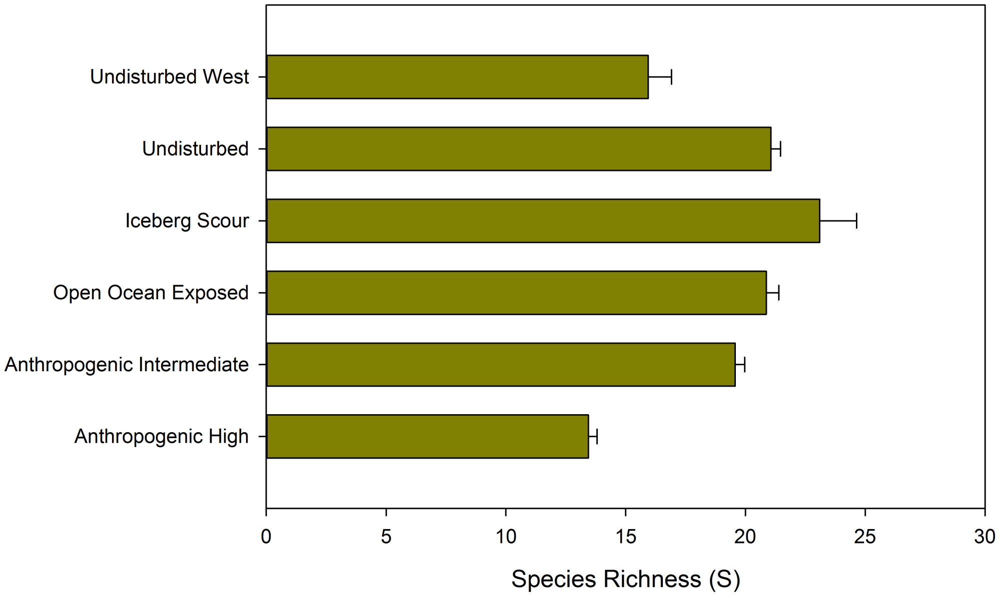

Figure 13. Species richness (S) per sample at each disturbance regime (Anthropogenic Intermediate, Anthropogenic High, Iceberg Scour, Open Ocean Exposed, Undisturbed West, Undisturbed) in McMurdo Sound. Error bars represent standard error from the mean.

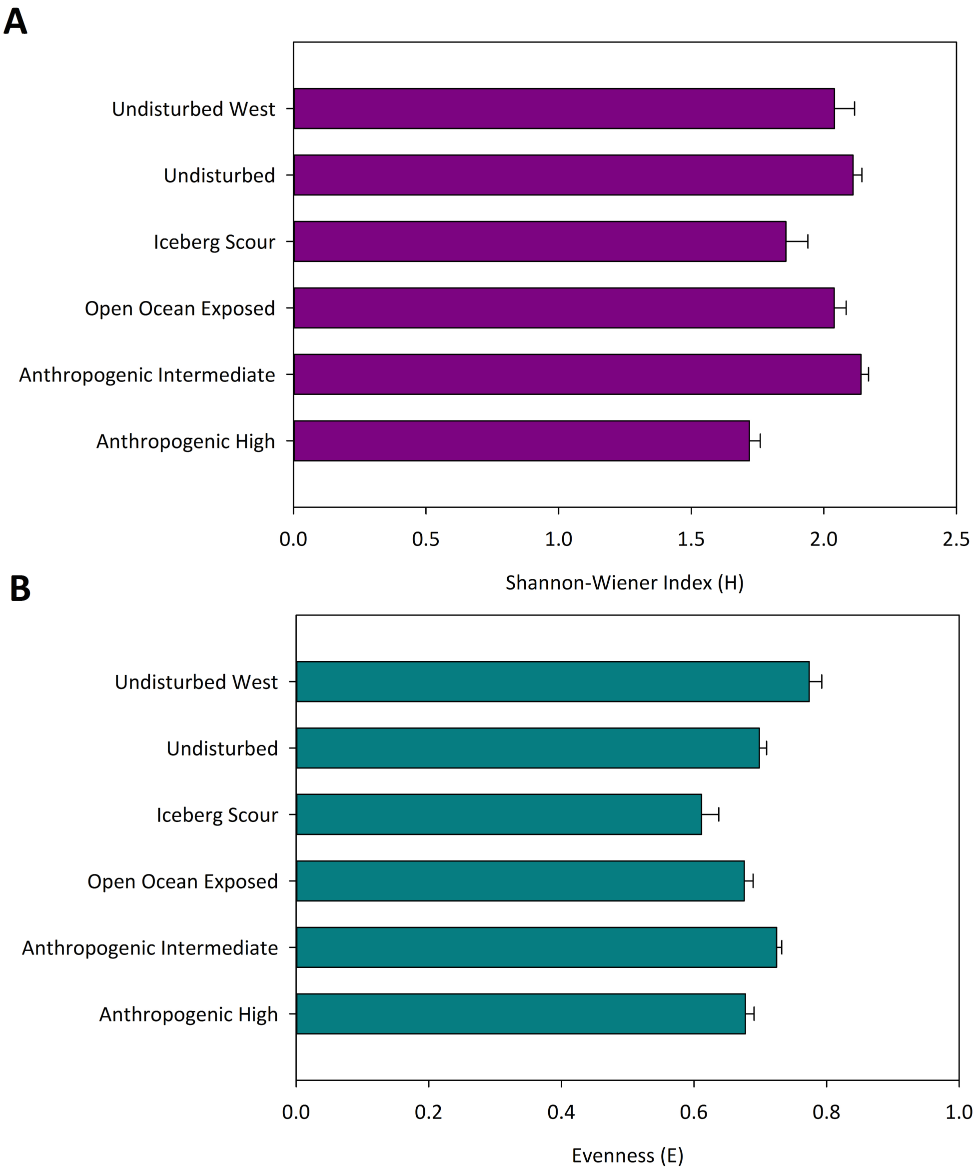

Figure 14. Diversity measures for A) Shannon-Wiener Diversity Index (H) and B) Evenness (E) diversity measures at each disturbance regime (Anthropogenic Intermediate, Anthropogenic High, Iceberg Scour, Open Ocean Exposed, Undisturbed West, Undisturbed) in McMurdo Sound. Error bars represent standard error from the mean.

To investigate the influence of sampling year over the course of the study, additional analysis was performed that incorporated disturbance regimes. Two-way PERMANOVA analysis revealed significant differences based upon disturbance regime and year, yet there was a significant interaction effect (Table 9). Disturbance regime explained the highest percentage of variance, but further analysis was performed to explore the interaction between disturbance regime and year. All samples and regimes were pooled to examine any patterns in total number of individuals across all sampling years (Fig. 15). The reduction in abundances from 2002-2004 coincided with the presence of the B-15 iceberg that blocked normal sea ice retreat from 2000-2005. Thought it was within the range of other years, abundances continually decreased following the arrival of B-15. It is possible that non-normal environmental conditions created by the presence of B-15 influenced the entire sound, as a potential reason for a significant interaction effect between disturbance regime and year.

Table 9

Two-way PERMANOVA analysis tests for differences in assemblages by disturbance regime and year. Based upon 4th root transformed abundances. An asterisk (*) denotes significant differences.

PERMANOVA Tests						
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P**	**% Variance**
Disturbance Regime*	5	2.69 E5	53915	52.84	0.001	28.13
Year*	12	1.54 E5	12878	12.62	0.001	12.13
Disturbance Regime x Year*	30	1.88 E5	6296	6.17	0.001	16.53
Residual	629	6.41 E5	1020.4			43.20
Total	676	1.39 E6				

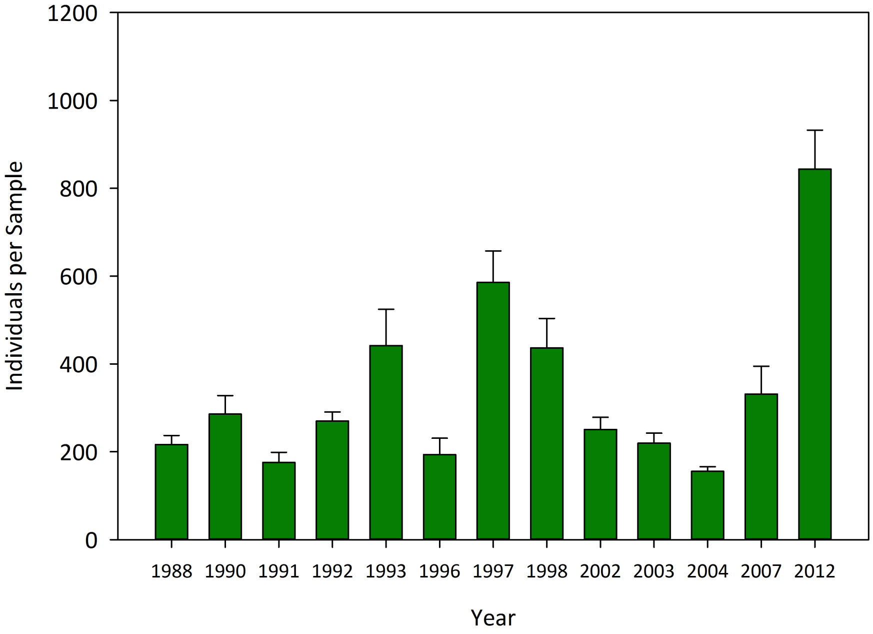

Figure 15. Total individuals per sample for all disturbance regimes across all sampling years in McMurdo Sound. Error bars represent standard error from the mean.

Discussion

Iceberg scours altered infaunal abundances and species composition in relatively predictable fashions at Cinder Cones, McMurdo Sound, Antarctica. Following iceberg disturbance, infaunal abundance was markedly lower inside the newly formed iceberg scours relative to undisturbed reference sediments. Similar declines in invertebrate abundance in response to iceberg scour were reported in studies from other regions in Antarctica (Richardson & Hedgepeth, 1977; Bromberg *et al.*, 2000; Smale, 2007; 2008) and Arctic waters (Conlan & Kvitek, 2005; Conlan *et al.,* 2008). Previous studies demonstrated slow recovery rates, taking anywhere from eight years (Conlan & Kvitek, 2005) to multiple decades (Gutt *et al.*, 1996; Gutt & Starmans, 2001) before scour locations were similar to adjacent undisturbed communities. This slow pace of succession in polar regions has been attributed to diverse assemblages of species, as well as the presence of slow-growing sponges. Recovery of infaunal communities at Cinder Cones appears to be a much faster process, mirroring findings reported in Smale (2008) at a site that also regularly experiences iceberg disturbance and is apparently well adapted to rapid recovery. An attempt to resample 2012 scour locations was made in 2014, but the lack of any visual boundary between previous scours and reference areas made sampling impossible. Though wholly qualitative, this is a good indicator of the speed at which recovery takes place at Cinder Cones and other sites commonly exposed to icebergs in McMurdo Sound.

