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Community Structure and Zonation of Antarctic Benthic Invertebrates: Using a Remotely Operated Vehicle under Ice to Define Biological Patterns

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COMMUNITY STRUCTURE AND ZONATION OF ANTARCTIC BENTHIC INVERTEBRATES: USING A REMOTELY OPERATED VEHICLE UNDER ICE TO DEFINE BIOLOGICAL PATTERNS

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by

Dorota Szuta

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COMMUNITY STRUCTURE AND ZONATION OF ANTARCTIC BENTHIC INVERTEBRATES: USING A REMOTELY OPERATED VEHICLE UNDER ICE TO DEFINE BIOLOGICAL PATTERNS

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ABSTRACT

COMMUNITY STRUCTURE AND ZONATION OF ANTARCTIC BENTHIC INVERTEBRATES: USING A REMOTELY OPERATED VEHICLE UNDER ICE TO DEFINE BIOLOGICAL PATTERNS

by Dorota Szuta

The Ross Sea, Antarctica is a deep bay of the Southern Ocean that exhibits seasonal sea ice and is adjacent to a permanent ice shelf overlying seawater. In 2008 and 2009, imagery of the seafloor under the McMurdo Ice Shelf and under the seasonal ice in the Ross Sea was collected via remotely operated vehicle (ROV) at depths to 300 m. Distinct differences in Antarctic benthic communities were observed over multiple environmental gradients. Species abundance typically exhibited a unimodal distribution with depth with mid-depth peaks, reflecting a food limitation at the deep end and potentially ice disturbance on the shallow end. Diversity and depth had a unimodal relationship at two of three sites encompassing a depth gradient. In terms of functional groups, the proportion of suspension feeders decreased with depth at one site, and no pattern was found at other sites. The group of sessile predators, comprised of several species of anemones, increased with depth proportionally, suggesting that they use a range of feeding strategies to adapt to life at depth. Benthic communities under seasonal ice were different than those under permanent ice shelves, with higher overall species diversity, a greater proportion of suspension feeders, and a degree of magnitude higher abundance.

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Introduction

The structure of benthic communities is determined by a number of environmental and biological factors. Environmental factors such as substrate type, light, currents, pressure, and nutrients influence the distribution of benthic fauna (Tait et al., 1998). Biological factors including competition, predation, and interrelationships such as mutualism and parasitism further determine the distribution and composition of benthic communities (Tait et al., 1998). In all systems, there is typically a limiting factor. In the example of the coastal Californian intertidal, environmental stress in the form of desiccation is the limiting factor in the upper zones, whereas interspecific competition for space becomes a limiting factor in the lower zones (Dayton, 1971). In hydrothermal vent communities, high temperatures and low oxygen are some of the primary limiting factors affecting benthic organisms (Van Dover, 2000). On the Antarctic seafloor, where the present study takes place, ice shelves and seasonal sea ice block light from entering the water column, seasonally in the case of sea ice and year-round in the case of ice shelves, preventing *in situ* primary productivity and thus creating a system limited by food availability (Arntz, 1994; Oliver et al., 1976). Additionally, ice creates disturbance in shallow depths via anchor ice and ice scouring. The structure of sub-ice benthic communities in the Antarctic and the potential limiting factors shaping them will thus be explored in the present study.

McMurdo Sound, the Ross Sea, Antarctica

Antarctica is thermally and biologically isolated from the rest of the planet. The Southern Ocean surrounds the continent, and encircling the Southern Ocean is the

Antarctic Circumpolar Current (ACC), driven by strong westerly winds. The ACC links the Pacific, Atlantic, and Indian Ocean basins and keeps warm waters away from Antarctica (Klinck & Nowlin, 2001). Associated with the ACC is the Polar Front, in which the cold northward-flowing waters of the Antarctic sink below the warmer subantarctic waters. Through these processes, the Polar Front and the ACC physically and thermally isolate Antarctic biota and limit the introduction of new fauna into the ecosystem (White, 1984). This isolation contributes to the high endemism that is seen in terrestrial as well as marine Antarctic fauna (Arntz et al., 1994).

The Ross Sea is a deep bay of the Southern Ocean off the coast of Antarctica with a unique physical environment. Encompassing the furthest south open water in the world, the Ross Sea faces extreme contrasts in seasonality, with 24 hours of sunlight in the summer and 24 hours of darkness in the winter. While light changes drastically according to season, most other environmental factors remain relatively constant. Waters in the Ross Sea are characterized by low but fairly constant temperatures that fluctuate only ±0.07ºC around mean temperature of -1.89º C, just above the freezing point of seawater (Picken, 1984). Salinity, pH, and oxygen levels remain relatively constant throughout the year as well (Arntz et al., 1994). Marine organisms in the Ross Sea have adapted to this stable situation over time, and conditions outside of this narrow environmental band could exceed their tolerances (Peck & Conway, 2000; Peck et al., 2014). Ross Sea organisms are thus vulnerable to large-scale processes causing rapid change in oceanic conditions (Convey, 2007).

In areas of open water, the Ross Sea is a productive region with underlying diverse seafloor communities. The continental shelf of the Ross Sea exhibits the highest rates of productivity in the Southern Ocean, averaging 180 g C m^{-2} yr^{-1} (Arrigo et al., 1998). Rich seasonal blooms of phytoplankton sustain populations of krill, Antarctic silverfish, and higher trophic levels (Smith et al., 2007). While the pelagic zone of the Ross Sea exhibits low diversity, with few species of fish and plankton, the species richness of the shelf fauna is quite high, comparable to that of temperate and tropical non-reef areas (Clarke, 2003).

The southern part of the Ross Sea is covered by the Ross and McMurdo Ice Shelves, which are permanent features that have been in place for tens of thousands of years. (Brachfeld et al., 2003). The Ross and McMurdo Ice Shelves are up to 300 meters thick and make up the largest body of floating ice in the world (Depoorter et al., 2013). North of the McMurdo Ice Shelf in McMurdo Sound, surface waters are covered by fast ice, a type of sea ice that is “fastened” to the coast in a continuous sheet, for nine or more months a year (Figure 1). Fast ice, roughly 1 m thick (Worby et al., 2008), disperses and reforms annually in conjunction with seasonal changes in air temperature, water temperature, and wind (Arntz, 1994). Further north is pack ice, a highly mobile type of seasonal ice that consists of broken pieces of various sizes and ages, often with areas of open water in between. The boundary of pack ice and fast ice is a hub of activity, with areas of open water experiencing *in situ* productivity, thus providing higher trophic levels with abundant food.

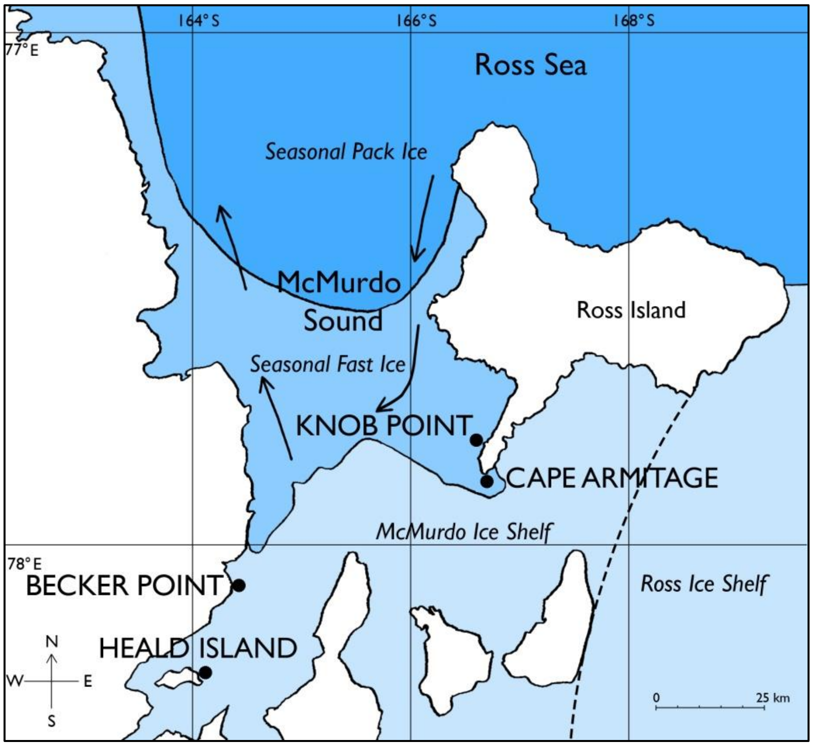


Figure 1. Map of sites Knob Point & Cape Armitage under the seasonal sea ice, and Becker Point & Heald Island under a permanent ice shelf. Arrows depict ocean current flow. White = land or glaciers overlying land; Light blue = ice shelf; Medium blue = seasonal fast ice; Dark blue = seasonal pack ice. See text for further discussion of ice types.

Though the details of current patterns under the ice shelves are not known, general current patterns of McMurdo Sound are fairly well described. A clockwise gyre in the Ross Sea drives south-moving water under the Ross and McMurdo Ice Shelves to an unknown distance. This water is deflected west and ultimately resurfaces in McMurdo Sound, heading north, resulting in the western Sound being bathed by a slow, oligotrophic current from under the McMurdo Ice Shelf year-round (Figure 1). The eastern sound, on the other hand, receives a northerly flow of supercooled water from below the McMurdo Ice Shelf in the winter and spring, but receives south flowing plankton-rich water from the Ross Sea in the summer (Barry & Dayton, 1988).

Anthropogenic impacts in the Ross Sea area have thus far been relatively minimal, both in a direct and indirect sense. While other parts of the Antarctic, such as the West Antarctic Peninsula, have experienced substantial increases in water temperatures and CO_2 levels due to climate change, resulting in sea ice decline at rates comparable to the Arctic (Cazenave & Llovel, 2010; Maksym et al., 2012) and pH levels low enough to impede the larval development and shell formation of some invertebrates (Bednaršek et al., 2012; Fabry et al., 2008; Gazeau et al., 2013), the Ross Sea has not yet experienced these destructive effects. Antarctic sea ice extent is largely driven by large-scale climate patterns such as El Nino-Southern Oscillation and the Southern Annual Mode, which have opposing effects around the continent. Consequently, the most notable effects of climate change in the Ross Sea to date have been increased winds and increased sea ice (Maksym et al., 2012).

Though there have been various direct anthropogenic impacts throughout history, the Ross Sea is considered one of the least anthropogenically-influenced ecosystems on earth (Halpern et al., 2008). Beginning in the 19th century through the 1980s, Weddell seals (*Leptonychotes weddellii*) were hunted for consumption by humans and sled dogs. Since these practices have stopped, seal populations have partially recovered (Ainley, 2010). In the 1920s, blue whales *(Balaenoptera musculus intermedia*) were hunted to extirpation in the area, from which the population has not recovered (Branch et al., 2007). Minke whales *(Balaenoptera bonaerensis*) were hunted in the 1970s and 1980s, and populations have since recovered fully (Clapham & Baker, 2002). Ongoing direct impacts include the commercial fishery for Antarctic Toothfish (*Dissostichus mawsoni*), that began in 1996, and local contamination surrounding research stations (Tin et al., 2009). Though these exploitative actions have certainly influenced the Ross Sea area, they are relatively minor compared to the impacts humans have had in the other oceans of the world. Furthermore, unlike many other marine habitats, the Ross Sea has not been subject to mining or oil drilling. This comparatively undisturbed state offers the opportunity to establish a baseline of benthic communities against which future changes can be evaluated before both direct and indirect anthropogenic impacts further change ecosystems, and the opportunity to study them in such a state is lost.

Food Availability and Gradients in the Ross Sea

Primary production comprises the base of the trophic web with all subsequent trophic levels relying on it. In most marine systems, the major primary producers are algae. In McMurdo Sound where there are almost no benthic macroalgae, the main primary production is from microalgae in the water column (Stark et al., 2014). The greatest factor limiting the primary production of algae is light (Lizotte, 2003), and given the extreme seasonality of light in the Ross Sea, primary production can only occur *in situ* during a short season each year.

In areas of thick ice cover (e.g. under ice shelves) where conditions are aphotic and *in situ* primary production cannot take place, planktonic food sources are laterally advected from areas with open water. Under the Ross and McMurdo Ice Shelves, food is advected from nearby open water in the Ross Sea (Arntz, 1994). Even under annual sea ice, seasonal ice thinning and dispersal only allows for a short period of *in situ* primary productivity during the austral summer (Oliver et al., 1976). North of the Ross and

McMurdo Ice Shelves in McMurdo Sound, much of which is covered by sea ice most of the year, lateral advection from the Ross Sea is the main source of productivity as well (Jaeger et al., 1996; Langone et al., 2000). Prior to the dispersal of ice in late January to March, the spring phytoplankton bloom is swept in from the north under the seasonal sea ice (Gow et al., 1998; Smith et al., 2000). The flagellate *Phaeocystis* tends to be the bloom's dominant phytoplankton in the spring, followed by the diatom *Nitzschia curta* (Palmisano et al., 1986; Smith & Nelson, 1985).

As the seasonal sea ice disperses in the summer and most of the western Ross Sea becomes open water, another source of food in areas under sea ice can come from flora and fauna associated with the ice itself. Attached to and embedded within the seasonal sea ice are numerous species of algae, bacteria, flagellates, crustaceans, and other organisms (Garrison et al., 1986, 2005). As the underside of the sea ice degrades, the communities associated with it fall to the seafloor, thus supplying the benthic community in areas of seasonal ice with an additional large seasonal input of food (Smith et al., 2007).

Making up the largest proportion of Antarctic benthic fauna, suspension feeders are well suited to the Antarctic sea floor as they are able to feed on particles suspended in the water column in otherwise low-food circumstances (Sorokin, 1991; Orejas et al., 2000). The viscosity of seawater allows phytoplankton and particulate matter to be suspended in the water column and slowly sink. Suspension feeding allows animals to capture food that is highly diluted in the water column and too small to be captured individually (Gili & Coma, 1998). Because they are adapted to moving fluid environments, sessile suspension feeders are able to capture food in bulk, which works particularly well in the Antarctic summer, when there is a rich seasonal input of food. As phytodetritus from the summer bloom sinks, it accumulates on the Antarctic sea floor forming a sediment "food bank" (*sensu* Mincks et al., 2005; Smith et al., 2006) Through the winter when food in the water column is scarce, benthic animals feed on the food bank via resuspension processes (Orejas et al., 2000) or by switching feeding modes (Riisgård et al., 2001; Slattery et al., 1997).

Environmental gradients often influence the distribution of fauna (Gutt, 2000). Physical proximity to a photosynthesizing food supply is one such gradient that influences benthic communities in shallow water (Dayton & Oliver, 1997), and may also influence deep water communities. Because the open surface waters of the Ross Sea are the source of primary production, in McMurdo Sound the food gradient occurs laterally (advective) and vertically (depth). In shallow water (<40m) in McMurdo Sound, ice disturbance is another defining gradient. Anchor ice (explained in greater detail later on) forms on substrates and organisms down to at least 33 m depth, and greatly affects zonation patterns in shallow benthic communities (Dayton et al., 1969). Pressure can covary with depth, and affect species distributions via range restrictions or adaptations of deep-sea organisms to high-pressure environments (Carney, 2005; Gaston, 2000). Though temperature is usually a covarying factor in other environments, the water column in the Antarctic is essentially isothermic (Dayton et al., 1982; Starmans et al., 1999).