Mobile crustaceans dominated the inside of scours, most noticeably the tanaid *N. dimorphus.* This species is thought to regulate the species composition and population-size structure of soft-bodied infauna, especially polychaetes, by preying on small species and small individuals of large species (Oliver & Slattery, 1985). This pattern appears to hold true, as higher proportions of crustaceans, driven by *N. dimorphus,* were correlated with drastically reduced numbers of polychaetes and *E. meridionalis* in communities inside scour zones. The number of *L. elliptica*, which produce pelagic nonfeeding larvae (Pearse *et al.*, 1987; 1990), was higher at scour edge and inside scour locations. Iceberg scours might be opening up favorable habitat for this species by removing larger and more mature organisms, allowing for a reduction in inter- and intra-specific competition (Woodin & Jackson, 1979; Brenchley, 1982).

Scour edges were characterized by higher numbers of total individuals per sample, due to higher abundances of *N. dimorphus,* the spionid polychaete *S. tcherniai,* and the burrowing anemone *E. meridionalis.* These three taxa often made up over half of the individuals within these samples. The greater influx of *E. meridionalis* and the pioneer polychaete *S. tcherniai* (Thrush & Cummings, 2011) at scour edge areas compared to inside scour areas suggests that the source of organisms for recolonization in scours was from adjacent locations, as opposed to the settlement of pelagic larvae. Experimental manipulations demonstrated similar patterns of recolonization, with edge locations and small plots having higher total abundance, and higher abundance of *S. tcherniai* and *E. meridionalis*. *Spiophanes* are known to have planktotrophic larvae (Blake & Arnofsky, 1999), but these results suggest that *S. tcherniai* may be brooding its young or has a strong proclivity for recruitment to conspecifics. *Edwardsia meridionalis* is known to have pelagic embryos and pelagic lecithotrophic larvae (Pearse *et al.*, 1986) and may be recruiting to conspecifics; however these results suggest that this species may be asexually reproducing by transverse fission, a common reproductive mode in other edwardsiids (Shick, 1991). The higher number of total individuals at scour edge locations suggests that either predators are satiated and no longer able to reduce soft-bodied organisms abundances in this area, or that inputs of organisms to these areas are too high to be regulated, or potentially a mixture of both.

Diversity at inside scour locations was lower compared to outside reference areas but was higher than edge locations, driven by a higher diversity of arthropods. The higher number of crustacean species at inside scour locations was likely driven by the movement of adults. Many of these crustaceans are detritivores and scavengers, and may benefit from the accumulating detritus found in the trap-like depressions formed after iceberg scour (Gerdes *et al.*, 2008), and first access to any dead and dying organisms left in the wake of an iceberg scour. Diversity was considerably lower at the edge of iceberg scours, yet this pattern could potentially be the result of a small sampling effort at these locations. Though species richness (S) did not differ across sampling locations, all other diversity indices demonstrated lower diversity inside and on the edge of iceberg scours, driven by a drop in evenness as a result of disturbance. This drop in diversity can be expected at the start of the successional process, when recolonization is dominated by a few opportunistic species that are capable of responding rapidly to a disturbance and monopolizing resources (Connell, 1978; Sousa 1979), in this case driven by *S. tcherniai*.

Recolonization varied from year to year, with a myriad of potential mechanisms. Though iceberg movement is dependent on open water and is therefore seasonal in the nearshore Antarctic, scours could have taken place at different times of the austral summer. This variation of timing would allow specific taxa to benefit from the increase of open space if it corresponds with their reproductive timing (Pearse *et al.,* 1991). In addition, sea ice extent and ice production varies year-to-year in the Ross Sea (Comiso *et al.,* 2011), as does fast-ice (sea ice that is "fastened" to the coastline); both were influenced by the arrival and persistence of several large tabular icebergs in the Ross Sea from 2001-2005 (Brunt *et al.,* 2006). The icebergs B-15A and C-19 restricted the normal ebb and flow of summer sea ice movements, increasing overall ice cover, reducing phytoplankton growth and the length of the algal growing season, and resulting in reduced primary productivity throughout the region (Arrigo *et al*., 2002; Seibel and Dierssen, 2003; Arrigo and van Dijken, 2003; 2004). Poor feeding conditions could have lowered reproductive rates (Thorson, 1950) of species that commonly dominate these areas. This reduction of productivity appears to have impacted recovery of scour samples from 2002 based upon the absence of two common and dominant members of this community, *S. tcherniai* and *E. meridionalis.* It appears that recolonization was altered by the presence of B-15, suggesting that environmental conditions may play a large role in community recovery following iceberg scour.

Iceberg scour appears to be exerting selective pressures on ecological traits within communities normally exposed to these types of disturbance. Ice-related disturbance, including icebergs and anchor ice formation, decreases with increasing depths (Smale, 2007). As a result, body size and the relative abundance of sessile taxa increase with increasing greater depths throughout Antarctica (Zamorano, 1983; Barnes & Brockington, 2003; Smale, 2007; 2008). Sessile and sedentary taxa have no way of avoiding approaching icebergs; therefore mobile taxa may have the advantage of moving away and back, initially recolonizing the open area, as suggested by these results.

The brief but intense summer period of productivity in the Antarctic is in stark contrast to the low light and low productivity periods of the winter (Clarke, 1988). Organisms must be able to adapt to these changes, and many switch feeding strategies throughout the year (Barnes & Clarke, 1995; Gili *et al*., 2001). The seasonal disparities in food availability and exposure to varying degrees of disturbance may have selected for generalist feeding strategies in a wide variety of species (McClintock, 1987; Clarke & Crame, 1989; Conlan *et al*., 2006). Higher abundances of generalist consumers, mostly scavengers and omnivores, occurred inside of scour locations. Many crustacean families, e.g. tanaids, chelicerates, amphipods, and isopods, were able to opportunistically exploit recently disturbed areas as previously noted (Lenihan & Oliver, 1995; Conlan *et al.,* 1998; Stanwell-Smith *et al.,* 1999; Smale, 2008). These species are common members of most McMurdo Sound infaunal communities (Stark *et al.,* 2014), yet they appear to cluster at recent disturbance areas.

Perhaps most noteworthy was the higher number of taxa with a low dispersal range within disturbed areas. This agrees with one previous study from Hangar Cove (Smale, 2008), yet contrasts with previous studies, which suggest that taxa with high dispersal ability are and should be dominant at disturbed Antarctic sites (Poulin *et al.,* 2002; Pearse & Lockhart; 2004; Palma *et al.,* 2007). Models predict that habitat instability favors species with high dispersal capabilities (McPeek & Holt, 1992; Lytle, 2001), as larval propagation is the only method for movement for many sessile species. The community at Cinder Cones appears to go against these predictions, most likely due to a high proportion of mobile organisms with direct development in nearby areas. The frequency at which iceberg disturbances occur at Cinder Cones may prevent the recruitment of organisms with slower growth (Clarke, 1980; 1983; 1988; Luxmoore, 1982; Arntz *et al.*, 1994) and episodic reproduction (Dayton *et al.,* 2013), which are commonly found at greater depths. Additionally, many organisms with planktotrophic larvae spawn in late winter and early spring to synchronize with increasing food availability during summer plankton blooms (Pearse *et al*., 1991). These species may have first access to freshly scoured areas that generally occur in mid-to-late summer (Smale *et al*., 2008). In contrast, species that produce lecithotrophic larvae and brooded embryos tend to spawn year-round (Pearse *et al*., 1991), and may arrive at a disadvantage, to a community of predators and competitors that have already been established for some time.

Although experiencing different types of disturbances, benthic communities in McMurdo Sound had overall similar community composition. By nominally classifying the communities based upon disturbance regimes (adapted from Stark *et al.,* 2014, Appendix B), differences became much more apparent. Different types and levels of disturbance alter these communities when compared to undisturbed samples (Fig. 9). The east region of the McMurdo Sound has been exposed to a variety of persistent organic and chemical toxicants from former military establishments and the current research station located on Ross Island since 1956 (Risebrough *et al.,* 1990). Environmental impacts include fuel and oil spills, landfill and marine waste disposal sites, and sewage and wastewater disposal (Lenihan *et al.*, 1990; Lenihan 1992; Conlan *et al.,* 2004). High levels of anthropogenic disturbances resulted in declines in abundance and diversity, as only a small subset of species, most of them being polychaetes (Stark *et al.,* 2014), were tolerant to these pollutants. Intermediate levels of anthropogenic disturbance were tolerated by a wider range of species, but still had lower abundances when compared to undisturbed locations.

North of McMurdo station are areas (Turtle Rock, Cape Evans, Cinder Cones) that have been used as control locations for comparisons with sites at the research base (Conlan *et al.,* 2000; 2004; 2006; 2010; Stark *et al.,* 2014), due to their geographic isolation from sites exposed to human impacts. These areas have higher likelihoods of episodic physical disturbance by icebergs due to their relative exposure to the open Ross Sea, and may be in various stages of recovery as a result. These areas also have higher levels of access to food-rich open ocean currents. Communities in areas north of McMurdo station were similar to undisturbed locations around the station, yet had significantly higher abundances driven by an increase in crustaceans. Open ocean exposed communities were also similar to samples taken from inside scours at Cinder Cones. Both are located in the same proximity to the open ocean, and both benefit from access to food-rich waters, as demonstrated by high levels of abundance in these samples. Although iceberg scours can have severe impacts on seafloor communities, these results suggest that ample access to food can aid recovery, providing resources for a community well prepared for such a disturbance.

Conclusions

Overall, there is a gradient of changes in communities across a spectrum of disturbance and environmental conditions (Table 13). Communities in the west region of McMurdo Sound had the lowest abundances and diversity levels similar to the most disturbed sites. The west region is further downstream from food-rich currents originating in the open Ross Sea (Barry & Dayton, 1988; Barry, 1988), suggesting that access to food is an important factor shaping Antarctic benthic communities, and that community response to stress, whether from contamination or lack of food, has some commonality. In the eastern region, sites and communities exposed to anthropogenically-derived pollutants and naturally occurring iceberg disturbances exist on opposite ends of a spectrum of disturbance (Fig. 12). Infaunal communities in Antarctica have had the chance to adapt to iceberg scour and other forms of ice disturbance, as the continent came into its current climate around 34 million years ago (Lear *et al.,* 2008). This study suggests that these communities are well-adapted to physical disturbances from icebergs, with abundances and species diversity (S) higher in scours than undisturbed samples due to a suite of species that are adapted to these pressures. In contrast, these infaunal communities have difficulty coping with anthropogenically-derived contaminants, resulting in drastic reductions in abundance and diversity. Human activities and the subsequent direct contamination of near-shore waters around McMurdo Station began in 1956 following the establishment of Naval Air Facility McMurdo. This span of time is too short for any evolutionary adaptations to manifest, and as a result only species with inherent tolerance to metals, hydrocarbons, and human waste can persist in contaminated areas. Luckily direct local contamination in Antarctica and the Southern Ocean is sparse and generally only found near research and former military establishments (Lenihan *et al.,* 1990; Lenihan, 1992; Cripps, 1992; Green and Nichols, 1995; Conlan *et al.,* 2004; Hughes & Thompson, 2004; Santos *et al.*, 2005; Kennicutt, 2010; Stark *et al.,* 2014).

There are currently no known invasive species in the benthos of the Ross Sea, and it has been isolated for at least 25 million years (Tavares & De Melo, 2004; Barnes, 2002). This insular and relatively unchanged suite of species, and the lack of any opportunistic invasive species, has kept infaunal communities similar regardless of exposure to various forms and severities of disturbance. Assertions could be made that

Table 13
Summary table of disturbance regime dissimilarity compared to undisturbed samples in the McMurdo Sound. Rank dissimilarity based upon PERMANOVA tests for average similarity between regimes compared to undisturbed samples. ↑ and ↓ represent significantly higher and lower values, respectively, for each factor (Abundance, Species Richness, Shannon-Wiener Diversity, and Evenness) compared to undisturbed samples based upon Tukey HSD test. – represents no significant differences compared to undisturbed samples.

Rank Dissimilarity	Disturbance Regime	Abundance	Species Richness (S)	Shannon-Wiener Diversity (H)	Evenness (E)
1	Undisturbed West	↓	↓	–	–
2	Anthropogenic High	↓	↓	↓	–
3	Iceberg Scour	↑	–	–	–
4	Open Ocean Exposed	↑	–	–	–
5	Anthropogenic Intermediate	↓	–	–	–

benthic infaunal communities are resilient to changing environmental conditions and disturbance pressures, but if polar warming (Purkey & Johnson, 2010; Durack & Wijffels, 2010; Aronson *et al.,* 2011) leads to changes in the oceanographic barrier formed by freezing temperatures in circumpolar currents (Barnes 2002), these communities may be in for wholesale transformations.

References

Ahn, I.-Y. (1993). Enhanced particle flux through the biodeposition by the Antarctic suspension-feeding bivalve Laternula elliptica in Marian Cove, King George Island. *Journal of Experimental Marine Biology and Ecology*, *171*(1), 75–90.

Åkesson, B. (1976). Morphology and life cycle of Ophryotrocha diadema, a new polychaete species from California. *Ophelia*, *15*(1), 23–35.

Allen, J. A., Ewel, K. C., & Jack, J. (2001). Patterns of natural and anthropogenic disturbance of the mangroves on the Pacific Island of Kosrae. *Wetlands Ecology and Management*, *9*, 291–301.

Amsler, M. O., Mcclintock, J. B., Amsler, C. D., Angus, R. A., & Baker, B. J. (2009). An evaluation of sponge-associated amphipods from the Antarctic Peninsula. *Antarctic Science*, *21*, 579–589.

Anderson, M. J., Gorley, R. N., & Clarke, R. K. (2005). Permanova. *Permutational Multivariate Analysis of Variance, a Computer Program. Department of Statistics, University of Auckland*, 24 pp.

Arntz, W., Brey, T., & Gallardo, V. A. (1994). Antarctic zoobenthos. *Oceanography and Marine Biology*, *32*, 241–304.

Aronson, R. B., Thatje, S., McClintock, J. B., & Hughes, K. A. (2011). Anthropogenic impacts on marine ecosystems in Antarctica. *Annals of the New York Academy of Sciences*, *1223*(1), 82–107.

Arrigo, K. R., & van Dijken, G. L. (2003). Impact of iceberg C‐19 on Ross Sea primary production. *Geophysical Research Letters*, *30*, 1836-1848.

Arrigo, K. R., & van Dijken, G. L. (2004). Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*(1), 117–138.

Arrigo, K. R., van Dijken, G. L., Ainley, D. G., Fahnestock, M. A., & Markus, T. (2002). Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters*, *29*(7), 1–8.

Aumack, C. F., Amsler, C. D., McClintock, J. B., & Baker, B. J. (2011). Changes in amphipod densities among macroalgal habitats in day versus night collections along the Western Antarctic Peninsula. *Marine Biology*, *158*, 1879–1885.

Ballantyne, J., & Long, D. G. (2002). A multidecadal study of the number of Antarctic icebergs using scatterometer data. *Geoscience and Remote Sensing Symposium, 2002. IGARSS'02. 2002 IEEE International*. *5*, 3029-3031.

Bargagli, R., Monaci, F., Sanchez-Hernandez, J. C., & Cateni, D. (1998). Biomagnification of mercury in an Antarctic marine coastal food web. *Marine Ecology Progress Series*, *169*(6), 65-76.

Barnes, D. K. A. (2002). Biodiversity: invasions by marine life on plastic debris. *Nature*, *416*, 808–809.

Barnes, D. K. A., & Brockington, S. (2003). Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica. *Marine Ecology Progress Series*, *249*, 145–155.

Barnes, D. K. A., & Clarke, A. (1995). Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom*, *75*, 689–703.

Barnes, D. K. A., & Conlan, K. E. (2007). Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*, 11–38.

Barnes, P. W., & Lien, R. (1988). Icebergs rework shelf sediments to 500 m off Antarctica. *Geology*, *16*, 1130–1133.

Barry, J. P. (1988). Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. *Polar Biology*, *8*, 377–391.

Barry, J. P., & Dayton, P. K. (1988). Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. *Polar Biology*, *8*, 367–376.

Berkman, P. A., Waller, T. R., & Alexander, S. P. (1991). Unprotected larval development in the Antarctic scallop Adamussium colbecki (Mollusca: Bivalvia: Pectinidae). *Antarctic Science*, *3*, 151–157.

Berry, A. J. (1982). Predation by Natica maculosa Lamarck (Naticidae: Gastropoda) upon the trochacean gastropod Umbonium vestiarium (L.) on a Malaysian shore. *Journal of Experimental Marine Biology and Ecology*, *64*(1), 71–89.

Blake, J. A., & Arnofsky, P. L. (1999). Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Reproductive strategies and developmental patterns in annelids*. pp. 57–106. Springer.

Blazewicz-Paszkowycz, M., & Ligowski, R. (2002). Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea). *Antarctic Science*, *14*(1), 11–15.

Bolker, B. M., & Pacala, S. W. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *The American Naturalist*, *153*, 575–602.

Bowden, D. A. (2005). Seasonality of recruitment in Antarctic sessile marine benthos. *Marine Ecology Progress Series*, *297*, 101–118.

Brenchley, G. A. (1982). Mechanisms of spatial competition in marine soft-bottom communities. *Journal of Experimental Marine Biology and Ecology*, *60*(1), 17–33.

Bromberg, S., Ferraz Nonato, E., Corbisier, T. N., & Varella Petti, M. A. (2000). Polychaete distribution in the near-shore zone of Martel inlet, admiralty bay (King George island, Antarctica). *Bulletin of Marine Science*, *67*, 175–188.

Bromley, H. J. (1974). Morphology and anatomy of Maccabeus tentaculatus (Priapulida: Seticoronaria). *Journal of Zoology*, *173*, 173–197.

Brown, K. M., Fraser, K. P. P., Barnes, D. K. A., & Peck, L. S. (2004). Links between the structure of an Antarctic shallow-water community and ice-scour frequency. *Oecologia*, *141*, 121–129.

Brunt, K. M., Sergienko, O., & MacAyeal, D. R. (2006). Observations of unusual fast-ice conditions in the southwest Ross Sea, Antarctica: preliminary analysis of iceberg and storminess effects. *Annals of Glaciology*, *44*, 183–187.

Burke, R. D. (1983). The induction of metamorphosis of marine invertebrate larvae: stimulus and response. *Canadian Journal of Zoology*, *61*, 1701–1719.

Choudhury, M., & Brandt, A. (2009). Benthic isopods (Crustacea, Malacostraca) from the Ross Sea, Antarctica: species checklist and their zoogeography in the Southern Ocean. *Polar Biology*, *32*, 599–610.

Clarke, A. (1980). A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. *Biological Journal of the Linnean Society*, *14*, 77–92.

Clarke, A. (1983). Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanography and Marine Biology*, *21*, 341–453.

Clarke, A. (1988). Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, *90,* 461–473.

Clarke, A. (1992). Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction & Development*, *22*, 175–183.

Clarke, A., Barnes, D. K. A., & Hodgson, D. A. (2005). How isolated is Antarctica? *Trends in Ecology & Evolution*, *20*, 1–3.

Clarke, A., & Crame, J. A. (1989). The origin of the Southern Ocean marine fauna. *Geological Society, London, Special Publications*, *47*, 253–268.

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K. A., & Smith, R. C. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 149–166.

Clarke, K. R., & Gorley, R. N. (2001). PRIMER v6 PRIMER-E Ltd. *Plymouth, UK*.

Clarke, K. R., & Green, R. H. (1988). Statistical design and analysis for a“ biological effects” study. *Marine Ecology Progress Series*, *46*(1), 213–226.

Clarke, K. R., & Warwick, R. M. (2001). An approach to statistical analysis and interpretation. *Change in Marine Communities*, *2*. PRIMER-E Ltd. *Plymouth, UK*.

Clarke, K. R., Warwick, R. M., & Brown, B. E. (1993). An index showing breakdown of seriation, related to disturbance, in a coral-reef assemblage. *Marine Ecology Progress Series*, *102(1)*, 153–160.

Coleman, C. O. (1989). Burrowing, grooming, and feeding behaviour of Paraceradocus, an Antarctic amphipod genus (Crustacea). *Polar Biology*, *10*, 43–48.

Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. 2006. *Consultado En: Http://viceroy. Eeb. Uconn. Edu/estimates*.

Comiso, J. C., Kwok, R., Martin, S., & Gordon, A. L. (2011). Variability and trends in sea ice extent and ice production in the Ross Sea. *Journal of Geophysical Research*. *116,* CO4021.

Conlan, K., Aitken, A., Hendrycks, E., McClelland, C., & Melling, H. (2008). Distribution patterns of Canadian Beaufort shelf macrobenthos. *Journal of Marine Systems*, *74*, 864–886.

Conlan, K. E., Kim, S. L., Lenihan, H. S., & Oliver, J. S. (2004). Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. *Marine Pollution Bulletin*, *49*(1), 43–60.

Conlan, K. E., Kim, S. L., Thurber, A. R., & Hendrycks, E. (2010). Benthic changes at McMurdo Station, Antarctica following local sewage treatment and regional iceberg-mediated productivity decline. *Marine Pollution Bulletin*, *60*(3), 419–432.

Conlan, K. E., & Kvitek, R. G. (2005). Recolonization of soft-sediment ice scours on an exposed Arctic coast. *Marine Ecology Progress Series*, *286*, 21–42.

Conlan, K. E., Lenihan, H. S., Kvitek, R. G., & Oliver, J. S. (1998). Ice scour disturbance to benthic communities in the Canadian High Arctic. *Marine Ecology Progress Series*, *166*, 1–16.

Conlan, K. E., Rau, G. H., & Kvitek, R. G. (2006). δ 13 C and δ 15 N shifts in benthic invertebrates exposed to sewage from McMurdo Station, Antarctica. *Marine Pollution Bulletin*, *52*, 1695–1707.