While food availability is often identified as a potential factor controlling benthic communities, it is in turn influenced by other important factors such as currents, which determine the amount of primary production that is advected to an under-ice location (Gili et al., 2001). Previous studies have shown current patterns on the seafloor to be important in governing benthic communities under ice (Barry & Dayton, 1988; Dayton & Oliver, 1977). In their studies throughout the McMurdo Sound, Dayton & Oliver (1977) found that the eutrophic East Sound had extremely high infaunal densities, while the oligotrophic West Sound had low infaunal density, similar to that of the deep sea (Figure 1). This disparity was thought to be due in part to differences in source waters and currents at the two sites.

Depth Zonation

Many studies have examined the depth distribution of benthic organisms in areas exhibiting seasonal sea ice in the Ross Sea, but due to depth limitations of SCUBA diving, much of our detailed knowledge extends to only roughly 60 m. (Cattaneo-Vietti et al., 2000a; Dayton et al., 1970; Dayton et al., 1974). In eastern McMurdo Sound, where the bulk of the following studies took place, the benthic invertebrate assemblages were found to be diverse and to differ greatly with depth. Additionally, differences in community structure occurred in discrete bands rather than in a continuous gradient.

In the uppermost 15 m, physical factors such as anchor ice, ice scouring, and substrate type have been found to be the driving factors of the benthic community (Dayton et al., 1970; Gutt et al., 1996). Melting under permanent ice shelves creates supercooled water, which forms anchor ice when it sinks to the seafloor and ice forms on the benthos. When anchor ice grows large enough and achieves sufficient buoyancy, it lifts to the surface, taking with it any attached benthic organisms and parts of the substratum (Dayton, 1969). Consequently, these shallow depths are primarily populated by mobile grazers or scavengers such as sea urchins, sea stars, and nemerteans, as opposed to sessile invertebrates (Clarke, 1996). This zonation pattern is seen in several places in Antarctica. At Cape Armitage (Figure 2 site 2), a site off the coast of Ross Island that is only seasonally covered by sea ice, Dayton et al. (1970) describe the uppermost 15 m as characterized by a "general organic barrenness" due to frequent ice scouring and heavy anchor ice formation. In areas far from ice shelves where anchor ice does not form, pack ice, or large pieces of broken up ice at the shore line, scours the seafloor and creates a similarly barren band in shallow water. Studies in other regions of Antarctica such as at Signy Island

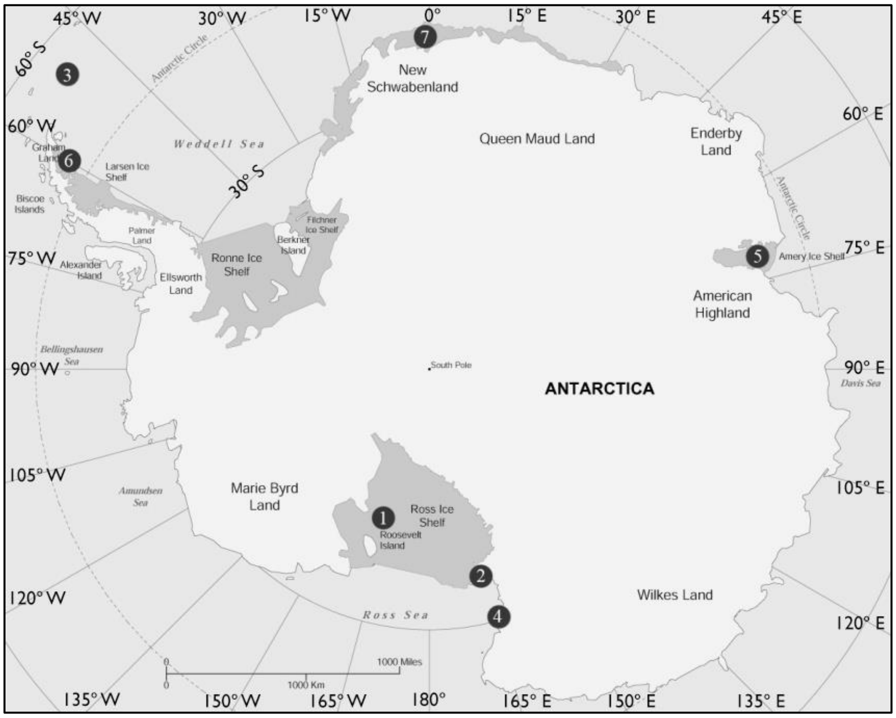


Figure 2. Map showing areas of sub-ice or vertical zonation studies of benthic communities. Site 1—Ross Ice Shelf; Site 2—Cape Armitage, Ross Sea; Site 3—Signy Island; Site 4—Terra Nova Bay; Site 5—Amery Ice Shelf; Site 6—Larsen Ice Shelf; Site 7—Fimbul Ice Shelf.

(Figure 2 site 3) (Barnes, 1995a) and Terra Nova Bay (Figure 2 site 4) (Cattaneo-Vietti et al., 2000a) have found similar zonation patterns with the most shallow zone (upper 15 m) being a relatively uninhabited area due to apparent physical disturbance.

The underlying zone, between 15 and 30 m, is frequently disturbed by anchor ice and occasionally by grounded icebergs. At Cape Armitage, this zone is described as having a cobble and volcanic substratum and is populated by numerous sessile and motile animals, dominated by sea anemones, hydroids, and fast-growing soft corals (Dayton et al., 1970). Studies in other parts of the continent such as at Signy Island (Barnes 1995a; Barnes & Clark, 1995) and Terra Nova Bay (Cattaneo-Vietti et al., 2000a) have also found this zone to have a more diverse community dominated by suspension-feeders.

Due to depth limitations of SCUBA, it is unknown to what depths this zone extends at Cape Armitage, but sponge-dominated communities similar to those found in the work of Dayton et al. (1970; 1974; 1979) have been found in other regions of Antarctica at greater depths (Cattaneo-Vietti et al., 2000a). Cattaneo-Vietti et al. (2000a) found that at a depth of 70-120 m in Terra Nova Bay, the sponge and anthozoan communities were the most complex of the Ross Sea to date, comparable to those found in the 30-60 m zone (Dayton et al., 1970). One study at the edge of the Fimbul Ice Shelf (Figure 2 site 7) found similar suspension-feeder-dominated communities with megafaunal density decreasing from 245 m to 510 m depth, and diversity varying independent of depth (Jones et al., 2007). Though the shallow-water benthic communities in the Ross Sea are known to be high in species richness and abundance (Cattaneo-Vietti et al., 2000a; Dell, 1972; Oliver & Slattery, 1985), the lower sublittoral zone (deeper than 25 m) has been generally understudied and, especially under the McMurdo and Ross Ice Shelves, the benthic community composition is largely unknown.

Benthic Fauna under Antarctic Ice Shelves

Few studies have examined benthic communities under ice shelves due to their inherent inaccessibility. The first study to obtain photographic imagery of the seafloor under an ice shelf found an assemblage of mobile scavengers with no sessile animals or living infauna in the Ross Sea at a depth of nearly 600 m (Figure 2, site 1) (Lipps et al., 1979). Prior to this, Littlepage & Pearse (1962) and Heywood & Light (1975) found evidence of seafloor communities under the Ross Ice Shelf, but both of these studies utilized natural tide cracks, meaning conditions were not truly aphotic and communities could have been responding to local primary productivity.

Once ice shelves collapse, the marine environment becomes more easily accessible for surveying, but conditions change rapidly. The disintegration of ice shelves due to regional warming can cause regime shifts because of a large and sudden increase in primary productivity (Bertolin & Schloss, 2009). Furthermore, the discharge of icebergs can create areas of high benthic disturbance due to scour (Gutt et al., 2011).

Several studies have examined benthic communities following the disintegration of ice shelves. Larsen A & B, two ice shelves off the coast of the West Antarctic Peninsula, collapsed in 1995 and 2002, respectively (Gutt et al., 2013). Studies such as the LARISSA (Larsen Ice Shelf System, Antarctica) Project (Figure 2 site 6) have examined the impact of climate change on these ice shelf systems by surveying areas post-collapse, and have found interesting and surprising benthic communities, such as a chemotrophic ecosystem consisting of an association of microbial mats and cold seep clam communities (Domack et al., 2005; Gutt et al., 2013). In the Ross Sea, Dayton et al. (2013) described very fast growth in an ecologically important species of hexactinellid sponge due to a large increase in primary productivity associated with the calving of a large iceberg (Figure 2 site 4). A similar response was reported by Fillinger et al. (2013) following the collapse of the Larsen A Ice Shelf in which hexactinellid sponges were found to have large increases in biomass and abundance (Figure 2 site 6). While these few isolated studies give us valuable insight into sub-ice marine communities and how they change once ice shelves have disintegrated, a baseline is lacking, and accurately evaluating change without baseline data is impossible.

Hot water drilling systems have made access to the marine environment under ice shelves possible and more common, but most studies utilizing these systems are thus far focused on oceanographic data rather than seafloor ecology (Browning et al., 1979; Nicholls et al., 1991). In 2007, Riddle et al. utilized hot water drilling systems to collect seafloor imagery under the Amery Ice Shelf at a depth of approximately 800 m, 100 km away from the ice edge (Figure 2 site 5). This study was the first to find a benthic community dominated by suspension feeders at this distance under an ice shelf.

Questions and Objectives

It is of ecological importance to survey seafloor communities under ice cover while ice shelves and the underlying habitats are intact. This work provides the first description of a benthic community under the McMurdo Ice Shelf, and the first estimate of spatial variability in communities under ice shelves. The communities found under ice shelves will be compared to communities under seasonal ice, and the relationship of community structure to food availability will be examined. Shallow water communities under seasonal sea ice near McMurdo Station are known to exhibit zonation along a depth gradient, and the extent of that zonation in deeper water will be tested.

The limiting factor in these benthic communities is expected to be food availability. Food is known to vary with vertical distance, that is, depth. As depth increases, food availability decreases (Barnes & Mann, 2009). Similarly, it is expected to vary with horizontal distance, or distance from open water and photosynthesizing food sources. I expect to see zonation patterns along depth gradients with primary feeding type changing with depth due to decreasing food availability. As depth increases, the proportion of suspension feeders is predicted to increase because of their ability to feed on suspended organic matter in the water column, and thus to form assemblages in environments where food availability is low (Dayton, 1989; Gili & Coma, 1998). Though I expect to see depth zonation patterns under both seasonal ice and the ice shelf, I expect patterns to be more pronounced under the seasonal sea ice due to higher productivity gradient in those areas (Barry & Dayton, 1987). Organismal abundance is expected to decrease as depth increases, since lower food availability will sustain smaller populations. Similarly, greater food availability has been shown to sustain more biodiverse populations (Chase, 2010; Tittensor et al., 2010). Thus, biodiversity is expected to decrease with depth due to decreased access to primary productivity, that is, less food availability.

In marine communities, abundance and diversity have been found to increase with greater food availability (Chase, 2010; Tittensor et al., 2010). The closer a site is to open water where algal photosynthesis occurs, the greater the food availability, and thus the greater diversity and abundance are expected to be on the sea floor. Communities at sites with seasonally open water are expected to exhibit greater diversity and abundance than communities at sites under the permanent ice shelf, because in addition to being physically closer to year-round open water, seasonally open water allows for *in situ* and ice-sourced primary productivity in addition to that which is laterally advected. At sites under the ice shelf, the proportion of suspension feeders is predicted to be greater than at sites under sea ice because of suspension feeders' ability to feed on suspended organic matter in the water column, and thus to form assemblages in environments where food availability is low (Dayton, 1989; Gili & Coma, 1998).

Here I explore the structure of sub-ice benthic communities and their limiting factors. In sum, I asked the following questions: 1.) How do benthic community assemblages change with depth? 2.) Do abundance and diversity decrease with depth? 3.) Will sites with seasonally open water exhibit greater diversity and abundance than sites under the permanent ice shelf? 4.) Will sites under the seasonally open water have a lower proportion of suspension feeders compared to those under the ice shelf?

Methods

Study Sites

Four sites in the Ross Sea were surveyed in 2008 and 2009, two under seasonal sea ice and two under a permanent ice shelf (Figure 1). Knob Point, commonly known as Cinder Cones (77º48’S 166º40’E) and Cape Armitage (77º51’S 166 º40’E) lie on the Hut Point peninsula of Ross Island, and the surface waters of both of these sites exhibit seasonal ice cover. These sites were chosen due to the fairly steep bathymetry, allowing surveys to be conducted along a depth gradient, and the known vertical zonation of benthic communities up to depths of 40 m (Arndt et al., 2013; Dayton et al., 1970). Whereas Cape Armitage and Knob Point have previously been surveyed extensively at shallow depths by Dayton et al. (1970, 1974), this study expands the currently known zonation to greater depths and deduces the ecosystem drivers there.

Becker Point (78º8’S 164º13’E) and Heald Island (78º15’S 163º49’E) lie near the coast of the Antarctic mainland, and both of these sites are under the McMurdo Ice Shelf (Figure 1). These two sites were chosen because ice movement has made the ice shelf in these areas relatively thin along linear cracks (approximately 7 m), making the ocean accessible with a hand drill. Heald Island and Becker Point seafloor communities have never before been studied due to their inaccessibility, and these data will be the first to document these communities.

Data Collection

The Submersible Capable of under Ice Navigation and Imaging (SCINI) is a Remotely Operated Vehicle (ROV) designed specifically to be used in remote conditions of the Antarctic, and so is rugged and easily repairable. Because of its narrow torpedo shape, SCINI fits through a hole in the ice of only 20 cm diameter (Cazenave et al., 2011). SCINI features propellers that allow it to move in all directions, scaling lasers, lights, and two 5 megapixel cameras. SCINI's depth capacity is 300 m, and depth is measured for each frame using a depth sensor. All data are streamed real-time to computers at the surface for monitoring and subsequent post-processing. In 2008, SCINI was still in development, and as such, was lacking some features that were present in 2009. In 2008, a short baseline (SBL) navigation system was used as opposed to a long baseline (LBL) acoustic positioning system in 2009. Also, in 2008 SCINI had only one forward facing camera which was usually run at ¼ or ½ binning, resulting in images of lower resolution. In 2009, an additional downward facing camera and accompanying lights and scaling lasers were installed. The downward facing camera always operated at full resolution, resulting in higher quality images in 2009 (McPike, 2010).

To deploy the ROV, holes were drilled through the seasonal ice and permanent ice shelf using a Jiffy hand drill with a 10 inch bit. Between one and three holes were drilled at each site, depending on the steepness of the slope, with flatter bathymetry requiring the drilling of more holes. For instance, at Knob Point where the bathymetry is relatively steep, one hole was sufficient to access a depth gradient, through which all dives were conducted. Surveys at three of the four sites encompassed a depth gradient; in the case of Heald Island, a depth gradient did not occur within the range of the ROV, despite drilling three holes covering >1 km horizontal distance.