Conlan, K. E., Rau, G. H., McFeters, G. N. A., & Kvitek, R. G. (2000). Influence of McMurdo Station sewage on Antarctic marine benthos, evidence from stable isotopes, bacteria, and biotic indices. *Antarctic Ecosystems, Models for Wider Ecological Understanding Davison W, Howard-Williams C, Broady P*, 315–318.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*, 1302–1310.

Cripps, G. C. (1992). The extent of hydrocarbon contamination in the marine environment from a research station in the Antarctic. *Marine Pollution Bulletin*, *25*, 288–292.

Crisp, D. J. (1984). Overview of research on marine invertebrate larvae, 1940-1980. *Marine Biodeterioration: An Interdisciplinary Study*, 103–126.

Cutler, E. B. (1994). *The Sipuncula: their systematics, biology, and evolution*. Cornell University Press. 480 pp.

Da Silva, A. A., & Gooday, A. J. (2009). Large organic-walled Protista (Gromia) in the Arabian Sea: density, diversity, distribution and ecology. *Deep Sea Research Part II: Topical Studies in Oceanography*, *56*, 422–433.

Dayton, P. K. (1989). Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Science*, *243*, 1484–1486.

Dayton, P. K., & Hessler, R. R. (1972). Role of biological disturbance in maintaining diversity in the deep sea. *Deep Sea Research and Oceanographic Abstracts,19*, 199–208.

Dayton, P. K., Kim, S., Jarrell, S. C., Oliver, J. S., Hammerstrom, K., Fisher, J. L., … Barry, J. (2013). Recruitment, growth and mortality of an Antarctic hexactinellid sponge, Anoxycalyx joubini. *PloS One*, *8*(2), e56939.

Dayton, P. K., & Oliver, J. S. (1977). Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science*, *197*, 55–58.

Dayton, P. K., Watson, D., Palmisano, A., Barry, J. P., Oliver, J. S., & Rivera, D. (1986). Distribution patterns of benthic microalgal standing stock at McMurdo Sound, Antarctica. *Polar Biology*, *6*, 207–213.

De Broyer, C., Nyssen, F., & Dauby, P. (2004). The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*, 1733–1752.

Dial, R., & Roughgarden, J. (1998). Theory of marine communities: the intermediate disturbance hypothesis. *Ecology*, *79*, 1412–1424.

Dinniman, M. S., Klinck, J. M., & Smith, W. O. (2007). Influence of sea ice cover and icebergs on circulation and water mass formation in a numerical circulation model of the Ross Sea, Antarctica. *Journal of Geophysical Research: Oceans, 112*, C11.

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Knowlton, N. (2012). Climate change impacts on marine ecosystems. *Marine Science*, *4*, 11-37.

Durack, P. J., & Wijffels, S. E. (2010). Fifty-year trends in global ocean salinities and their relationship to broad-scale warming. *Journal of Climate*, *23*, 4342–4362.

Fabiano, M., & Danovaro, R. (1999). Meiofauna distribution and mesoscale variability in two sites of the Ross Sea (Antarctica) with contrasting food supply. *Polar Biology*, *22*, 115–123.

Fauchald, K., & Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology, Annual Review,* 17, 193-284.

Gabbott, P. A., & Larman, V. N. (1987). The chemical basis of gregariousness in cirripedes: a review (1953–1984). *Barnacle Biology*, 377–388.

Gallardo, V. A. (1987). The sublittoral macrofaunal benthos of the Antarctic shelf. *Environment International*, *13*(1), 71–81.

Gallardo, V. A., Castillo, J. G., Retamal, M. A., Yanez, A., Moyano, H. I., & Hermosilla, J. G. (1977). Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic bays. *Adaptations within Antarctic Ecosystems. Gulf, Houston*, 361–387.

Gerdes, D., Hilbig, B., & Montiel, A. (2003). Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. *Polar Biology*, *26*, 295–301.

Gerdes, D., Isla, E., Knust, R., Mintenbeck, K., & Rossi, S. (2008). Response of Antarctic benthic communities to disturbance: first results from the artificial Benthic

Disturbance Experiment on the eastern Weddell Sea Shelf, Antarctica. *Polar Biology*, *31*, 1469–1480.

Giere, O., & Pfannkuche, O. (1982). Biology and ecology of marine Oligochaeta, a review. *Oceanography and Marine Biology*, *20*, 173–309.

Gili, J.-M., & Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology & Evolution*, *13*, 316–321.

Goosse, H., Arzel, O., Bitz, C. M., de Montety, A., & Vancoppenolle, M. (2009). Increased variability of the Arctic summer ice extent in a warmer climate. *Geophysical Research Letters*, *36*(23). L23702.

Graeve, M., Dauby, P., & Scailteur, Y. (2001). Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. *Polar Biology*, *24*, 853–862.

Grassle, J. P., & Grassle, J. F. (1976). Sibling species in the marine pollution indicator Capitella (Polychaeta). *Science*, *192*, 567–569.

Gravier, C. J. (1923). *La ponte et l'incubation chez les annélides polychètes*. Masson. 247 pp.

Grebmeier, J. M., & Barry, J. P. (1991). The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *Journal of Marine Systems*, *2*, 495–518.

Green, G., & Nichols, P. D. (1995). Hydrocarbons and sterols in marine sediments and soils at Davis Station, Antarctica: a survey for human-derived contaminants. *Antarctic Science*, *7*, 137–144.

Gusso, C. C., & Gravina, M. F. (2001). Faunistic and biological traits of some Antarctic Pycnogonida. *Italian Journal of Zoology*, *68*, 335–344.

Gutt, J. (2001). On the direct impact of ice on marine benthic communities, a review. *Polar Biology*, 24, 553-563.

Gutt, J., & Piepenburg, D. (2003). Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series*, *253(1)*, 77–83.

Gutt, J., & Starmans, A. (1998). Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biology*, *20*, 229–247.

Gutt, J., & Starmans, A. (2001). Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biology*, *24*, 615-619.

Gutt, J., Starmans, A., & Dieckmann, G. (1996). Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series*, *137*(1), 311–316.

Hain, S., & Arnaud, P. M. (1992). Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. *Polar Biology*, *12*(2), 303–312.

Hale, R. C., Kim, S. L., Harvey, E., La Guardia, M. J., Mainor, T. M., Bush, E. O., & Jacobs, E. M. (2008). Antarctic research bases: local sources of polybrominated diphenyl ether (PBDE) flame retardants. *Environmental Science & Technology*, *42*, 1452–1457.

Hanes, T. L. (1971). Succession after fire in the chaparral of southern California. *Ecological Monographs*, 27–52.

Hessler, R. R., & Strömberg, J.-O. (1989). Behavior of janiroidean isopods (Asellota), with special reference to deep-sea genera. *Sarsia*, *74*, 145–159.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 1–23.

Hughes, K. A., & Thompson, A. (2004). Distribution of sewage pollution around a maritime Antarctic research station indicated by faecal coliforms, Clostridium perfringens and faecal sterol markers. *Environmental Pollution*, *127*, 315–321.

Jĝrgensen, C. B. (1990). *Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology*. Olsen & Olsen. 140 pp.

JMP®, Version *12.0*. SAS Institute Inc., Cary, NC, 1989-2015.

Kanneworff, E. (1965). Life cycle, food, and growth of the amphipod Ampelisca macrocephala Liljeborg from the Øresund. *Ophelia*, *2*, 305–318.

Karanovic, I. (2012). *Recent freshwater ostracods of the world: crustacea, ostracoda, podocopida*. Springer Science & Business Media. 640 pp.

Keenan, R. J., & Kimmins, J. P. (1993). The ecological effects of clear-cutting. *Environmental Reviews*, *1*, 121–144.

Kennicutt II, M. C., Klein, A., Montagna, P., Sweet, S., Wade, T., Palmer, T., Denoux, G. (2010). Temporal and spatial patterns of anthropogenic disturbance at McMurdo Station, Antarctica. *Environmental Research Letters*, *5*, 34010.

Kersken, D., Göcke, C., Brandt, A., Lejzerowicz, F., Schwabe, E., Seefeldt, M. A., Janussen, D. (2014). The infauna of three widely distributed sponge species (Hexactinellida and Demospongiae) from the deep Ekström Shelf in the Weddell Sea, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography*, *108*, 101–112.

Kimmerer, W. J., Gartside, E., & Orsi, J. J. (1994). Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. *Marine Ecology Progress Series. 113*(1), 81–93.

Koltun, V. M. (1969). *Porifera-Part 1: Antarctic sponges*. I. Tetraxonida and Cornacuspongida. Biological Reports of the Soviet Antarctic Expedition (1955-1958). Issledovania Fauni Mo-rei, 2, 6-116.

Koltun, V. M. (1970). Sponges of the Arctic and Antarctic: a faunistic review. In *Symposia of the Zoological Society of London*, *25*, 285–297.

Lear, C. H., Bailey, T. R., Pearson, P. N., Coxall, H. K., & Rosenthal, Y. (2008). Cooling and ice growth across the Eocene-Oligocene transition. *Geology*, *36*, 251–254.

Lee, H. J., Gerdes, D., Vanhove, S., & Vincx, M. (2002). Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biology, 24*, 926-933.

Lee, H., Vanhove, S., Peck, L. S., & Vincx, M. (2001). Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biology*, *24*, 918–925.

Lenihan, H. S. (1992). Benthic marine pollution around McMurdo Station, Antarctica: a summary of findings. *Marine Pollution Bulletin*, *25*, 318–323.

Lenihan, H. S., Kiest, K. A., Conlan, K. E., Slattery, P. N., Konar, B. H., & Oliver, J. S. (1995). Patterns of survival and behavior in Antarctic benthic invertebrates exposed to contaminated sediments: field and laboratory bioassay experiments. *Journal of Experimental Marine Biology and Ecology*, *192*, 233–255.

Lenihan, H. S., & Oliver, J. S. (1995). Anthropogenic and Natural Disturbances to Marine Benthic Communities in Antarctica. *Ecological Applications*, *5*, 311–326.

Lenihan, H. S., Oliver, J. S., Oakden, J. M., & Stephenson, M. D. (1990). Intense and localized benthic marine pollution around McMurdo Station, Antarctica. *Marine Pollution Bulletin*, *21*, 422–430.

Lowry, J. K. (1975). Soft bottom macrobenthic community of Arthur Harbor, Antarctica. *Antarctic Research Series, 23*, 1-19.

Luxmoore, R. A. (1982). The reproductive biology of some serolid isopods from the Antarctic. *Polar Biology*, *1*, 3–11.

Luxmoore, R. A. (1985). The energy budget of a population of the Antarctic isopod Serolis polita. *Antarctic Nutrient Cycles and Food Webs* (pp. 389–396). Springer.

Lytle, D. A. (2001). Disturbance regimes and life‐history evolution. *The American Naturalist*, *157*, 525–536.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*, 94–100.