To conduct the surveys, SCINI was flown at a height of about 1 m above the seafloor using scaling lasers set 10 cm apart as a guide. Inconsistencies in flying height above the seafloor resulted in images with a range of areas surveyed. The number of dives conducted at each site varied: seven dives were conducted at Becker Point in the available depth range of 15-149 m, five dives were conducted at Knob Point in the available depth range of 30-315 m, two dives were conducted at Cape Armitage in the depth range of 15-119 m, and one dive was conducted at Heald Island in the depth range of 180-209 m. At Knob Point, no images were taken in the depth strata 165-179 m or 255-269 m; these strata were not covered during dives. Because SCINI was still in development in 2008 when sampling took place at Cape Armitage and Heald Island, images at these sites were taken with a lower resolution forward-facing camera, and consequently images from these sites were of poorer quality than images at sites sampled in 2009 (Knob Point and Becker Point). Originally seven dives were conducted at both Cape Armitage and Heald Island, but only two and one, respectively, produced images of sufficient quality for analysis. These few dives, however, were generally representative of the content of the imagery at each site.

Imagery from each dive was sorted in 15 m depth bins (e.g. 30-44 m, 45-59 m, etc.) and if available, 10 non-overlapping clear stills that fell within an image area of 0.077 and 2.17 m^2 were randomly chosen per depth bin per dive for photo processing. Occasionally dives within a site overlapped in depth, and images from each dive were used per depth strata resulting in more than 10 images per depth class. Since sites Heald Island and Cape Armitage were limited both by number of dives (one and two, respectively) and by image quality, all images that fell within the criteria at these sites were used (Table 1). For example, in the 180-194 m depth interval at Heald Island, 12 images from one dive were used because it was the only dive with adequate imagery at the site. Ultimately, nine depth strata were surveyed at Becker Point, 19 depth strata were surveyed at Knob Point, two depth strata were surveyed at Heald Island, and seven depth strata were surveyed at Cape Armitage for a total of 448 images analyzed (Table 1).

Table 1

Total Number of Images Analyzed

Depth Class (m)	Becker Point	Heald Island	Knob Point	Cape Armitage
15-29	10 (1)	0	0	8 (1)
30-44	10 (1)	0	9 (1)	14 (2)
45-59	20 (2)	0	20 (2)	9 (2)
60-74	30 (3)	0	10 (1)	2 (2)
75-89	30 (3)	0	10 (1)	7 (2)
90-104	20 (2)	0	10 (1)	8 (2)
105-119	20 (2)	0	18 (2)	11 (1)
120-134	30 (2)	0	20 (2)	0
135-149	10 (1)	0	9 (1)	0
150-164	0	0	10 (1)	0
180-194	0	12 (1)	10 (1)	0
195-209	0	2 (1)	10 (1)	0
210-224	0	0	10 (1)	0
225-239	0	0	10 (1)	0
240-254	0	0	10 (1)	0
270-284	0	0	10 (1)	0
285-299	0	0	10 (1)	0
300-314	0	0	9 (1)	0
Total	180	14	195	59

Note. Number of dives at each site and depth class in parentheses.

Image Processing and Analysis

Image area was calculated using the program ImageJ. In the case of Knob Point and Becker Point where images were taken with a downward-facing camera, calculations were made using one set of scaling lasers set 10 cm apart. At Cape Armitage and Heald Island, where a forward-facing camera was used with two sets of lasers 12.5 and 6.5 cm apart, images were cropped just beyond the height of both lasers and area was measured using the average distance of the two lasers, 9.5 cm, as a scale. Images were binned into five equal categories based on image area for analysis to ensure there were no patterns with image area (Table 2).

Table 2

Image Area Categories and Range of Values

Image area category	Image area (m^2) min.	Image area (m^2) max.
A	0.08	0.50
B	0.51	0.91
C	0.92	1.33
D	1.34	1.75
E	1.76	2.17

Images were processed in PhotoQuad with 100 stratified random points per image. Organisms were identified to the lowest possible taxon using primarily Peter Brueggeman’s Underwater Field Guide to Ross Island & McMurdo Sound, Antarctica (Brueggeman, 1998), and were subsequently placed into operational taxonomic categories (Appendix A). “Operational taxonomic units” (OTUs) in this instance are primarily groupings of phylum with the following exceptions: In the case of phylum Annelida, all annelids found were polychaetes, so “Polychaeta” was used as a taxonomic unit. There were many instances of bryozoans, colonial tunicates, and hydroids, many of which were identified to species. However, some hydroids couldn’t be differentiated from bryozoans with certainty, or bryozoans from certain colonial tunicates. Furthermore, colonial organisms were often found growing in an indistinguishable mass, so the operational taxonomic unit for bryozoans, hydrozoans, and colonial tunicates adopted was “colonial invertebrate”. In the phylum Cnidaria, only hydrozoans and anthozoans were present, and since all hydrozoans were part of the “colonial invertebrate” category, “Anthozoa” became the remaining operational unit.

For analysis of feeding type, organisms were placed into one of the following functional groups according to the available literature: mobile grazers, mobile scavengers, deposit feeders, suspension feeders, mobile predators, sessile predators, and spongivores (Table 3). Points that fell on substrate were assigned to one of the following categories: fine sediment (<0.5 cm diameter grain size), gravel (0.5- 5 cm), boulder (<5 cm), echinoderm ossicles, spicule mat, or benthic diatoms.

Table 3

Lowest Taxonomic Designation, Operational Taxonomic Unit (OTU), and Functional Group for All Organisms Identified

Lowest taxonomic designation	Operational taxonomic unit (OTU)	Functional group	Source for functional group designation
Alcyonaceae- Sea whip	Anthozoa	Suspension feeder	Wildish & Kristmanson, 2005
Alcyonaceae- Soft coral	Anthozoa	Suspension feeder	Wildish & Kristmanson, 2005
Anemone	Anthozoa	Sessile predator	Shick, 1991; Dayton et al., 1970
Artemidactis victrix	Anthozoa	Sessile predator	Shick, 1991
Isotealia antarctica	Anthozoa	Sessile predator	Dayton et al., 1974
Gersemia antarctica	Anthozoa	Deposit feeder	Slattery, 1997
Decapoda- Shrimp	Arthropoda	Mobile scavenger	Brueggeman, 1998
Glyptonotus antarcticus	Arthropoda	Mobile scavenger	Wägele, 1991
Pycnogonida	Arthropoda	Mobile scavenger	Brueggeman, 1998
Bryozoa	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Bryozoa sp. A	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Bryozoa sp. B	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Bryozoa sp. C	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Camptoplites sp.	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998

Cellaria sp.	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Cellarinella sp.	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Distaplia cylindrica	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Hornera sp.	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Hydrodendron arboreum	Colonial invertebrate	Suspension feeder	Barnes & Clarke, 1995; Gili & Coma, 1998
Hydrozoa	Colonial invertebrate	Suspension feeder	Barnes & Clarke, 1995; Gili & Coma, 1998
Reteporella sp.	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Tunicate sp. A	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Tunicate sp. B	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Tunicate sp. C	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Tunicate sp. D	Colonial invertebrate	Suspension feeder	Gili & Coma, 1998
Zyzzyzus parvula	Colonial invertebrate	Suspension feeder	Barnes & Clarke, 1995
Lyrocteis flavopallidus	Ctenophora	Suspension feeder	Robilliard & Dayton, 1972
Acondontaster sp.	Echinodermata	Spongivore	Dayton et al., 1974; McClintock, 1994
Asteroidea	Echinodermata	Mobile predator	Brueggeman, 1998
Bathyplotes bongraini	Echinodermata	Deposit feeder	Gutt, 1991
Diplasterias brucei	Echinodermata	Mobile predator	Dayton et al., 1974
Holothuroidea	Echinodermata	Suspension feeder	Gutt, 1991; McClintock, 1994
Macroptychaster accrescens	Echinodermata	Mobile predator	Dearborn, 1977; Dayton et al., 1974; McClintock, 1994
Odontaster validus	Echinodermata	Mobile scavenger	Dayton, 1974; McClintock, 1994
Ophionotus victoriae	Echinodermata	Mobile predator	McClintock, 1994
Ophiosparte gigas	Echinodermata	Mobile predator	Dearborn, 1977; McClintock, 1994
Ophiuroidea	Echinodermata	Mobile predator	McClintock, 1994
Perknaster aurorae	Echinodermata	Mobile predator	McClintock et al., 2008
Perknaster fuscus antarcticus	Echinodermata	Spongivore	Dayton et al., 1974; McClintock, 1994
Promachocrinus kerguelensis	Echinodermata	Suspension feeder	McClintock, 1994
Sterechinus neumayeri	Echinodermata	Mobile grazer	Pearse & Giese, 1966; McClintock, 1994
Chordata- Fish	Chordata		
Cuthona crinita	Mollusca	Mobile grazer	Cattaneo-Vietti, 1991
Doris kerguelensis	Mollusca	Spongivore	McClintock et al., 2005
Laternula elliptica	Mollusca	Suspension feeder	Ahn, 1994
Nuttallochiton mirandus	Mollusca	Mobile grazer	Brand, 1976
Parborlasia corrugatus	Nemertea	Mobile scavenger	Gibson, 1983

Chaetopterus variopedatus	Polychaeta	Suspension feeder	Flood & Fiala-Médioni, 1982
Flabelligera mundata	Polychaeta	Deposit feeder	Shepherd & Thomas, 1982
Perkinsiana sp.	Polychaeta	Suspension feeder	Rouse & Pleijel, 2001
Serpula narconensis	Polychaeta	Suspension feeder	Dales, 1957
Phymatolithon foecundum	Rhodophyta (Algae)	Autotrophic	
Alga	Rhodophyta (Algae)	Autotrophic	
Cnemidocarpa verrucosa	Tunicata (solitary)	Suspension feeder	Tatián et al., 2002
Cinachyra antarctica	Porifera	Suspension feeder	Gili & Coma, 1998
Cladocroce gaussiana	Porifera	Suspension feeder	Gili & Coma, 1998
Clathria nidificata	Porifera	Suspension feeder	Gili & Coma, 1998
Demospongia	Porifera	Suspension feeder	Gili & Coma, 1998
Dendrilla antarctica	Porifera	Suspension feeder	Gili & Coma, 1998
Guitarra cf. antarctica	Porifera	Suspension feeder	Gili & Coma, 1998
Haliclona scotti	Porifera	Suspension feeder	Gili & Coma, 1998
Haliclona sp.	Porifera	Suspension feeder	Gili & Coma, 1998
Hemigellius fimbriatus	Porifera	Suspension feeder	Gili & Coma, 1998
Homaxinella balfourensis	Porifera	Suspension feeder	Gili & Coma, 1998
Inflatella belli	Porifera	Suspension feeder	Gili & Coma, 1998
Isodictya setifera	Porifera	Suspension feeder	Gili & Coma, 1998
Leucascus leptoraphis	Porifera	Suspension feeder	Gili & Coma, 1998
Mycale (Oxymycale) acerata	Porifera	Suspension feeder	Gili & Coma, 1998
Polymastia invaginata	Porifera	Suspension feeder	Gili & Coma, 1998
Porifera	Porifera	Suspension feeder	Gili & Coma, 1998
Porifera- Budding sponge	Porifera	Suspension feeder	Gili & Coma, 1998
Rossella antarctica	Porifera	Suspension feeder	Gili & Coma, 1998
Rossella levis	Porifera	Suspension feeder	Gili & Coma, 1998
Rossella podagrosa	Porifera	Suspension feeder	Gili & Coma, 1998
Rossella sp.	Porifera	Suspension feeder	Gili & Coma, 1998
Sphaerotylus antarcticus	Porifera	Suspension feeder	Gili & Coma, 1998
Sponge sp. A	Porifera	Suspension feeder	Gili & Coma, 1998
Sponge sp. B	Porifera	Suspension feeder	Gili & Coma, 1998
Sponge sp. C	Porifera	Suspension feeder	Gili & Coma, 1998
Sponge sp. D	Porifera	Suspension feeder	Gili & Coma, 1998
Sponge sp. E	Porifera	Suspension feeder	Gili & Coma, 1998
Stylochordata chupachups	Porifera	Suspension feeder	Gili & Coma, 1998

Suberites sp.	Porifera	Suspension feeder	Gili & Coma, 1998
Tetilla leptoderma	Porifera	Suspension feeder	Gili & Coma, 1998

Data Analysis

Community-level analyses were performed in PRIMER 6 with the PERMANOVA add-on package. Data were fourth root-transformed to reduce the influence of abundant taxonomic groups and Bray-Curtis similarity matrices were generated. Community assemblage data were analyzed at the lowest taxonomic designation and in broader "operational taxonomic units" (OTUs). When making comparisons within sites or between sites with similar image quality, lowest taxonomic designations were used. When comparing sites with disparate image quality, OTUs were used to keep taxonomic designations at a similar level across sites, as lower image resolution at Cape Armitage and Heald Island potentially impeded precise species designations and designations at these sites were often made at higher taxonomic levels.

Three factors were tested in the multivariate analysis—depth, site, and image area. A PERMANOVA (Permutational Multivariate Analysis of Variance) test was applied to examine if the sites differed from one another, if there were differences between the depth strata, and to test if there were patterns with image area. Because of the significant interaction term of "Site x Depth" in the overall PERMANOVA, each site was examined individually for differences in depth using analysis of similarities (ANOSIM) pairwise comparisons. Non-metric multidimensional scaling (nMDS) plots were created to visualize similarities in benthic communities within and between sites. For groupings determined by the nMDS analysis, an ANOSIM tested whether differences in communities were significant. ANOSIM analyses were conducted as opposed to PERMANOVA because ANOSIM is more robust to unequal sample sizes. P-values were adjusted for multiple comparisons using sequential Bonferroni corrections in order to lower the probably of making a type 1 error. Similarity percentage (SIMPER) analyses were used to identify which taxa drove the differences between communities. Species richness and Shannon-Weiner diversity indices were calculated in PRIMER and compared among sites and depth classes. Image was used as the level of replication because of unequal sampling within and between sites. Though diversity within individual images represents a small subset of the overall site diversity, the averages of diversity per image were useful to compare within and between sites, though overall area sampled per site differed.

All univariate statistical analyses were executed in JMP 12.01 Pro. When making comparisons within a site, images at all depths were used in the analysis. When making comparisons between sites, only images at depth intervals that co-occur across sites were used. Percent cover data served as a proxy for abundance, as images consisted of mostly colonial organisms, for which individual counts were not appropriate. Data met assumptions of normality, and thus patterns in faunal abundance, diversity, and relative abundance of functional groups with depth were evaluated using various statistical tests. To examine differences between assemblages under sea ice to those under the ice shelf, one-way ANOVAs with site nested in type of ice cover, and two-sample t-tests with post-hoc Tukey HSD tests were conducted, as appropriate. Differences with depth within sites were evaluated using least-squares regressions. For regressions, data were statistically tested for linear and quadratic relationships to explore the question of how communities change with depth. Best-fit relationships were determined using model selection techniques with corrected Aikake's information criteria (Burnham & Anderson, 1998). Models were considered statistically significant when the difference in AICc values was greater than or equal to 2. Substrate categories were removed in the univariate analysis so only living fauna were considered. When necessary, p-values were adjusted for multiple comparisons using sequential Bonferroni corrections in order to lower the probability of making a type 1 error.