Mack, M. C., & D'Antonio, C. M. (1998). Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, *13*, 195–198.

Malaquias, M. A. E., Condinho, S., Cervera, J. L., & Sprung, M. (2004). Diet and feeding biology of Haminoea orbygniana (Mollusca: Gastropoda: Cephalaspidea). *Journal of the Marine Biological Association of the UK*, *84*, 767–772.

Martin, J. W., Vetter, E. W., & Cash-Clark, C. E. (1996). Description, external morphology, and natural history observations of Nebalia hessleri, new species (Phyllocarida: Leptostraca), from southern California, with a key to the extant families and genera of the Leptostraca. *Journal of Crustacean Biology*, *16*, 347–372.

Martin, S., Drucker, R. S., & Kwok, R. (2007). The areas and ice production of the western and central Ross Sea polynyas, 1992–2002, and their relation to the B-15 and C-19 iceberg events of 2000 and 2002. *Journal of Marine Systems*, *68*(1), 201–214.

McClintock, J. B. (1987). Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctica. *Marine Biology*, *94*, 479–487.

McCune, B., Grace, J. B., & Urban, D. L. (2002). *Analysis of ecological communities* (Vol. 28). MjM software design. 300 pp.

McPeek, M. A., & Holt, R. D. (1992). The evolution of dispersal in spatially and temporally varying environments. *American Naturalist*, 1010–1027.

Meadows, P. S., & Campbell, J. I. (1972). Habitat selection and animal distribution in the sea: the evolution of a concept. *Proceedings of the Royal Society of Edinburgh. Section B. Biology*, *73*, 145–157.

Nedwell, D. B., Walker, T. R., Ellis-Evans, J. C., & Clarke, A. (1993). Measurements of seasonal rates and annual budgets of organic carbon fluxes in an Antarctic coastal environment at Signy Island, South Orkney Islands, suggest a broad balance between production and decomposition. *Applied and Environmental Microbiology*, *59*, 3989–3995.

O'hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

Oliver, J. S., & Slattery, P. N. (1985). Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica. *Ophelia*, *24*, 155–175.

Orejas, C., Gili, J., López-González, P. J., & Arntz, W. (2001). Feeding strategies and diet composition of four Antarctic cnidarian species. *Polar Biology*, *24*, 620–627.

Overpeck, J. T., Rind, D., & Goldberg, R. (1990). Climate-induced changes in forest disturbance and vegetation. *Nature, 343,* 51-53.

Paine, R. T., & Levin, S. A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs*, *51*, 145–178.

Palma, A. T., Poulin, E., Silva, M. G., San Martín, R. B., Muñoz, C. A., & Díaz, A. D. (2007). Antarctic shallow subtidal echinoderms: is the ecological success of broadcasters related to ice disturbance? *Polar Biology*, *30*, 343–350.

Pawlik, J. R. (1992). Induction of marine invertebrate larval settlement: evidence for chemical cues. *Ecological Roles of Marine Natural Products.* Cornell University Press, 189–236.

Pearse, J. S., Bosch, I., McClintock, J. B., Marinovic, B., & Britton, R. (1986). Contrasting tempos of reproduction by shallow-water animals in McMurdo Sound, Antarctica. *Antarctic J*, *31*, 182–184.

Pearse, J. S., & Lockhart, S. J. (2004). Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*, 1533–1549.

Pearse, J. S., McClintock, J. B., & Bosch, I. (1991). Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *American Zoologist*, *31*, 65–80.

Pickett, S. T. A., & White, P. S. (2013). *The ecology of natural disturbance and patch dynamics*. Elsevier. 472 pp.

Ponder, W. F. (1985). A revision of the genus Botelloides (Mollusca: Gastropoda: Trochacea). *Stratigraphy, Palaeontology, Malacology: Papers in Honour of Dr. Nell Ludbrook*, *5*, 301.

Poulin, E., Palma, A. T., & Féral, J.-P. (2002). Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology & Evolution*, *17*, 218–222.

Pritchard, H. D., Ligtenberg, S. R. M., Fricker, H. A., Vaughan, D. G., Van den Broeke, M. R., & Padman, L. (2012). Antarctic ice-sheet loss driven by basal melting of ice shelves. *Nature*, *484*, 502–505.

Pugh, P. J. A., & King, P. E. (1985). Feeding in intertidal Acari. *Journal of Experimental Marine Biology and Ecology*, *94*, 269–280.

Purkey, S. G., & Johnson, G. C. (2010). Warming of global abyssal and deep Southern Ocean waters between the 1990s and 2000s: contributions to global heat and sea level rise budgets. *Journal of Climate*, *23*, 6336–6351.

Quetin, L. B., & Ross, R. M. (2003). Episodic recruitment in Antarctic krill Euphausia superba in the Palmer LTER study region. *Marine Ecology Progress Series*, *259*, 185–200.

Raimondi, P. T. (1988). Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology*, 400–407.

Raimondi, P. T. (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs*, 283–309.

Read, G. B. (1984). Persistence of infaunal polychaete zonation patterns on a sheltered, intertidal sand flat. *New Zealand Journal of Marine and Freshwater Research*, *18*, 399–416.

Richards, T. L. (1967). Reproduction and development of the polychaete Stauronereis rudolphi, including a summary of development in the superfamily Eunicea. *Marine Biology*, *1*, 124–133.

Richardson, M. D., & Hedgpeth, J. W. (1977). Antarctic soft-bottom, macrobenthic community adaptations to a cold, stable, highly productive, glacially affected environment. *Adaptations within Antarctic ecosystems: proceedings of the third SCAR symposium on Antarctic biology*, 181–196.

Risebrough, R. W., De Lappe, B. W., & Younghans-Haug, C. (1990). PCB and PCT contamination in Winter Quarters Bay, Antarctica. *Marine Pollution Bulletin*, *21*, 523–529.

Robertson, R., Visbeck, M., Gordon, A. L., & Fahrbach, E. (2002). Long-term temperature trends in the deep waters of the Weddell Sea. *Deep Sea Research Part II: Topical Studies in Oceanography, 49,* 4791-4806.

Roxburgh, S. H., Shea, K., & Wilson, J. B. (2004). The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*, *85*, 359–371.

Sahade, R., Tatián, M., & Esnal, G. B. (2004). Reproductive ecology of the ascidian Cnemidocarpa verrucosa at Potter Cove, South Shetland Islands, Antarctica. *Marine Ecology Progress Series*, *272*, 131–140.

Santos, I. R., Silva-Filho, E. V, Schaefer, C. E. G. R., Albuquerque-Filho, M. R., & Campos, L. S. (2005). Heavy metal contamination in coastal sediments and soils near the Brazilian Antarctic Station, King George Island. *Marine Pollution Bulletin*, *50*, 185–194.

Sarà, M., Balduzzi, A., Barbieri, M., Bavestrello, G., & Burlando, B. (1992). Biogeographic traits and checklist of Antarctic demosponges. *Polar Biology*, *12*, 559–585.

Scheltema, R. S. (1974). Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugosl*, *10*, 263–296.

Schick, M. J. (1991). *Functional biology of sea anemones*. Chapman & Hall. 118 pp.

Schüller, M., Ebbe, B., & Wägele, J.-W. (2009). Community structure and diversity of polychaetes (Annelida) in the deep Weddell Sea (Southern Ocean) and adjacent basins. *Marine Biodiversity*, *39*(2), 95–108.

Seibel, B. A., & Dierssen, H. M. (2003). Cascading trophic impacts of reduced biomass in the Ross Sea, Antarctica: Just the tip of the iceberg? *The Biological Bulletin*, *205*, 93–97.

Slattery, P. N., & Oliver, J. S. (1986). Scavenging and other feeding habits of lysianassid amphipods (Orchomene spp.) from McMurdo Sound, Antarctica. *Polar Biology*, *6*, 171–177.

Smale, D. A. (2008). Continuous benthic community change along a depth gradient in Antarctic shallows: evidence of patchiness but not zonation. *Polar Biology*, *31*, 189–198.

Smale, D. A., Barnes, D. K. A., & Fraser, K. P. P. (2007). The influence of depth, site exposure and season on the intensity of iceberg scouring in nearshore Antarctic waters. *Polar Biology*, *30*, 769–779.

Smale, D. A., Barnes, D. K. A., Fraser, K. P. P., & Peck, L. S. (2008). Benthic community response to iceberg scouring at an intensely disturbed shallow water site at Adelaide Island, Antarctica. *Marine Ecology Progress Series*, *355*, 85–94.

Solomon, S. (2007). *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge University Press. 996 pp.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, *60*, 1225–1239.

Sousa, W. P. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 353–391.

Sousa, W. P. (2001). Natural disturbance and the dynamics of marine benthic communities. *Marine Community Ecology*, *4*, 85–130.

Srivastava, M. S., & Hui, T. K. (1987). On assessing multivariate normality based on Shapiro-Wilk W statistic. *Statistics & Probability Letters*, *5*(1), 15–18.

Stanwell-Smith, D., Peck, L. S., Clarke, A., Murray, A. W. A., & Todd, C. D. (1999). The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*, 471–484.

Stark, J. S., Kim, S. L., & Oliver, J. S. (2014). Anthropogenic Disturbance and Biodiversity of Marine Benthic Communities in Antarctica: A Regional Comparison. *PloS One*, *9*(6), e98802.

Swanson, F. J., & Dyrness, C. T. (1975). Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. *Geology*, *3*, 393–396.

Tatian, M., Sahade, R., & Esnal, G. B. (2004). Diet components in the food of Antarctic ascidians living at low levels of primary production. *Antarctic Science*, *16*, 123–128.

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

Teixidó, N., Garrabou, J., Gutt, J., & Arntz, W. (2004). Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms. *Marine Ecology Progress Series*, *278*, 1-16.

Thayer, C. W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science*, *203*, 458–461.

Thompson, D. W. J., & Solomon, S. (2002). Interpretation of recent Southern Hemisphere climate change. *Science, 296*, 895–899.

Thomson, M. (2014). Ovoviviparous reproduction in Australian specimens of the intertidal isopod Cirolana harfordi. *Invertebrate Reproduction & Development*, *58*, 218-225.

Thorson, G. (1946). Reproduction and larval development of Danish bottom invertebrates. *Medd. Komm. Danm. Fisk Og Havunders*. 523 pp.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, *25*, 1–45.

Thrush, S. F., & Cummings, V. J. (2011). Massive icebergs, alteration in primary food resources and change in benthic communities at Cape Evans, Antarctica. *Marine Ecology*, *32*, 289–299.

Thrush, S. F., Hewitt, J. E., Dayton, P. K., Coco, G., Lohrer, A. M., Norkko, A., Chiantore, M. (2009). Forecasting the limits of resilience: integrating empirical research with theory. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3209-3217.

Uhl, C., & Kauffman, J. B. (1990). Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology*, *71*, 437–449.

Uhl, C., Nepstad, D., Buschbacher, R., Clark, K., Kauffman, B., Subler, S., & Anderson, A. B. (1990). Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines for designing sustainable land-use systems in Amazonia. *Alternatives to Deforestation: Steps towards Sustainable Use of the Amazon Rain Forest*, 24–42.