Results

Site Descriptions

Becker Point Communities under the ice shelf at Becker Point were sparse with variable percent cover (Table 4). The substrate at Becker Point was primarily fine sediment and gravel with what appeared to be echinoderm ossicles mixed into the substrate. In terms of “operational taxonomic units” (OTUs), groups Porifera (1.65% avg. cover) and Anthozoa (1.46% avg. cover) were the most common throughout Becker Point (Table 4). The anemone species *Artemidactis victrix* (1.21% avg. cover), budding sponges of unknown species (0.62% avg. cover), and demosponges of unknown species (0.57% avg. cover) were the most abundant groups of lowest taxonomic designation. Also present but less common were groups Echinodermata, colonial invertebrates, and Polychaeta (Table 4). With regard to functional groups, suspension feeders were most common at Becker Point (2.37% avg. cover), followed by sessile predators (1.43% avg. cover), mobile predators (1.12% avg. cover), mobile grazers (0.10% avg. cover), mobile scavengers (0.03% avg. cover), spongivores (0.03% avg. cover), and deposit feeders (0.02% avg. cover) (Table 5).

Table 4

Average Percent Cover and Standard Error of Fauna at Becker Point

Lowest taxonomic unit	M	SE
Porifera	1.65	0.27
Unknown sp. budding sponge	0.62	0.08
Unknown sp. demosponge	0.57	0.21
Polymastia invaginata	0.20	0.07
Hemigellius fimbriatus	0.04	0.02
Homaxinella balfourensis	0.03	0.01
Sphaerotylus antarcticus	0.03	0.01

Anthozoa	1.46	0.20
Artemidactis victrix	1.21	0.19
Unknown sp. anemone	0.17	0.06
Isotealia antarctica	0.05	0.02
Unknown sp. soft coral	0.02	0.02
Colonial invertebrate	0.37	0.08
Unknown sp. bryozoa	0.23	0.07
Cellarinella sp.	0.05	0.02
Zyzzyzus parvula	0.02	0.01
Cellaria sp.	0.02	0.01
Echinodermata	0.41	0.10
Promachocrinus kerguelensis	0.14	0.08
Unidentified ophiuroid	0.06	0.02
Sterechinus neumayeri	0.08	0.03
Ophiosparte gigas	0.05	0.02
Polychaeta	0.14	0.03
Perkinsiana sp.	0.12	0.03
Mollusca	0.02	0.01
Arthopoda	0.02	0.01
Tunicata (solitary)	0.02	0.06

Note. All OTUs present and lowest taxonomic units with greater than or equal to 0.02% average cover were included.

Table 5

Average Percent Cover, Standard Error, and Relative Percent of All Fauna at Becker Point by Functional Group

Functional group	M	SE	% of fauna
Suspension feeder	2.37	0.33	57.80
Sessile predator	1.43	0.20	34.90
Mobile predator	0.12	0.03	2.92
Mobile grazer	0.10	0.03	2.44
Mobile scavenger	0.03	0.01	0.73
Spongivore	0.03	0.02	0.73
Deposit feeder	0.02	0.02	0.48

Heald Island Communities under the ice shelf at Heald Island were the most sparse of this study. The substrate at Heald Island was very fine, homogenous, soft sediment. Few fauna were present at this site, and low image resolution prevented identifications from being made at the species level. Most common were sea whips (0.29% avg. cover) and anemones of undetermined species (0.29% avg. cover), belonging to the OTU category Anthozoa (Table 6). Other fauna present were ophiuroids (0.14% avg. cover) and sponges of undetermined species (0.14% avg. cover) (Table 6). In terms of functional groups, suspension feeders were most common (0.43% avg. cover), followed by sessile predators (0.29% avg. cover), and mobile predators (0.14% avg. cover) (Table 7).

Table 6

Average Percent Cover and Standard Error of All Fauna Present at Heald Island, by OTUs and Lowest Taxonomic Units

Lowest taxonomic unit	M	SE
Anthozoa	0.57	0.20
Unknown sp. anemone	0.29	0.19
Unknown sp. sea whip	0.29	0.13
Porifera	0.14	0.10
Unknown sp. budding sponge	0.07	0.07
Unknown sp. sponge	0.07	0.07
Echinodermata	0.14	0.10
Unidentified ophiuroid	0.14	0.10

Table 7

Average Percent Cover, Standard Error, and Relative Percent of All Fauna at Heald Island by Functional Group

Functional group	M	SE	% of fauna
Suspension feeder	0.43	0.14	50
Sessile predator	0.29	0.19	34
Mobile predator	0.14	0.10	16

Knob Point Benthic communities under the seasonal sea ice at Knob Point were dense and diverse, with faunal groups often growing atop one another or mixed together. The substrate at shallow Knob Point sites was primarily fine sediment and shells of the bivalve *Laternula elliptica* with a high abundance of diatomaceous film. With regards to OTUs, colonial invertebrates were the most common group present at Knob Point (26.29% avg. cover) (Table 8). Also fairly common were groups Porifera (8.18% avg. cover) and Polychaeta (2.79% avg. cover), followed by Echinodermata (1.11% avg. cover). In terms of lowest taxonomic designations, the bryozoan *Cellaria* sp. (11.86% avg. cover) and unidentified bryozoans were most common (9.34% avg. cover) (Table 8). When looking at the fauna in functional groups, suspension feeders were by far the most abundant, comprising 96.42% of all fauna at Knob Point (Table 9).

Table 8

Average Percent Cover and Standard Error of Fauna at Knob Point

Lowest taxonomic unit	M	SE
Colonial invertebrate	26.29	1.38
Cellaria sp.	11.86	1.25
Unknown sp. bryozoan	9.34	0.79
Hydrodendron arboreum	1.13	0.29
Bryozoa sp. *B*	0.94	0.17
Tunicate sp. *D*	0.75	0.21
Cellarinella sp.	0.45	0.08
Tunicate sp. *A*	0.43	0.07
Unknown sp. hydroid	0.41	0.12
Tunicate sp. *C*	0.33	0.09
Reteporella sp.	0.31	0.05
Bryozoa sp. A	0.10	0.05
Tunicate sp. B	0.09	0.07
Distaplia cylindrica	0.08	0.03
Hornera sp.	0.05	0.02
Porifera	8.18	0.70

Rossella podagrosa	1.12	0.42
Hemigellius fimbriatus	1.11	0.31
Unknown sp. demosponge	1.02	0.12
Rossella sp.	1.02	0.41
Polymastia invaginata	0.96	0.15
Sponge sp. D	0.45	0.11
Sponge sp. E	0.35	0.09
Mycale (Oxymycale) acerata	0.33	0.20
Homaxinella balfourensis	0.27	0.01
Sphaerotylus antarcticus	0.22	0.05
Isodictya setifera	0.21	0.12
Rossella antarctica	0.21	0.09
Tetilla leptoderma	0.19	0.14
Rossella levis	0.17	0.11
Dendrilla antarctica	0.16	0.05
Leucascus leptoraphis	0.12	0.04
Inflatella belli	0.07	0.03
Polychaeta	2.79	0.28
Perkinsiana sp.	2.62	0.28
Serpula narconensis	0.17	0.04
Echinodermata	1.11	0.24
Unidentified ophiuroid	0.51	0.05
Promachocrinus kerguelensis	0.25	0.22
Odontaster validus	0.12	0.04
Macroptychaster accrescens	0.07	0.04
Perknaster aurorae	0.06	0.04
Rhodophyta (Algae)	0.36	0.22
Phymatholithon foecundum	0.27	0.22
Algae sp. A	0.09	0.01
Anthozoa	0.16	0.05
Unknown sp. soft coral	0.13	0.04
Ctenophora	0.08	0.08
Lyrocteis flavopallidus	0.08	0.08
Nemertea	0.07	0.03
Parborlasia corrugatus	0.07	0.03
Arthropoda	0.06	0.02
Mollusca	0.04	0.02

Note. All OTUs present and lowest taxonomic units with greater than or equal to 0.05% average cover were included.

Table 9

Average Percent Cover, Standard Error, and Relative Percent of All Fauna at Knob Point by Functional Group

Functional group	M	SE	% of fauna
Suspension feeder	37.73	1.44	96.42
Mobile predator	0.69	0.08	1.76
Mobile scavenger	0.25	0.07	0.64
Spongivore	0.05	0.03	0.13
Mobile grazer	0.02	0.01	0.05
Sessile predator	0.03	0.03	0.08
Deposit feeder	0.02	0.01	0.05

Cape Armitage Under the sea ice at Cape Armitage, dense assemblages of benthic species covered the seafloor. The substrate at Cape Armitage was primarily spicule mat with embedded shells. Most abundant were colonial invertebrates (11.67% avg. cover) and individuals of the group Porifera (11.52% avg. cover), followed by the groups Anthozoa (0.86% avg. cover), Echinodermata (0.44% avg. cover), and Polychaeta (0.42% avg. cover) (Table 10). The groups Arthropoda and Mollusca were present as well, each with 0.05% or less cover. With regards to functional groups, suspension feeders were by far the most abundant group, with average cover of 23.80%, or 95% of all fauna (Table 11).

Table 10

Average Percent Cover and Standard Error of Fauna at Cape Armitage

Lowest taxonomic unit	M	SE
Colonial invertebrate	11.67	1.94
Cellaria sp.	5.81	1.77
Unknown sp. bryozoan	3.23	0.60
Hydrodendron arboreum	1.83	0.75
Tunicate sp. D	0.36	0.15
Bryozoa sp. A	0.34	0.26

Reteporella sp.	0.09	0.06
Porifera	11.52	1.2
Unknown sp. demosponge	2.17	0.33
Tetilla leptoderma	2.11	0.35
Polymastia invaginata	2.05	0.51
Rossella sp.	0.92	0.48
Rossella podagrosa	0.91	0.42
Unknown sp. sponge	0.84	0.31
Hemigellius fimbriatus	0.56	0.26
Cinachyra antarctica	0.39	0.12
Rossella levis	0.33	0.22
Mycale (Oxymycale) acerata	0.31	0.20
Suberites sp.	0.25	0.12
Leucascus leptoraphis	0.22	0.12
Haliclona scotti	0.14	0.08
Sponge sp. D	0.08	0.06
Sponge sp. A	0.08	0.06
Homaxinella balfourensis	0.05	0.03
Sphaerotylus antarcticus	0.03	0.02
Anthozoa	0.86	0.39
Unknown sp. anemone	0.73	0.39
Unknown sp. soft coral	0.13	0.06
Echinodermata	0.44	0.11
Unidentified ophiuroid	0.23	0.07
Promachocrinus kerguelensis	0.06	0.06
Polychaeta	0.42	0.13
Perkinsiana sp.	0.42	0.13
Arthropoda	0.05	0.03
Unknown sp. pycnogonid	0.05	0.03
Mollusca	0.03	0.02

Note. All OTUs present and lowest taxonomic units with greater than or equal to 0.05% average cover were included.

Table 11

Average Percent Cover, Standard Error, and Relative Percent of All Fauna at Cape Armitage by Functional Group

Functional group	M	SE	% of fauna
Suspension feeder	23.80	2.11	95.0
Sessile predator	0.73	0.39	2.9
Mobile predator	0.28	0.07	1.1
Spongivore	0.13	0.05	0.52
Mobile scavenger	0.05	0.05	0.2

Differences between Sites and Depths

An nMDS plot at the species level of the 448 images analyzed shows a distinction between communities at Cape Armitage, Knob Point, and the two ice shelf sites, Becker Point and Heald Island (Figure 3, Figure 4), as well as by depth within sites. Samples from Becker Point and Heald Island group together with no apparent organization by depth (Figure 3). Samples from Knob Point group together with a gradient in depth along axis nMDS 2. Samples from a depth of 30-44 m at Becker Point group more closely with shallow (45-59 m) Knob Point samples than they do to Becker Point samples from other depths. Cape Armitage samples group together fairly well with little visible organization with depth. A three factor PERMANOVA analysis determined that there was a significant interaction term of “Site x Depth,” confirming that changes in community among depth classes were different from site to site (p=0.001) (Table 12). The third factor, image area, was not found to be significant, allowing all images at each site to be used in the comparisons.

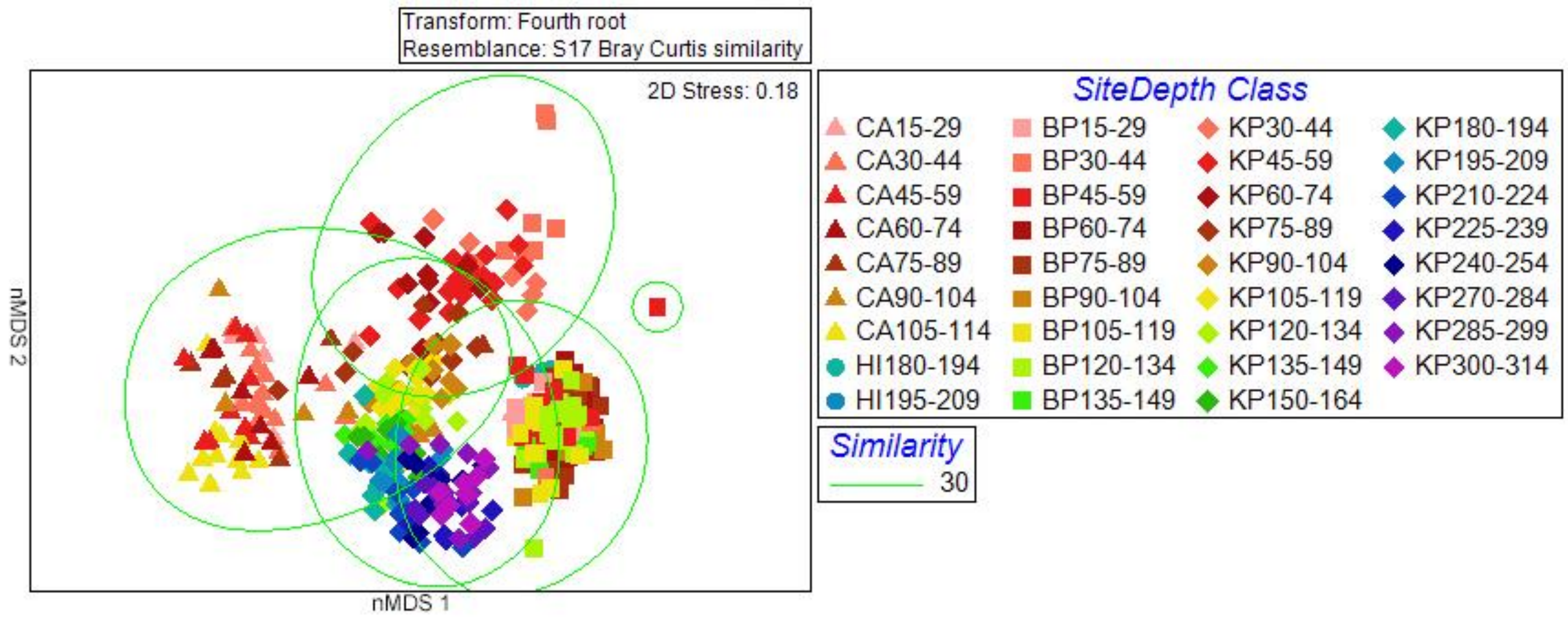


Figure 3. Two-dimensional nMDS ordination showing 448 images at all sites analyzed at the species level, sorted by site and depth in meters. Triangles represent images at Cape Armitage (CA), circles represent Heald Island (HI), squares represent Becker Point (BP), diamonds represent Knob Point (KP). Based on fourth root transformed percent cover and Bray-Curtis similarities. Similarity based on cluster analysis showing level of similarity between groups.