Vannier, J., Abe, K., & Ikuta, K. (1998). Feeding in myodocopid ostracods: functional morphology and laboratory observations from videos. *Marine Biology*, *132*, 391–408.

Villnäs, A., Norkko, J., Hietanen, S., Josefson, A. B., Lukkari, K., & Norkko, A. (2013). The role of recurrent disturbances for ecosystem multifunctionality. *Ecology*, *94*, 2275–2287.

Waples, R., Beechie, T., & Pess, G. R. (2009). Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific Salmon populations? *Ecology and Society, 14*, 3.

Ward, P., & Robins, D. B. (1987). The reproductive biology of *Euchaeta antarctica* Giesbrecht (Copepoda: Calanoida) at South Georgia. *Journal of Experimental Marine Biology and Ecology*, *108*, 127–145.

White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *The Botanical Review*, *45*, 229–299.

White, P. S., & Pickett, S. T. A. (1985). *Natural disturbance and patch dynamics: an introduction*. Academic Press, Inc. 457 pp.

Williams, R. N., Rees, W. G., & Young, N. W. (1999). A technique for the identification and analysis of icebergs in synthetic aperture radar images of Antarctica. *International Journal of Remote Sensing*, *20*, 3183–3199.

Wilson, W. H. (1991). Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science*, *48*, 500–516.

Winston, J. E. (1983). Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. *Bulletin of Marine Science*, *33*, 688–702.

Wong, Y. M., & Moore, P. G. (1995). Biology of feeding in the scavenging isopod Natatolana borealis (Isopoda: Cirolanidae). *Ophelia*, *43*, 181–196.

Woodin, S. A. (1986). Settlement of infauna: larval choice? *Bulletin of Marine Science*, *39*, 401–407.

Woodin, S. A., & Jackson, J. B. C. (1979). Interphyletic competition among marine benthos. *American Zoologist*, *19*, 1029–1043.

Word, J. Q. (1979). Extension of the infaunal trophic index to a depth of 800 meters. *Southern California Coastal Water Research Project Biennial Report*, *1980*, 95–101.

Zamorano, J. H. (1983). Zonación y biomasa de la macrofauna bentónica en Bahía South, Archipiélago de Palmer, Antártica. *INACH Ser Cient*, *30*, 27–38.

Appendix A. List of sites and sample replicates for infaunal samples in McMurdo Sound. n = total number of samples taken during each year.

Site	Year													Total
	1988	1990	1991	1992	1993	1996	1997	1998	2002	2003	2004	2007	2012	n
Cape Armitage	6	6			6			6	6	6	6	6	6	54
Cape Bernacchi									5	6	6			17
Cinder Cones	6						18	6	12	6	6	6	30	90
Cape Evans									6					6
Explorers Cove									6	6	6			18
Jetty									6	6	6			18
Jetty South	6	6		6	6	6	6	6			6			48
Outfall	6	6	6	6	6			6	6	6	6	6	6	66
Outfall South A		6	6	6	6			6	6	6	6			48
Outfall South B	6	5		6	6			6	6	6	6			47
Road										6	6			12
Transition									6	6	6			18
Turtle Rock									6	6	6			18
Winter Quarters Inner	6							6	6	6	6			30
Winter Quarters Middle	12	6	6	6	6			6	6	6	6			60
Winter Quarters Outer	6	6		6	6			6	5	6	6			47

Appendix B. List of latitude/longitude and disturbance regime for sites in McMurdo Sound.

Site	Latitude	Longitude	Disturbance Regime	Region
Cape Armitage	-77.85516	166.66783	Undisturbed	East
Cape Bernacchi	-77.47555	163.85221	Undisturbed	West
Cinder Cones	-77.80011	166.67200	Open Ocean Exposed	East
Cape Evans	-77.64018	166.41005	Open Ocean Exposed	East
Explorers Cove	-77.63601	163.41504	Undisturbed	West
Jetty	-77.85106	166.66444	Undisturbed	East
Jetty South	-77.85133	166.66642	Undisturbed	East
Outfall	-77.84814	166.65406	Anthropogenic High	East
Outfall South A	-77.84872	166.65586	Anthropogenic Intermediate	East
Outfall South B	-77.84889	166.65667	Anthropogenic Intermediate	East
Road	-77.85014	166.66181	Anthropogenic Intermediate	East
Transition	-77.84989	166.66056	Anthropogenic High	East
Turtle Rock	-77.73333	166.76667	Open Ocean Exposed	East
Winter Quarters Inner	-77.84536	166.65581	Anthropogenic High	East
Winter Quarters Middle	-77.84630	166.65258	Anthropogenic High	East
Winter Quarters Outer	-77.84722	166.64844	Anthropogenic High	East

Appendix C. List of species from McMurdo infaunal samples. Lowest taxonomic level of individuals observed in all samples.

Phylum	Class	Family	Species/Morphospecies
Annelida	Polychaeta	Nephtyidae	*Aglaophamus* sp.
Annelida	Polychaeta	Terebellidae	*Amaeana* sp.
Annelida	Polychaeta	Ampharetidae	Ampharetidae
Annelida	Polychaeta	Sabellidae	*Amphiglena* sp.
Annelida	Polychaeta	Sabellidae	*Amphiglena* sp. A
Annelida	Polychaeta	Sabellidae	*Amphiglena* sp. B
Annelida	Polychaeta	Sabellidae	*Amphiglena* sp. C
Annelida	Polychaeta	Cirratulidae	*Aphelochaeta* sp.
Annelida	Polychaeta	Maldanidae	*Axiothella* sp.
Annelida	Polychaeta	Polynoidae	*Barrrukia cristata*
Annelida	Polychaeta	Capitellidae	*Capitella capitata*
Annelida	Polychaeta	Capitellidae	*Capitella* sp. A
Annelida	Polychaeta	Chaetopteridae	Chaetopteridae
Annelida	Polychaeta	Sabellidae	*Chone* sp.
Annelida	Polychaeta		Cossuridae
Annelida	Polychaeta	Syllidae	*Exogone* sp.
Annelida	Polychaeta	Flabelligeridae	Flabelligeridae
Annelida	Polychaeta	Oweniidae	*Galathowenia scotiae*
Annelida	Polychaeta	Glyceridae	Glyceridae
Annelida	Polychaeta	Hesionidae	*Gyptis* sp.
Annelida	Polychaeta	Polynoidae	*Harmothoe* sp.
Annelida	Polychaeata	Hesionidae	*Kefersteinia fauveli*
Annelida	Polychaeta	Spionidae	*Laonice* sp.
Annelida	Polychaeta	Orbiniidae	*Leitoscoloplos kerguelensis*
Annelida	Polychaeta	Lumbrineridae	*Lumbrinereis* sp.
Annelida	Polychaeta	Oweniidae	*Myriochele heeri*
Annelida	Polychaeta	Nephtyidae	*Nephtys* sp.
Annelida	Polychaeta	Nereididae	Nereididae
Annelida	Clitellata		Oligochaeta
Annelida	Polychaeta	Opheliidae	*Ophelina breviata*
Annelida	Polychaeta	Dorvilleidae	*Ophryotrocha notialis*
Annelida	Polychaeta	Dorvilleidae	*Ophryotrocha puerilis*
Annelida	Polychaeta	Orbiniidae	Orbiniidae
Annelida	Polychaeta	Paraonidae	Paraonidae
Annelida	Polychaeata	Paraonidae	*Paraonidae* sp. A
Annelida	Polychaeata	Paraonidae	*Paraonidae* sp. B
Annelida	Polychaeata	Paraonidae	*Paraonidae* sp. C
Annelida	Polychaeta	Phyllodocidae	*Phyllodoce* sp.
Annelida	Polychaeta	Polygordiidae	*Polygordius* sp.
Annelida	Polychaeta	Polynoidae	*Polynoidae* sp.
Annelida	Polychaeta	Protodriloididae	*Protodriloides symbioticus*
Annelida	Polychaeta	Sabellidae	*Sabellidae* sp.
Annelida	Polychaeta	Spionidae	*Scolelepis* sp.
Annelida	Polychaeta	Serpulidae	Serpulidae
Annelida	Polychaeta	Sphaerodoridae	*Sphaerodoridae* sp.
Annelida	Polychaeta	Spionidae	*Spiophanes tcherniai*
Annelida	Polychaeta	Syllidae	Syllidae
Annelida	Polychaeta	Terebellidae	Terebellidae
Annelida	Polychaeta	Cirratulidae	*Tharyx* sp.
Annelida	Polychaeta	Terebellidae	*Thelepus* sp.
Annelida	Polychaeta	Scalibregmatidae	*Travisia kerguelensis*
Arthropoda	Malacostraca	Ampeliscidae	*Ampelisca* sp.
Arthropoda	Malacostraca	Paramunnidae	*Austronanus glacialis*
Arthropoda	Malacostraca	Paramunnidae	*Austrosignum glaciale*

Arthropoda	Malacostraca	Cirolanidae	*Cirolana* sp.
Arthropoda	Malacostraca		Cumacea sp. A
Arthropoda	Malacostraca	Leuconidae	*Eudorella splendida*
Arthropoda	Malacostraca	Gnathiidae	*Gnathia Antarctica*
Arthropoda	Arachnida	Halacaridae	Halacaridae
Arthropoda	Malacostraca	Corophiidae	*Haplocheira barbimana*
Arthropoda	Malacostraca	Phoxocephalidae	*Heterophoxus videns*
Arthropoda	Malacostraca	Lysianassidae	*Hippomedon kergueleni*
Arthropoda	Malacostraca	Hyperiidae	*Hyperiella* sp.
Arthropoda	Malacostraca		Isopoda sp. B
Arthropoda	Malacostraca		Isopoda sp. D
Arthropoda	Malacostraca		Isopoda sp. E
Arthropoda	Malacostraca		Isopoda sp. F
Arthropoda	Malacostraca	Jaeropsididae	*Jaeropsis* sp.
Arthropoda	Malacostraca	Leuconidae	*Leucon* sp.
Arthropoda	Malacostraca	Liljiborgiidae	*Liljiborgia* sp.
Arthropoda	Malacostraca	Lysianassidae	Lysianassidae
Arthropoda	Malacostraca	Oedicerotidae	*Monoculodes scabriculosus*
Arthropoda	Malacostraca	Munnidae	*Munna* sp.
Arthropoda	Malacostraca	Nebaliidae	*Nebalia* sp.
Arthropoda	Malacostraca	Janiridae	*Neojaera furcate*
Arthropoda	Malacostraca	Munnopsidae	*Notopais* sp.
Arthropoda	Malacostraca	Nototanaidae	*Nototanais dimorphus*
Arthropoda	Malacostraca	Paramunnidae	*Notoxenus* sp.
Arthropoda	Malacostraca	Calliopiidae	*Oradarea rossi*
Arthropoda	Malacostraca	Lysianassidae	*Orchomenella pinguides*
Arthropoda	Malacostraca	Paramunnidae	*Pagnonana rostrata*
Arthropoda	Malacostraca	Pontogeneiidae	*Paramoera walker*
Arthropoda	Malacostraca	Paramunnidae	*Paramunna* sp.
Arthropoda	Malacostraca	Paramunnidae	*Paramunna* sp. A
Arthropoda	Malacostraca	Paramunnidae	*Paramunna* sp. B
Arthropoda	Malacostraca	Paramunnidae	*Paramunna* sp. C
Arthropoda	Malacostraca	Paramunnidae	*Paramunna* sp. D
Arthropoda	Malacostraca	Philomedidae	*Philomedes sp.*
Arthropoda	Ostracoda		Podocopida
Arthropoda	Ostracoda		Podocopida sp. A
Arthropoda	Ostracoda		Podocopida sp. B
Arthropoda	Pycnogonida		Pycnogonida
Arthropoda	Malacostraca	Eusiridae	*Rhachotropis* sp.
Arthropoda	Malacostraca	Santiidae	*Santia charcoti*
Arthropoda	Malacostraca	Pontogeneiidae	*Schraderia* sp.
Arthropoda	Malacostraca	Sebidae	*Seba* sp.
Arthropoda	Malacostraca	Serolidae	*Serolis* sp.
Arthropoda	Malacostraca	Stenothoidae	Stenothoidae
Arthropoda	Malacostraca		Tanaidacea sp. A
Arthropoda	Malacostraca	Stenothoidae	*Thaumatelson herdmani*
Arthropoda	Malacostraca	Stenothoidae	*Torometopa antarctica*
Arthropoda	Malacostraca		Unknown Amphipoda
Arthropoda	Malacostraca		Unknown Isopoda
Cephalorhyncha	Priapula	Priapulidae	Priapulidae
Cercozoa	Gromiidea	Gromiidae	*Gromia oviformis*
Chordata	Ascidiacea		Tunicata
Cnidaria	Anthozoa		Actinaria
Cnidaria	Hydrozoa		Anthomedusae
Cnidaria	Anthozoa	Clavulariidae	*Clavularia frankliniana*
Cnidaria	Anthozoa	Coelenterateidae	Coelenteratea
Cnidaria	Anthozoa	Edwardsiidae	*Edwardsia meridionalis*
Cnidaria	Hydrozoa		Hydrozoa

Cnidaria	Anthozoa		Pennatulacea
Echinodermata	Echinoidea	Schizasteridae	*Abatus shackletoni*
Echinodermata	Asteroidea	Asteriidae	*Diplasterias brucei*
Echinodermata	Holothuroidea		Holothuroidea
Echinodermata	Asteroidea	Odontasteridae	*Odontaster validus*
Echinodermata	Ophiuroidea		Ophiuroidea
Echinodermata	Echinoidea	Echinidae	*Sterechinus neumayeri*
Echiura	Echiuroidea		Echiuroidea
Ectoprocta	Gymnolaemata		Bryozoa
Mollusca	Bivalvia	Pectinidae	*Adamussium colbecki*
Mollusca	Bivalvia		Bivalvia sp. A
Mollusca	Bivalvia		Bivalvia sp. B (Round)
Mollusca	Bivalvia		Bivalvia sp. C
Mollusca	Bivalvia		Bivalvia sp. D (Rusty)
Mollusca	Bivalvia		Bivalvia sp. E (Flat)
Mollusca	Bivalvia		Bivalvia sp. F (Pointed)
Mollusca	Bivalvia	Cyamiidae	*Cyamiocardium denticulatum*
Mollusca	Bivalvia	Yoldiidae	*Yoldia eightsi*
Mollusca	Gastropoda		Gastropoda sp. B
Mollusca	Gastropoda	Margaritidae	*Margarites* sp.
Mollusca	Gastropoda	Eulimidae	*Melanella* sp.
Mollusca	Gastropoda	Naticidae	Naticidae
Mollusca	Gastropoda	Cancellariidae	*Nothoadmete antarctica*
Mollusca	Gastropoda	Rissoidae	*Onoba/Eatonella* sp.
Mollusca	Gastropoda		Opisthobranchia
Mollusca	Gastropoda	Philinidae	*Philine Antarctica*
Mollusca	Gastropoda		Prosobranchia
Mollusca	Gastropoda		Unknown Gastropoda
Nemertea	Anopla	Lineidae	Nemertea
Platyhelminthes			Platyhelminthes
Sipuncula	Sipunculidea	Sipunculidae	Sipunculidae

Appendix D. List of ecological categories (Table 2) applied to each organism identified from McMurdo infaunal samples.

Species / Morphospecies	Reproduction Category	Mobility Category	Feeding Category	Citation
Abatus shackletoni	1	2	2	Pearse & McClintock, 1991, McClintock, 1994
Actinaria	0	1	0	Covadonga *et al.*, 2001
Adamussium colbecki	2	1	1	Berkman *et al.*, 1991
Aglaophamus sp.	1	2	2	Fauchald & Jumars, 1979
Amaeana sp.	0	1	2	Schüller *et al.*., 2009; Fauchald & Jumars, 1979
Ampelisca sp.	1	1	2	Kanneworff, 1965
Ampharetidae	0	1	1	Schüller *et al*.., 2009; Fauchald & Jumars, 1979
Amphiglena sp.	2	1	1	Schüller *et al*.., 2009; Fauchald & Jumars, 1979
Amphiglena sp. A	2	1	1	Schüller *et al*.., 2009; Fauchald & Jumars, 1979
Amphiglena sp. B	2	1	1	Schüller *et al*.., 2009; Fauchald & Jumars, 1979
Amphiglena sp. C	2	1	1	Schüller *et al*., 2009; Fauchald & Jumars, 1979
Anthomedusae	0	1	0	Covadonga *et al.*, 2001
Aphelochaeta sp.	0	1	2	Wilson 1991
Austronanus glacialis	1	2	1	Hessler & Strömberg 1989
Austrosignum glaciale	1	2	1	Pearse & McClintock, 1991
Axiothella sp.	1	1	2	Read, 1984
Barrrukia cristata	2	2	2	Fauchald & Jumars, 1979
Bivalvia sp. A	0	1	1	
Bivalvia sp. B (Round)	0	1	1	
Bivalvia sp. C	0	1	1	
Bivalvia sp. D (Rusty)	0	1	1	
Bivalvia sp. E (Flat)	0	1	1	
Bivalvia sp. F (Pointed)	0	1	1	
Bryozoa	2	1	1	Winston, 1983
Capitella capitata	1	1	2	Grassle & Grassle, 1976; Fauchald & Jumars, 1979
Capitella sp. A	1	1	2	Grassle & Grassle, 1976; Fauchald & Jumars, 1979
Chaetopteridae	2	1	1	Thorson, 1946
Chone sp.	2	1	1	Schüller *et al*., 2009; Fauchald & Jumars, 1979
Cirolana sp.	1	2	2	Thomson, 2014; Wong & Moore, 1995
Clavularia frankliniana	0	1	1	Covadonga *et al.*, 2001
Coelenterata	0	1	0	Covadonga *et al.*, 2001
Cossuridae	0	1	2	Fauchald & Jumars, 1979
Cumacea sp. A	1	2	2	Blazewicz-Paszkowycz, 2002

Cyamiocardium denticulatum	1	1	1	Hain & Arnaud, 1992
Diplasterias brucei	1	2	2	Pearse & McClintock, 1991, McClintock, 1994
Echiuroidea	2	2	0	Pearse & McClintock, 1991
Edwardsia meridionalis	0	1	2	Pearse *et al.,* 1986
Eudorella splendida	1	2	2	Blazewicz-Paszkowycz, 2002
Exogone sp.	1	2	1	Schüller *et al.,* 2009
Flabelligeridae	1	1	2	Gravier, 1923
Galathowenia scotiae	0	1	1	Fauchald & Jumars, 1979
Gastropoda sp. B	0	2	0	
Glyceridae	2	2	2	Schüller *et al.,* 2009
Gnathia antarctica	1	2	2	Broyer *et al.*, 2004
Gromia oviformis	1	2	2	Silva & Gooday, 2009
Gyptis sp.	2	2	2	Schüller *et al.,* 2009
Halacaridae	1	2	2	Pugh & King, 1985
Haplocheira barbimana	1	2	1	Lowry, 1975
Harmothoe sp.	2	2	2	Fauchald & Jumars, 1979
Heterophoxus videns	1	2	2	Pearse & McClintock, 1991
Hippomedon kergueleni	1	2	2	Broyer *et al.*, 2004
Holothuroidea	1	2	0	McEuen & Chia, 1991
Hydrozoa	0	1	0	Covadonga *et al.*, 2001
Hyperiella sp.	1	2	2	Hopkins, 1987
Isopoda sp. B	1	2	0	
Isopoda sp. D	1	2	0	
Isopoda sp. E	1	2	0	
Isopoda sp. F	1	2	0	
Jaeropsis sp.	1	2	0	
Kefersteinia fauveli	2	2	2	Schüller *et al.,* 2009
Laonice sp.	2	1	2	Fauchald & Jumars, 1979
Laternula elliptica	2	1	1	Pearse & McClintock, 1991
Leitoscoloplos kerguelensis	2	1	2	Fauchald & Jumars, 1979
Leucon sp.	1	2	2	Blazewicz-Paszkowycz, 2002
Liljiborgia sp.	1	2	2	Broyer *et al.*, 2003
Limatula hodgsoni	2	1	1	Pearse & McClintock, 1991
Lumbrinereis sp.	1	2	2	Richards, 1967
Lysianassidae	1	2	2	Broyer *et al.*, 2003
Margarites sp.	1	2	0	Pearse & McClintock, 1991
Melanella sp.	0	2	0	
Monoculodes scabriculosus	1	1	2	Pearse & McClintock, 1991; Coleman, 1989
Munna sp.	1	2	1	Choudhury 2009
Myriochele heeri	0	1	2	Word, 1979; Fauchald & Jumars, 1979
Naticidae	0	2	2	Berry, 1982