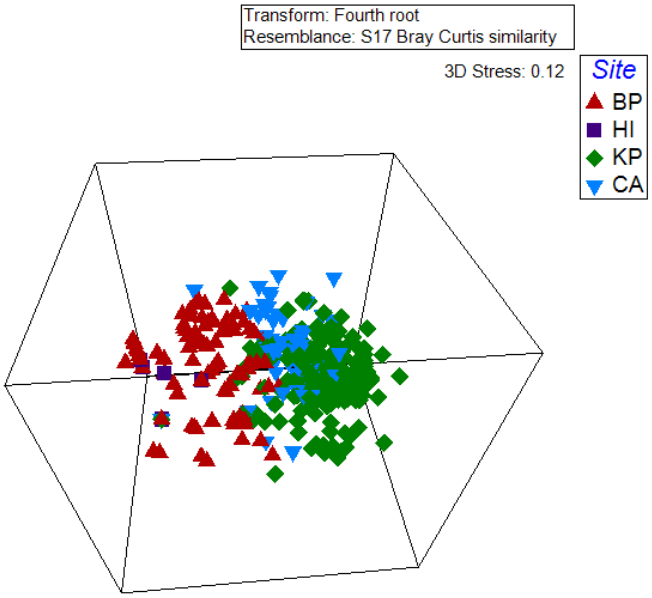


Figure 4. Three-dimensional nMDS ordination of images at all sites analyzed at the OTU level. Based on fourth root transformed percent cover and Bray-Curtis similarities. BP = Becker Point, HI = Heald Island, CA = Cape Armitage, KP = Knob Point.

Table 12

Permutational Multivariate Analyses of Variance (PERMANOVA) of the Effects of Three Crossed, Fixed factors, Depth, Site, and Image area, on the Transformed Abundance Community Data

Source	df	SS	MS	Pseudo-F	P(perm)	Perms
Depth	14	6894.1	492.43	1.735	0.011*	999
Site	1	7796.4	7796.4	27.467	0.001*	999
Image Area	2	94.779	47.39	0.167	0.906	998
Depth x Site	14	11051	789.33	2.781	0.001*	999
Depth x Image Area	30	4168.7	138.96	0.490	0.999	998
Site x Image Area	6	1715.1	285.84	1.007	0.468	999
Depth x Site x Image Area	17	3865.9	227.41	0.801	0.785	998
Res	353	1.00E+05	283.84			
Total	447	2.81E+05				

Note. df = degrees of freedom, SS = sum of squares, MS = mean squares, Pseudo-F = the pseudo F-value, P(perm) = the permutational probability value, and Perms = the number of permutations of residuals carried out. *p < 0.05.

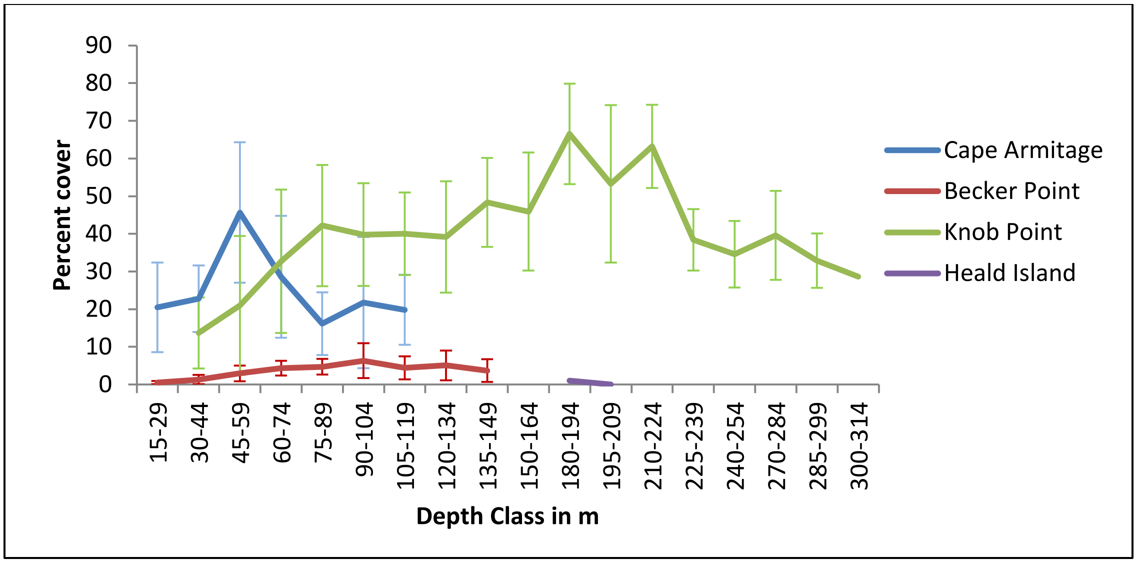


Figure 5. Line graph of average faunal percent cover at each site by depth class. Error bars indicate standard error.

Differences in Communities with Depth

Becker Point At Becker Point, a site under the permanent ice shelf, differences in community structure with depth were mostly subtle along a depth gradient of 15-149 m (Figure 6), with the exception of images from the depth class 30-44 m that were dissimilar from the other depths (Figure 7). Differences in community composition by depth class were significant (One-way ANOSIM, R= 0.255, p=0.001).

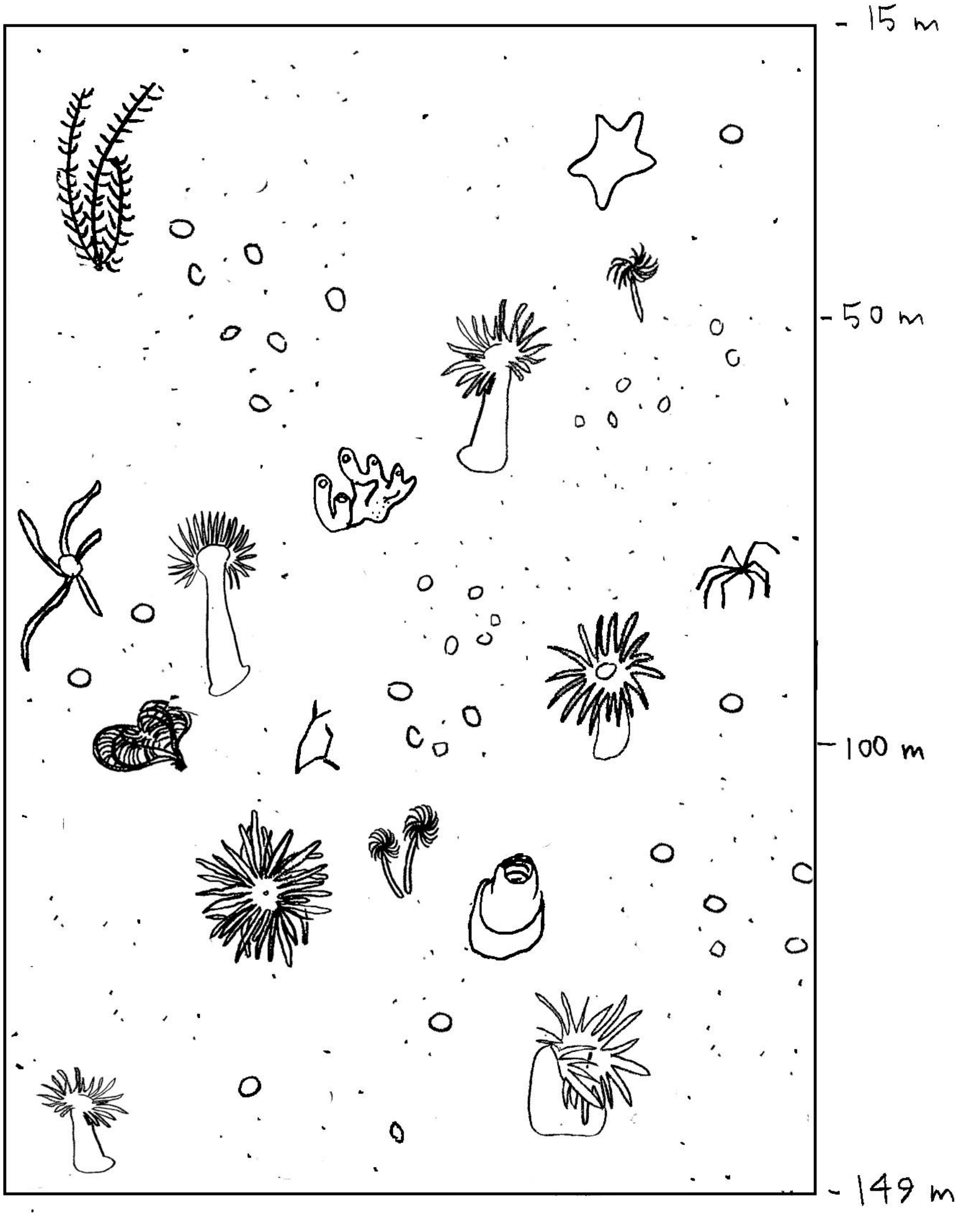


Figure 6. Illustration of distribution of fauna with depth between 15 and 149 m at Becker Point.

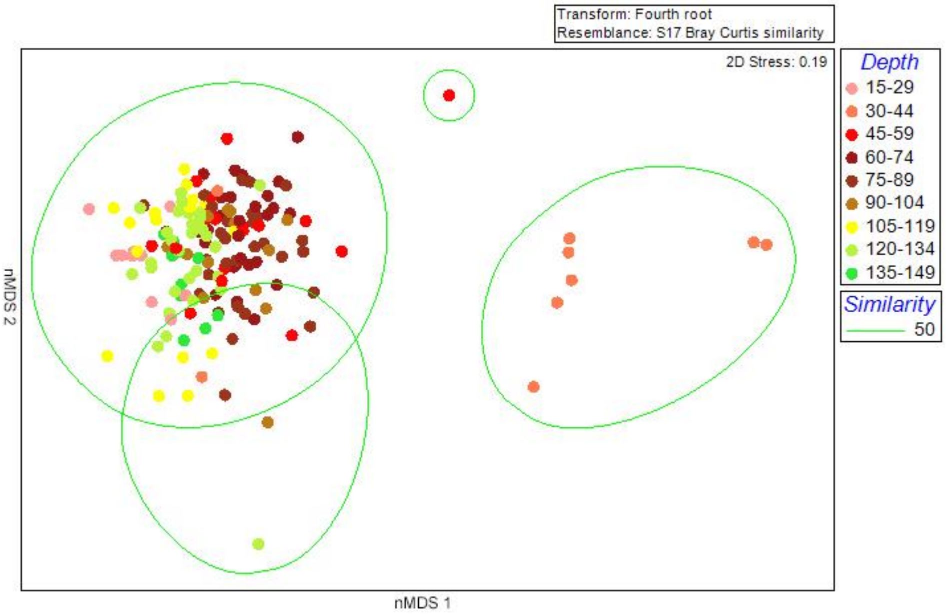


Figure 7. nMDS ordination of all 180 images at Becker Point analyzed at the species level, sorted by depth in meters. Based on fourth root transformed percent cover and Bray-Curtis similarities. Similarity based on cluster analysis showing level of similarity between groups.

ANOSIM pairwise comparisons found samples from depths of 15-29 m were statistically different from all other depths except 105-119 m (p=0.001) (Appendix B, Table 1). SIMPER analysis determined this group was characterized by a relatively high proportion of fine sediment, gravel, and shell (Appendix C, Table 1). Samples from depths of 30-44 m were statistically different from all other depths as well (p=0.001), with very high SIMPER dissimilarity values across all depth strata (minimum dissimilarity of 74.27 at 45-59 m, maximum dissimilarity of 77.94 at 105-119 m) (Table 13). The SIMPER analysis determined the community assemblage at 30-44 m was characterized by a high proportion of diatomaceous film growing on the fine sediment (2.5% average abundance). At 60-74 m and beyond, living fauna become relatively abundant. Budding sponges were most abundant at mid depth (0.79%, 0.70%, and 0.73% cover for depth strata 60-74 m, 75-89 m, and 90-104 m). The anemone *Artemidactis victrix* was the most common living organism at 105-119 m depth (0.62%). Beyond this depth, the community was characterized by sediment (fine sediment, gravel, echinoderm ossicles) and no living fauna (Appendix C, Table 1).

Table 13

Matrix of Dissimilarity between Depth Bins at Becker Point

Depth (m)	15-29	30-44	45-59	60-74	75-89	90-104	105-119	120-134	135-149
15-29									
30-44	76								
45-59	42	74							
60-74	45	76	35						
75-89	44	75	38	34					
90-104	42	77	37	34	35				
105-119	38	78	40	41	40	38			
120-134	36	76	37	38	39	36	36		
135-149	38	76	38	38	38	33	37	33	

Note. Dissimilarity values calculated by SIMPER. Color-coding represents percent dissimilarity with green = 70-79%, pink = 40-49%, and purple = 30-39%.

When looking at general patterns in OTU with depth, several patterns emerge (Figure 8a-f). Average total faunal percent cover followed a unimodal distribution with depth at Becker Point, that is, a quadratic relationship with one clear peak of 6.33% living cover at 90-104 m (r^2=0.950, p=0.0008) (Figure 5). The cover of colonial invertebrates stayed fairly constant throughout all depth classes at Becker Point, averaging around 0.35% cover (8b). At the shallowest zone at Becker Point, 15-29 m, colonial invertebrates were the dominant taxa with only 0.4% cover, but were 80% of all living fauna. At all other depth classes, anthozoans and/or sponges were the dominant fauna, with both groups

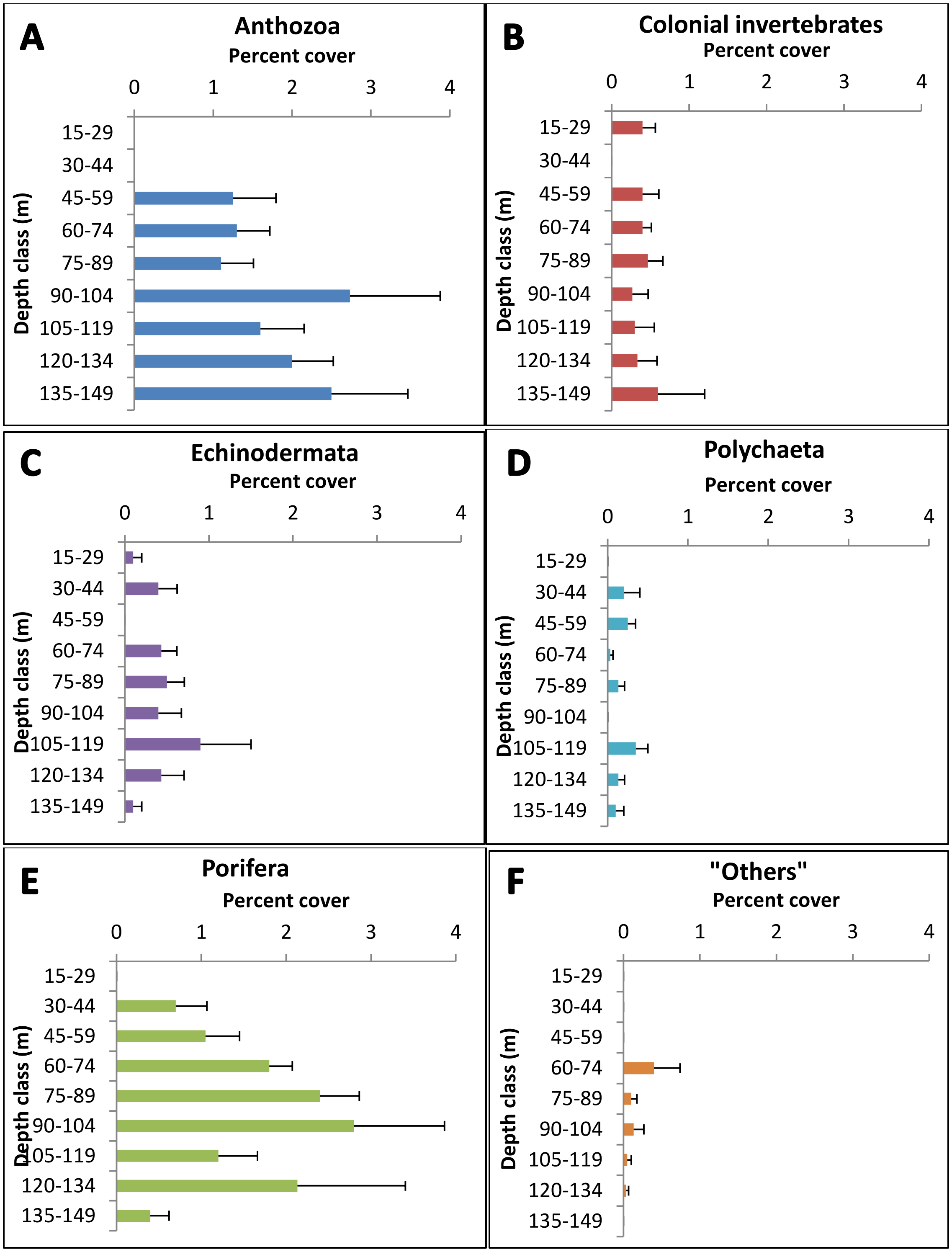


Figure 8a-f. Bar graphs of mean cover and standard error at Becker Point at operational taxonomic unit (OTU) level by depth class. a.) Anthozoa, b.) colonial invertebrates, c.) Echinodermata, d.) Polychaeta, e.) Porifera, f.) “others.”

increasing steadily to 2.73% and 2.8% respectively at 90-104 m before dropping off at greater depths.

With regards to differences in functional groups with depth, several patterns were observed. Whereas the raw cover of suspension feeders followed a unimodal pattern with depth (r^2=0.890, p=0.0013) (Table 14), the proportion of suspension feeders relative to other feeding types was found to decrease with depth in a linear fashion (r^2=0.663, p=0.0076) (Figure 9a). Sessile predators were also fairly common at Becker Point, with percent cover increasing with depth (r^2=0.812, p=0.0009) from 0% at the most shallow depth to a maximum of 61.56% of the fauna (2.6% total cover) at 90-104 m (Table 14, Figure 9b). Mobile scavengers, mobile grazers, spongivores, and mobile predators were all present at Becker Point, though consistently at low abundances (<0.3%).

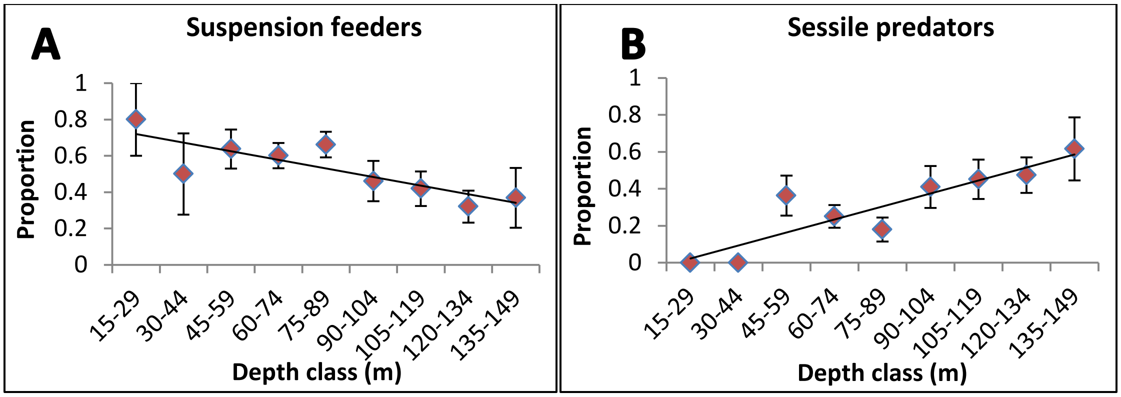


Figure 9a-b. Scatter plot of the proportion of a.) suspension feeders and b.) sessile predators and standard error with depth at Becker Point.

Species diversity was unimodal with depth at Becker Point (Figure 10). Both species richness and the Shannon-Wiener diversity index regressions were significant (r^2=0.87, p=0.0024; r^2=0.84, p=0.0043, respectively) (Figure 10).

Table 14

Average Percent Cover and Standard Error for Functional Groups at Becker Point by Depth Class

Depth class (m)	Sessile predators		Suspension feeders		Mobile predators		Spongivores		Mobile grazers		Deposit feeders		Mobile scavengers	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
15-29	0	0	0.4	0.16	0.1	0.1	0	0	0	0	0	0	0	0
30-44	0	0	0.9	0.48	0.2	0.13	0	0	0	0	0	0	0.2	0.2
45-59	1.25	0.55	1.7	0.48	0	0	0	0	0	0	0	0	0	0
60-74	1.3	0.42	2.57	0.46	0.1	0.07	0.13	0.13	0.2	0.01	0	0	0	0
75-89	1.03	0.41	3.27	0.58	0.17	0.84	0	0	0.23	0.1	0	0	0	0
90-104	2.6	1.12	3.2	1.24	0.13	0.09	0	0	0.27	0.21	0	0	0.13	0.13
105-119	1.6	0.55	2.5	0.87	0.1	0.07	0.05	0.05	0	0	0.1	0.1	0	0
120-134	2	0.52	2.8	1.5	0.17	0.07	0	0	0	0	0.07	0.07	0.03	0.03
135-149	2.5	0.97	1.1	0.62	0.1	0.1	0	0	0	0	0	0	0	0

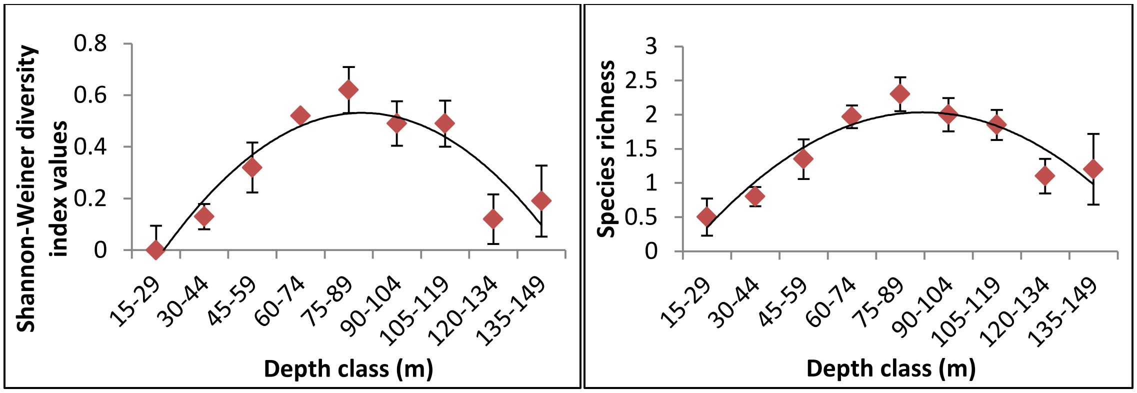


Figure 10. a.) Shannon-Weiner diversity values and b.) species richness and standard error by depth class at Becker Point.

Heald Island At Heald Island, the other site under the ice shelf, only two depth classes were present, 180-194 m and 195-209 m (Figure 11, Table 15). With only two images and no fauna in the latter group, there was an insufficient sample size to examine changes in species assemblages in this narrow depth gradient.

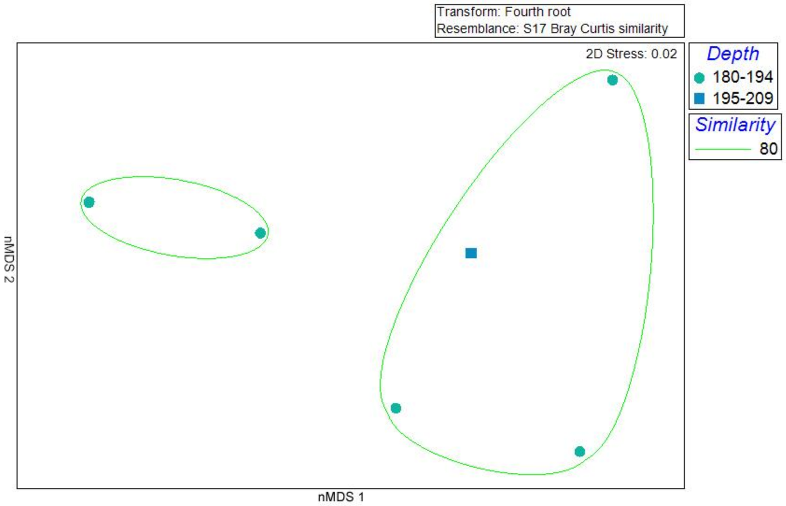


Figure 11. nMDS ordination of 14 images at Heald Island analyzed at the species level, 12 images at 180-194 m and two images at 195-209 m. Based on fourth root transformed percent cover and Bray-Curtis similarities. Green outlined similarity based on cluster analysis showing level of similarity between groups.

Table 15

Average and Standard Error Shannon-Wiener Diversity Index Values and Species Richness by Depth Class at Heald Island

Depth class (m)	Shannon-Weiner		Species richness	
	Avg.	SE	Avg.	SE
180-194	0.12	0.08	0.83	0.21
195-209	0	0	0	0

Knob Point At Knob Point, a site under seasonal ice, benthic assemblages differed greatly along a depth gradient of 30-314 m (Figure 12). Differences in community composition as a function of depth class were statistically significant (One-way ANOSIM, R= 0.624, p=0.001).

ANOSIM pairwise comparisons found most depth strata to be significantly different from one another (Appendix B, Table 2), with the starkest contrast at 75 m depth, between depths 30-74 m and 75-314 m according to SIMPER dissimilarities (Table 16). Samples at depth of 30-44 m, 45-59 m, and 60-74 m were found to be relatively similar to one another (minimum dissimilarity of 49.58 of 30-44 m and 60-74 m, maximum dissimilarity of 56.65 of 45-59 m and 60-74 m), but very different from samples at greater depths (minimum dissimilarity of 63.33 of 45-59 m and 75-89 m, maximum dissimilarity of 82.07 of 30-44 m and 180-194 m). This depth break in the community assemblage is visible in the nMDS plot, in which samples in the deep group (75-314 m) appear to be ordinated in a linear pattern along a depth gradient (Figure 13). It should be noted that with stress levels over 0.2, the two-dimensional image is slightly distorted and doesn’t as adequately represent the data as a 3-dimensional image, but is clearer to visualize and still allows a look at general patterns.