Nebalia sp.	1	2	2	Martin *et al*., 1996
Nemertea	2	2	2	Pearse & McClintock, 1991
Neojaera furcata	1	2	0	
Nephtys sp.	2	2	2	Fauchald & Jumars, 1979
Nereididae	2	2	2	Schüller *et al.,* 2009
Nothoadmete antarctica	0	2	0	
Notopais sp.	1	2	2	Jamieson *et al*., 2012
Nototanais dimorphus	1	2	2	Pearse & McClintock, 1991; Oliver & Slattery, 1985
Notoxenus sp.	1	2	1	Choudhury 2009
Odontaster validus	2	2	2	Pearse & McClintock, 1991, McClintock, 1994
Oligochaeta	0	1	2	Giere & Pfannkuche, 1982
Onoba/Eatonella sp.	0	2	2	Ponder, 1985
Ophelina breviata	2	1	2	Schüller *et al*., 2009; Fauchald & Jumars, 1979
Ophiuroidea	0	2	0	Pearse & McClintock, 1991
Ophryotrocha notialis	1	1	2	Akesson, 1973
Ophryotrocha puerilis	1	1	2	Akesson, 1973
Opisthobranchia	0	2	0	
Oradarea rossi	1	2	1	Graeve *et al*., 2001
Orbiniidae	0	1	2	Fauchald & Jumars, 1979
Orchomenella pinguides	1	2	2	Pearse & McClintock, 1991
Pagnonana rostrata	1	2	1	Choudhury 2009
Paramoera walkeri	1	2	2	Bargagli, 1998
Paramunna sp.	1	2	1	Choudhury 2009
Paramunna sp. A	1	2	1	Choudhury 2009
Paramunna sp. B	1	2	1	Choudhury 2009
Paramunna sp. C	1	2	1	Choudhury 2009
Paramunna sp. D	1	2	1	Choudhury 2009
Paraonidae	1	1	2	Fauchald & Jumars, 1979
Paraonidae sp. A	1	1	2	Fauchald & Jumars, 1979
Paraonidae sp. B	1	1	2	Fauchald & Jumars, 1979
Paraonidae sp. C	1	1	2	Fauchald & Jumars, 1979
Pennatulacea	2	1	0	Covadonga *et al*., 2001
Philine antarctica	1	2	2	Malaquias *et al*., 2004
Philomedes sp.	1	2	2	Vannier *et al*., 1998
Phyllodoce sp.	0	2	2	Fauchald & Jumars, 1979
Platyhelminthes	2	2	0	Stanwell-Smith *et al.,* 1999
Podocopida	1	2	1	Karanovic, 2012
Podocopida sp. A	1	2	1	Karanovic, 2012
Podocopida sp. B	1	2	1	Karanovic, 2012
Polygordius sp.	2	1	2	Fauchald & Jumars, 1979
Polynoidae sp.	2	2	2	Fauchald & Jumars, 1979

Priapulidae	1	1	2	Bromley, 1974
Prosobranchia	0	2	0	
Protodriloides symbioticus	2	1	2	Fauchald & Jumars, 1979
Pycnogonida	1	2	2	Gusso & Gravina, 2001
Rhachotropis sp.	1	2	2	Broyer *et al.*, 2003
Sabellidae sp.	2	1	1	Schüller *et al.,* 2009
Santia charcoti	1	2	0	
Schraderia sp.	1	1	2	Amsler *et al*., 2009
Scolelepis sp.	2	1	2	Fauchald & Jumars, 1979
Seba sp.	1	1	2	Kersken *et al.*, 2014
Serolis sp.	1	2	2	Luxmoore, 1985
Serpulidae	2	1	1	Fauchald & Jumars, 1979
Sipunculidae	2	1	0	Cutler, 1994
Sphaerodoridae sp.	2	2	2	Schüller *et al.,* 2009
Spiophanes tcherniai	0	1	2	Fauchald & Jumars, 1979; Blake & Arnofsky, 1999
Stenothoidae	1	2	1	Aumack *et al*., 2011
Sterechinus neumayeri	2	2	2	Pearse & McClintock, 1991; Brey *et al*., 1995
Syllidae	1	2	1	Schüller *et al.,* 2009
Tanaidacea sp. A	1	2	2	Pearse & McClintock, 1991; Oliver & Slattery, 1985
Terebellidae	0	1	2	Schüller *et al.*, 2009; Fauchald & Jumars, 1979
Tharyx sp.	0	1	2	Wilson 1991
Thaumatelson herdmani	1	2	1	Aumack *et al*., 2011
Thelepus sp.	0	1	2	Schüller *et al.*, 2009; Fauchald & Jumars, 1979
Torometopa antarctica	1	2	1	Aumack *et al*., 2011
Travisia kerguelensis	2	1	2	Schüller *et al.,* 2009
Tunicata	2	1	1	Sahade *et al., 2004*
Unknown Amphipoda	1	2	0	
Unknown Bivalvia	0	1	1	
Unknown Gastropoda	0	2	0	
Unknown Isopoda	1	2	0	
Yoldia eightsi	2	1	1	Clarke, 1992

Appendix E. Relative contribution of species to the observed differences in the overall community assemblage within and between sample locations. Similarity percentage (SIMPER) analysis listed for five species contributing most to dissimilarity. Analysis was performed on 4th root transformed species lists.

Location	**Species**	**Contribution %**	**Cumulative Contribution %**
Outside	*Nototanais dimorphus*	10.47	10.47
	Spiophanes tcherniai	10.02	20.49
	Philomedes sp.	9.52	30.00
	Austrosignum glaciale	8.00	38.00
	Edwardsia meridionalis	7.12	45.12
Edge	*Nototanais dimorphus*	10.14	10.14
	Spiophanes tcherniai	8.92	19.06
	Philomedes sp.	8.23	27.28
	Edwardsia meridionalis	5.89	33.18
	Axiothella sp.	5.24	38.42
Inside	*Nototanais dimorphus*	17.40	17.40
	Austrosignum glaciale	12.74	30.14
	Heterophoxus videns	9.18	39.32
	Eudorella splendida.	8.52	47.84
	Philomedes sp.	6.26	54.10
			Directionality in Abundance
Outside vs Inside	*Spiophanes tcherniai*	5.49	Outside > Inside
	Edwardsia meridionalis	4.45	Outside > Inside
	Polygordius sp.	4.33	Outside > Inside
	Philomedes sp.	3.88	Outside > Inside
	Nototanais dimorphus	3.08	Inside > Outside
Outside vs Edge	*Polygordius* sp.	5.10	Outside > Edge
	Laternula elliptica	4.20	Edge > Outside
	Spiophanes tcherniai	3.64	Edge > Outside
	Edwardsia meridionalis	3.52	Edge > Outside
	Tanaidacea sp. A	3.22	Edge > Outside
Edge vs Inside	*Spiophanes tcherniai*	6.20	Edge > Inside
	Edwardsia meridionalis	5.02	Edge > Inside
	Philomedes sp.	4.05	Edge > Inside
	Axiothella sp.	3.65	Edge > Inside
	Laternula elliptica	3.21	Edge > Inside

Appendix F. Relative contribution of species to the observed differences in the overall community assemblage separated based upon year. Similarity percentage (SIMPER) analysis listed for five species contributing most to dissimilarity. Analysis was performed on 4th root transformed species lists.

Year	Species	Average Abundance	Contribution %	Cumulative Contribution %
1997	*Nototanais dimorphus*	2.34	10.03	10.03
	Austrosignum glaciale	1.76	8.71	18.74
	Spiophanes tcherniai	2.13	8.06	26.74
	Philomedes sp.	1.82	7.56	34.35
	Eudorella splendida	1.84	7.50	41.85
2002	*Nototanais dimorphus*	3.63	20.41	20.41
	Austrosignum glaciale	2.85	16.89	37.30
	Heterophoxus videns	2.55	15.02	52.32
	Eudorella splendida	2.41	13.15	65.47
	Lysianassidae sp.	1.36	7.91	73.38
2012	*Nototanais dimorphus*	4.24	10.51	10.51
	Philomedes sp.	3.09	7.74	18.25
	Spiophanes tcherniai	3.36	7.27	25.52
	Austrosignum glaciale	2.24	5.58	31.10
	Laternula elliptica	2.25	5.34	36.43

Appendix G. Relative contribution of species to the observed differences in the overall community assemblage within experimental plot sample locations. Similarity percentage (SIMPER) analysis listed for seven species contributing most to dissimilarity. Analysis was performed on 4th root transformed species lists.

Location	**Species**	**Contribution %**	**Directionality in Abundance**
1 m Inside vs 1 m Edge	*Spiophanes tcherniai*	4.45	Edge > Inside
	Nototanais dimorphus	4.27	Edge > Inside
	Kefersteinia fauveli	4.19	Edge > Inside
	Edwardsia meridionalis	3.87	Edge > Inside
	Capitella sp. A	3.62	Edge > Inside
1 m Inside vs 10 cm	*Spiophanes tcherniai*	4.74	10 cm > Inside
	Isopoda B	3.97	10 cm > Inside
	Nototanais dimorphus	3.82	10 cm > Inside
	Capitella sp. A	3.66	10 cm > Inside
	Kefersteinia fauveli	3.63	10 cm > Inside
1 m Edge vs 10 cm	*Spiophanes tcherniai*	4.88	Edge > 10 cm
	Torometopa antarctica	3.92	Edge > 10 cm
	Edwardsia meridionalis	3.88	Edge > 10 cm
	Unknown Amphipoda	3.75	10 cm > Edge
	Axiothella sp.	3.68	Edge > 10 cm

Appendix F. Tests for differences between disturbance types within McMurdo Sound. Table sorted based upon average similarity between disturbance regimes. All samples are from the east region of the McMurdo Sound unless otherwise noted. Based upon one-way PERMANOVA and ANOSIM with 4^{th} root transformed abundances and Bray-Curtis similarities. An asterisk (*) denotes significant differences in both PERMANOVA and ANOSIM tests.

	PERMANOVA Tests				ANOSIM Tests	
Disturbance Level Comparison	**t**	**P (perm)**	**Average Similarity Between Groups**	**Distance Between Group Centroids**	**R**	**P**
Undisturbed West Region vs Anthropogenic High*	6.76	0.001	15.71	54.97	0.74	0.001
Undisturbed West Region vs Open Ocean Exposed*	6.43	0.001	21.76	51.49	0.85	0.001
Undisturbed West Region vs Iceberg Scour*	4.69	0.001	21.99	51.39	0.59	0.001
Undisturbed West Region vs Anthropogenic Intermediate*	7.94	0.001	24.72	52.34	0.93	0.001
Undisturbed West Region vs Undisturbed*	6.66	0.001	25.65	47.54	0.90	0.001
Iceberg Scour vs Anthropogenic High*	5.53	0.001	26.60	48.13	0.48	0.001
Open Ocean Exposed vs Anthropogenic High*	8.45	0.001	28.40	45.06	0.46	0.001
Undisturbed vs Anthropogenic High*	8.33	0.001	34.32	38.48	0.33	0.001
Iceberg Scour vs Anthropogenic Intermediate*	6.60	0.001	38.93	41.81	0.88	0.001
Anthropogenic High vs Anthropogenic Intermediate*	6.82	0.001	41.09	31.79	0.12	0.001
Open Ocean Exposed vs Anthropogenic Intermediate*	8.02	0.001	41.96	37.03	0.66	0.001
Undisturbed vs Iceberg Scour*	4.28	0.001	43.06	30.57	0.54	0.001
Undisturbed vs Open Ocean Exposed*	5.03	0.001	46.17	24.62	0.30	0.001
Open Ocean Exposed Exposed vs Iceberg Scour*	2.58	0.001	46.66	20.40	0.16	0.008
Undisturbed vs Anthropogenic Intermediate*	5.29	0.001	52.49	21.80	0.26	0.001