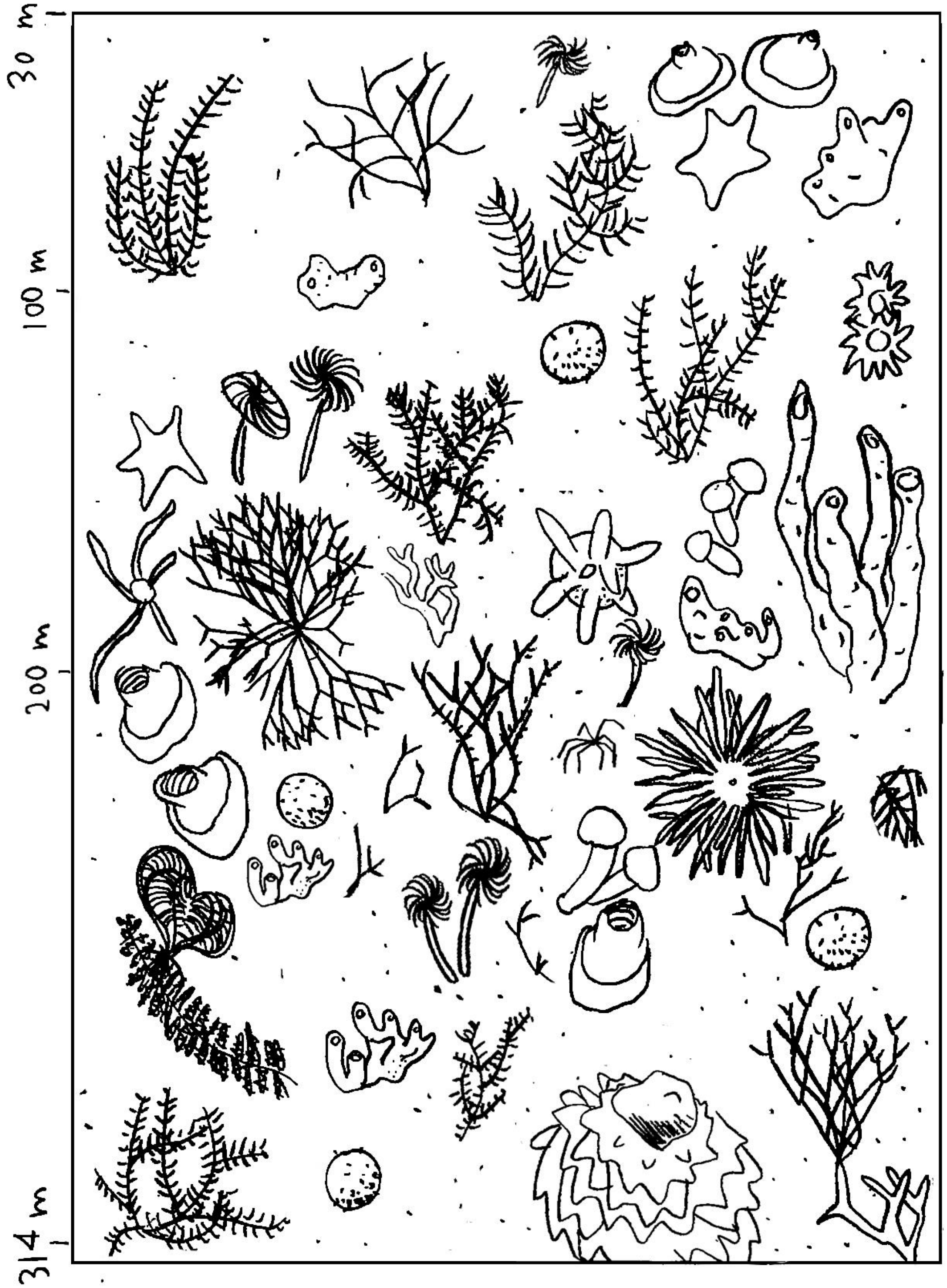
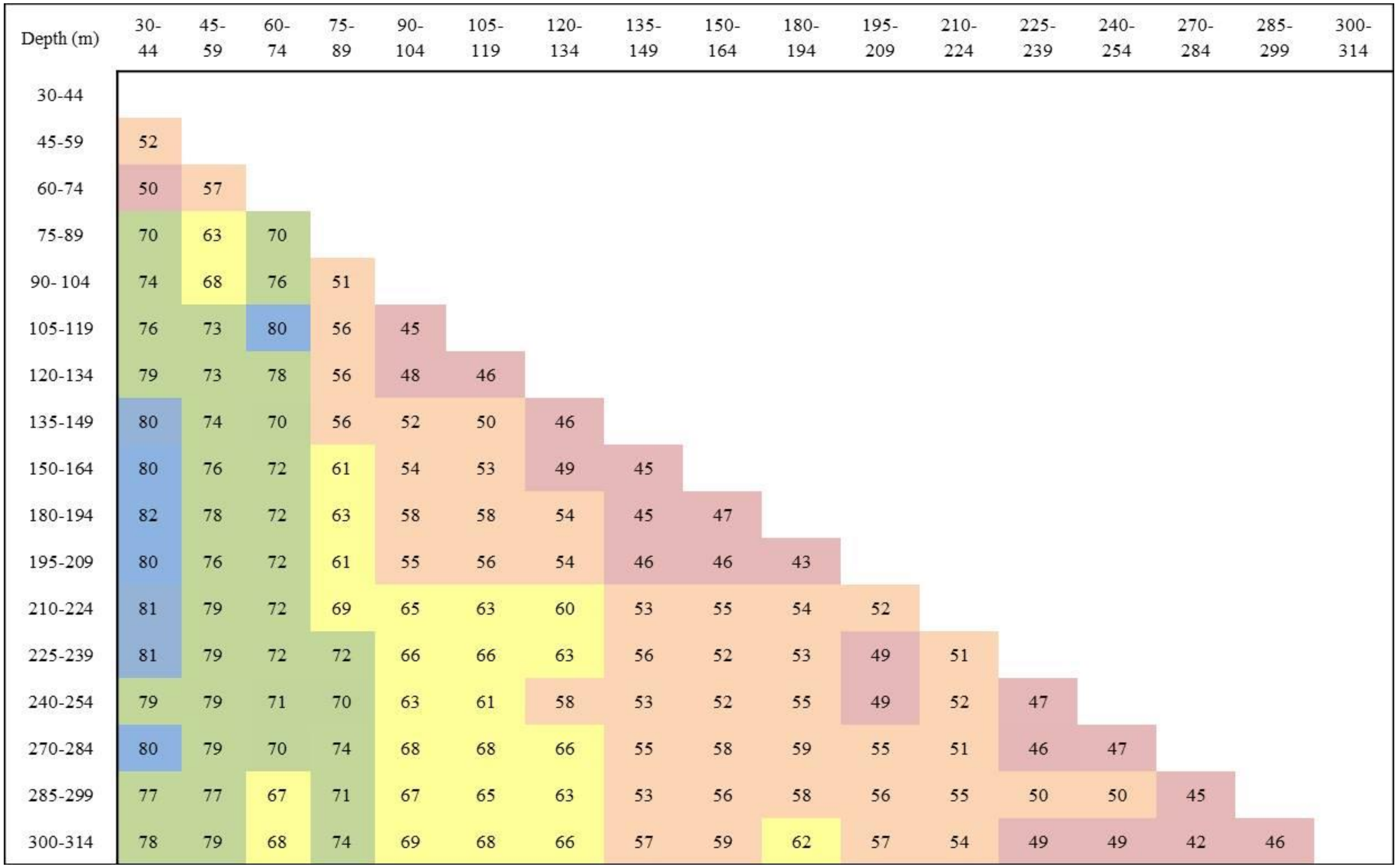


Figure 12. Illustration of distribution of fauna with depth between 30 m and 314 m at Knob Point.

Table 16

Matrix of Dissimilarity between Depth Bins at Knob Point



Depth (m)	30-44	45-59	60-74	75-89	90-104	105-119	120-134	135-149	150-164	180-194	195-209	210-224	225-239	240-254	270-284	285-299	300-314
30-44																	
45-59	52																
60-74	50	57															
75-89	70	63	70														
90- 104	74	68	76	51													
105-119	76	73	80	56	45												
120-134	79	73	78	56	48	46											
135-149	80	74	70	56	52	50	46										
150-164	80	76	72	61	54	53	49	45									
180-194	82	78	72	63	58	58	54	45	47								
195-209	80	76	72	61	55	56	54	46	46	43							
210-224	81	79	72	69	65	63	60	53	55	54	52						
225-239	81	79	72	72	66	66	63	56	52	53	49	51					
240-254	79	79	71	70	63	61	58	53	52	55	49	52	47				
270-284	80	79	70	74	68	68	66	55	58	59	55	51	46	47			
285-299	77	77	67	71	67	65	63	53	56	58	56	55	50	50	45		
300-314	78	79	68	74	69	68	66	57	59	62	57	54	49	49	42	46	

Note. Dissimmilarity values calculated by SIMPER. Color-coding represents percent dissimilarity with blue = 80-89%, green = 70-79%, yellow = 60-69%, coral = 50-59%, and pink = 40-49%.

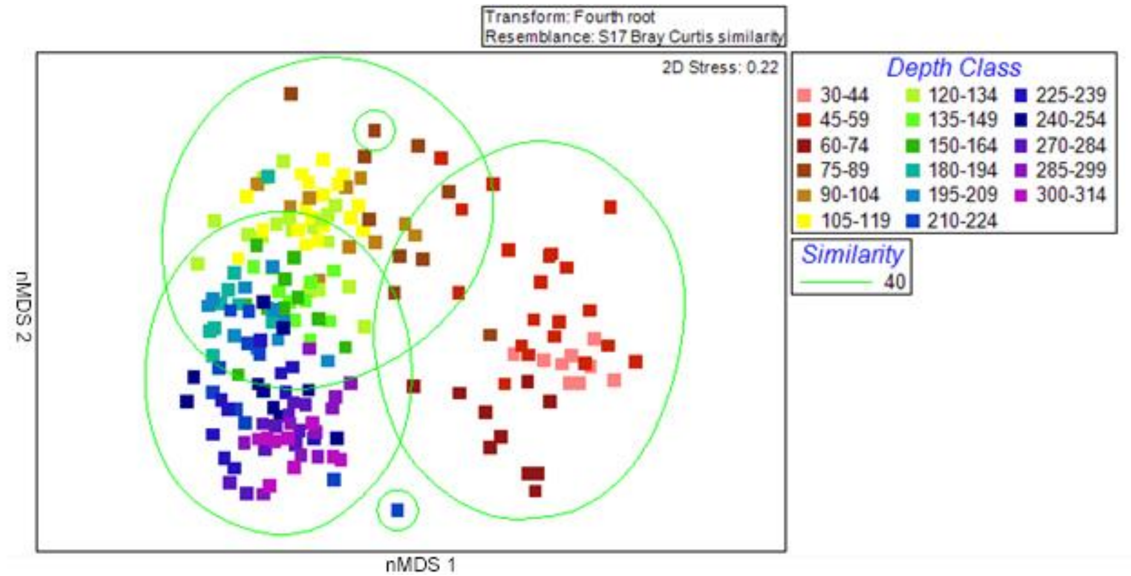


Figure 13. nMDS ordination of 195 images at Knob Point analyzed at the species level, sorted by depth in meters. Based on fourth root transformed percent cover and Bray-Curtis similarities. Green outlined similarity based on cluster analysis showing level of similarity between groups.

A SIMPER analysis revealed the contribution of faunal and substrate categories to the depth break at 75 m. Samples in the shallow groups of 30-74 m were characterized by high cover of diatomaceous film (avg. 2.58% cover at 30-44 m, avg. 2.38% cover at 45-59 m, avg. 2.69% cover at 60-74 m), fine sediment (avg. 2.23% cover at 30-44 m, avg. 2.00% cover at 45-59 m, avg. 1.32% cover at 60-74 m), and shells of the bivalve *Laternula elliptica* (avg. 1.62% cover at 30-44 m, avg. 0.78% cover at 45-59 m, avg. 1.18% cover at 60-74 m) (Appendix C, Table 2). Also relatively common at the shallower depths were the seastar *Odontaster validus* (0.61% cover at 30-44 m), hydroid *Hydrodendron arboreum* (0.85% cover at 45-59 m), sponge *Dendrilla antarctica* (0.65% cover at 45-59 m), unidentified bryozoans (1.71% cover at 60-74 m) and the polychaete *Perkinsiana* sp.(0.65% cover at 60-74 m). Samples from deeper depths had higher abundances of fauna, specifically the bryozoan *Cellaria* sp. (maximum 2.11% cover at

105-119 m depth), unknown bryozoans (maximum 2.03% cover at 300-314 m), the polychaete *Perkinsiana* sp. (maximum 1.38% cover at 180-194 m), and various species of unknown tunicates (maximum 1.09% cover of Tunicate sp. A at 180-194 m).

As depth increased at Knob Point, there were general patterns in terms of OTUs (Figure 14). Average total faunal cover changed following a unimodal pattern (r^2=0.729, p=0.0001) (Figure 5). Faunal abundance was highest at Knob Point at a depth of 180-194 m, averaging 66.5% cover, at which depth the substrate was fine sediment and the benthic community consisted primarily of bryozoans, tunicates, and demosponges. Sponges and colonial organisms were the dominant organisms at all Knob Point depths, though sponges decreased in abundance with depth. Bryozoans and other colonial invertebrates, however, increased in abundance with depth. With increasing depth, diatomaceous film growing on the substrate decreased in cover until it was entirely absent at 90 m depth. Shell as a substrate decreased with depth as well down to 240 m, at which depth it was no longer found.

With regards to functional groups, suspension feeders were found to be the dominant category at Knob Point across all depths, with no significant relationship with depth (r^2=0.12, p=0.18) (Table 17, Figure 15).

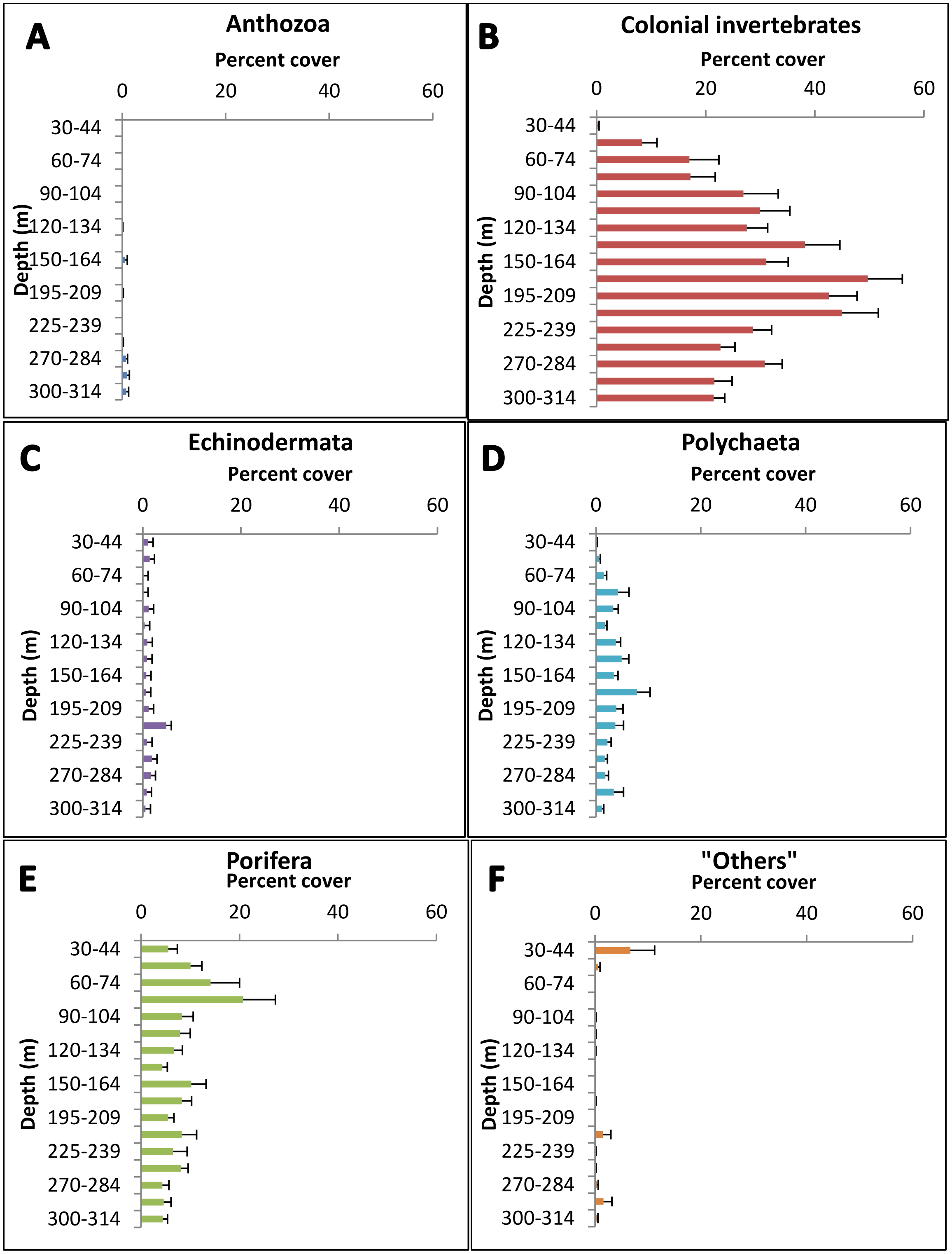


Figure 14a-f. Bar graph of mean cover and standard error of fauna at Knob Point at operational taxonomic unit (OTU) level by depth class. a.) Anthozoa, b.) colonial invertebrates, c.) Echinodermata, d.) Polychaeta, e.) Porifera, f.) “others”.

Table 17

Average Percent Cover and Standard Error for Functional Groups at Knob Point by Depth Class

Depth class (m)	Sessile predators		Suspension feeders		Mobile predators		Spongivores		Mobile grazers		Deposit feeders		Mobile scavengers	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
30-44	0	0	5.89	1.87	0.11	0.11	0	0	0	0	0.22	0.22	1.56	0.6
45-59	0	0	19.05	3.44	0.45	0.35	0.25	0.25	0.05	0.05	0.05	0.05	1.15	0.53
60-74	0	0	32.6	6.51	0.1	0.1	0	0	0	0	0	0	0	0
75-89	0	0	42.1	5.64	0	0	0	0	0	0	0	0	0.1	0.1
90-104	0	0	38.5	5.8	1.2	0.61	0	0	0	0	0	0	0.1	0.1
105-119	0	0	39.5	5.47	0.39	0.12	0	0	0.06	0.06	0	0	0.06	0.06
120-134	0	0	38.1	3.89	0.85	0.36	0.1	0.1	0.05	0.05	0	0	0.05	0.05
135-149	0	0	47.44	5.97	0.89	0.2	0	0	0	0	0	0	0	0
150-164	0	0	45.2	3.26	0.6	0.27	0	0	0	0	0	0	0.1	0.1
180-194	0	0	65.8	4.51	0.5	0.17	0.1	0.1	0	0	0	0	0.1	0.1
195-209	0	0	52.1	5.17	1.2	0.49	0	0	0	0	0	0	0	0
210-224	0	0	62.7	3.99	0.5	0.22	0	0	0	0	0	0	0	0
225-239	0	0	37.5	3.7	0.8	0.25	0	0	0	0	0	0	0.1	0.1
240-254	0	0	33.1	2.96	1.4	0.4	0.1	0.1	0	0	0	0	0	0
270-284	0	0	37.6	2.89	1.6	0.4	0	0	0	0	0	0	0.4	0.22
285-299	0.5	0.5	30	2.89	0.8	0.33	0	0	0	0	0	0	0	0
300-314	0	0	27.89	3.03	0.56	0.24	0	0	0	0	0	0	0	0

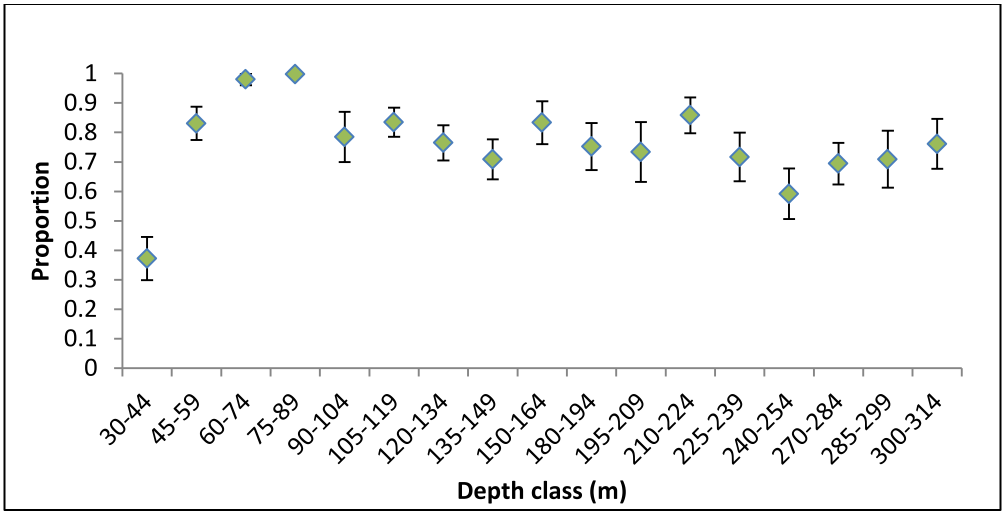


Figure 15. Scatter plot of mean proportion and standard error of suspension feeders at Knob Point by depth class.

Diversity and depth were correlated at Knob Point with regards to Shannon-Weiner indices. The Shannon-Weiner diversity index was found to change along a quadratic pattern (r^2=0.618, p<0.0001) (Figure 16). AICc model testing found neither a linear nor a quadric pattern to be a better fit with regards to species richness with depth. (ΔAICc = 1.87) (Figure 17).

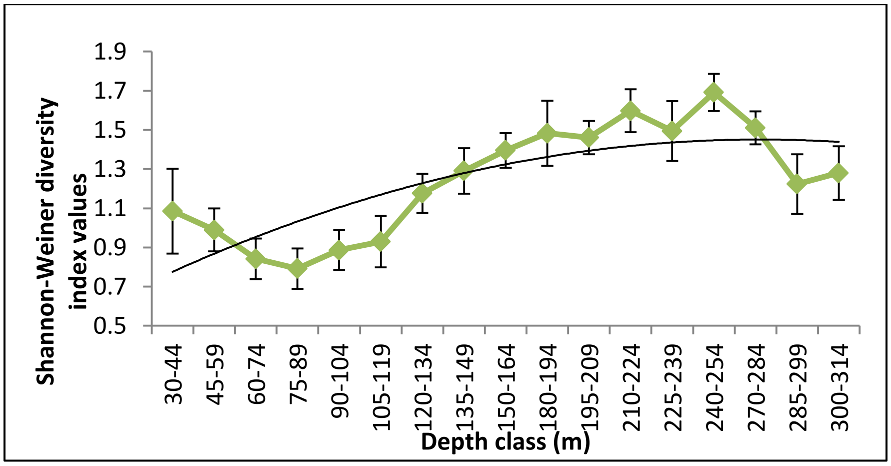


Figure 16. Shannon-Weiner diversity values and standard error by depth class at Knob Point.

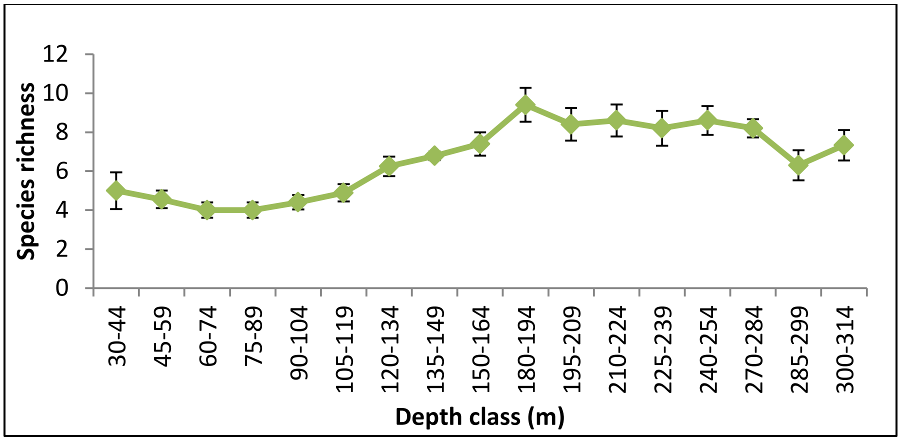


Figure 17. Species richness and standard error by depth class at Knob Point.

Cape Armitage Communities at Cape Armitage, the other site under seasonal sea ice, were found to change significantly with depth (One-way ANOSIM, R= 0.403, p=0.001).

ANOSIM pairwise comparisons found most depth strata to be significantly different from one another, except for depth classes 15-29 m and 30-44m, 15-29 m and 75-89 m, 45-59m and 60-74 m, 60-74 m and 75-89 m, and 75-89 m and 90-104 m (Appendix B, Table 3). Greatest differences in community structure were found between depths 15-29 m and 60-74 m, with a dissimilarity value of 72.71 (Table 18). This difference in community assemblage was indicated by the SIMPER analysis to be driven by a high proportion of the bryzoan *Cellaria* sp. in the deeper class (avg. 1.40% cover at 60-74 m; avg. 0.18% cover at 15-29 m) and high proportion of the sponge *Polymastia invaginata* in the shallower class (avg. 1.41% cover at 15-29 m; 0% cover at 60-74% m) (Appendix C, Table 3).

Table 18

Matrix of Dissimilarity Between Depth Bins at Cape Armitage

Depth (m)	15-29	30-44	45-59	60-74	75-89	90-104	105-119
15-29							
30-44	50						
45-59	69	54					
60-74	73	58	51				
75-89	65	58	61	62			
90-104	65	58	64	63	59		
105-119	70	55	57	57	64	57	

Note. Dissimilarity values calculated by SIMPER. Color-coding represents percent dissimilarity with green = 70-79%, yellow = 60-69%, and coral = 50-59%.

When looking at general patterns in overall faunal cover and OTUs with depth, some patterns emerge (Figure 18a-f). Total faunal cover was tested for linear and quadratic patterns with depth and was not found to have any predictable relationship (r^2=0.0696, p=0.568; r^2=0.267, p=0.537, respectively), and there was no clear pattern in the nMDS plot (Figure 19). Faunal cover had a mid-depth peak at the depth class of 45-59 m with 45.67% average cover. Colonial invertebrates were found to be the most abundant OTU, with a peak in cover at 45-59 m of 33.56% (Figure 18b). Sponges were also found to be fairly common, though sponge cover did not differ considerably with depth, staying fairly constant across all depth strata around an average of 11.16% cover (Figure 18e).

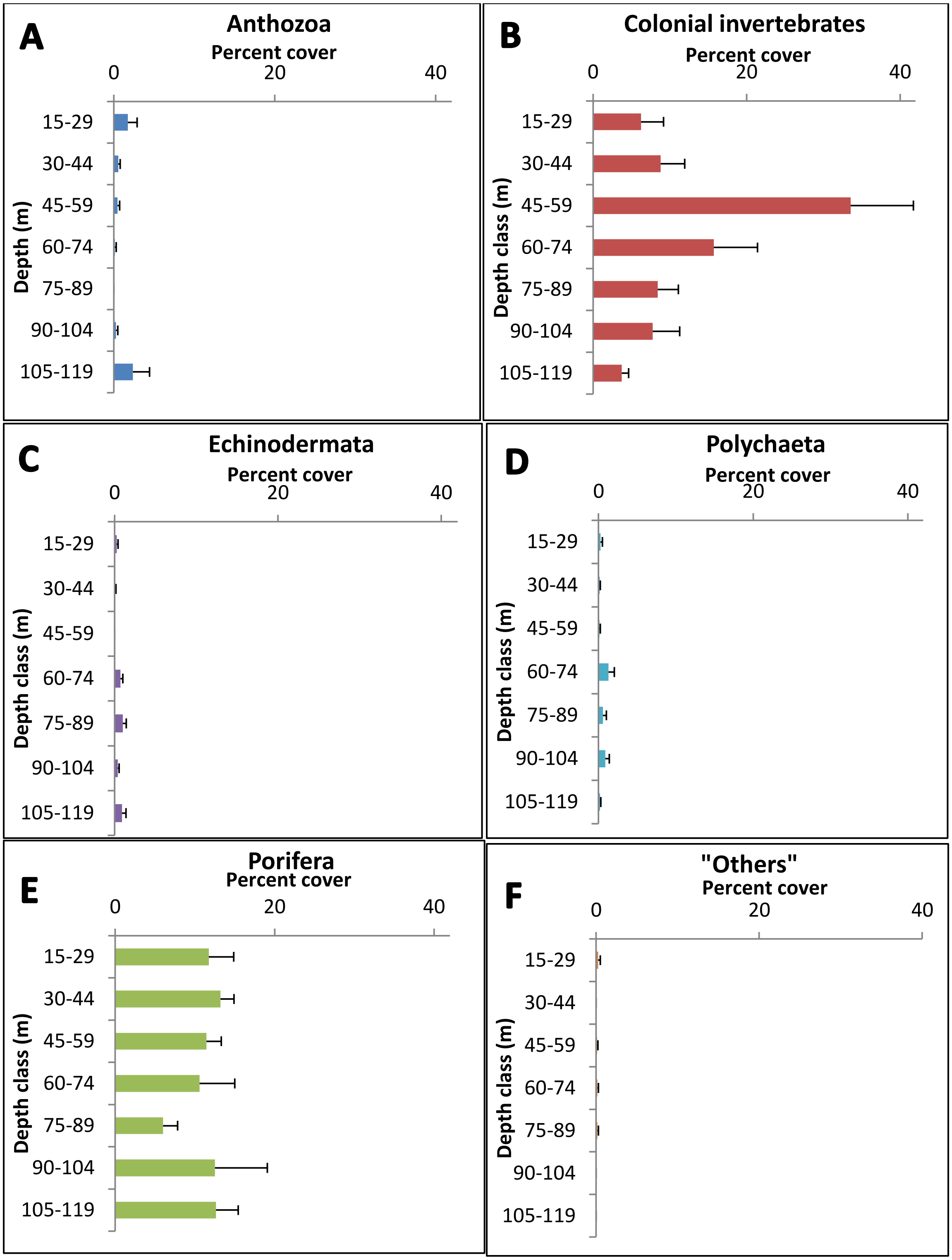


Figure 18a-f. Bar graphs of mean cover and standard error at Cape Armitage at operational taxonomic unit (OTU) level by depth class. a.) Anthozoa, b.) colonial invertebrates, c.) Echinodermata, d.) Polychaeta, e.) Porifera, f.) "others."

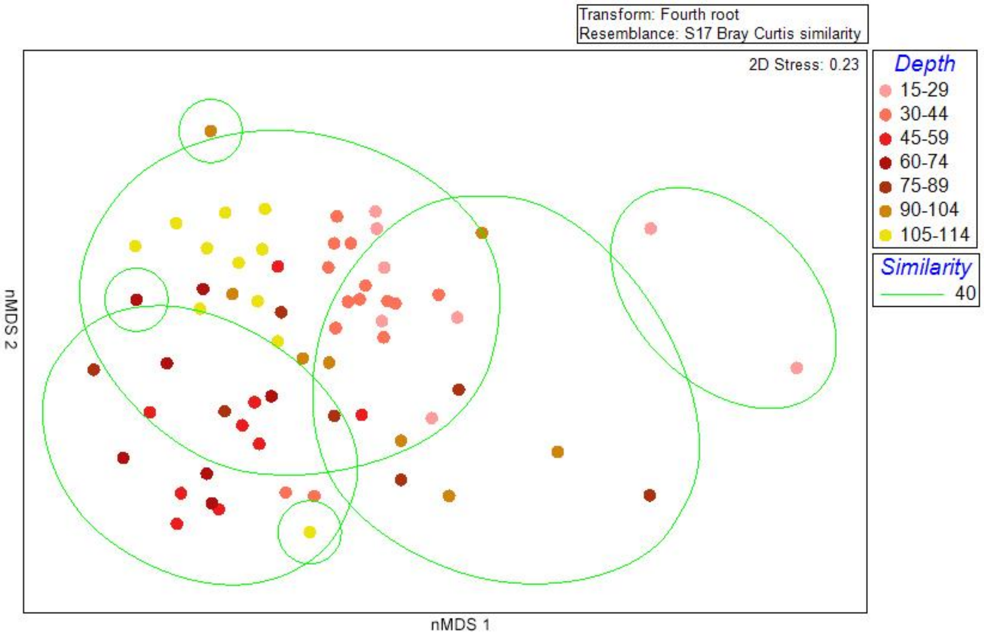


Figure 19. nMDS ordination showing 59 images at Cape Armitage analyzed at the species level, sorted by depth in meters. Based on fourth root transformed percent cover and Bray-Curtis similarities. Similarity based on cluster analysis showing level of similarity between groups.

In terms of functional groups, suspension feeders were most common at Cape Armitage, with 15% to 43% average cover and making up 86.69% to 99.27% of all living fauna throughout all depth classes (Table 19, Figure 10). No relationship was found between proportion of suspension feeders and depth (linear regression r^2=0.031, p=0.706) (Figure 20)

Table 19

Average Percent Cover and Standard Error for Functional Groups at Cape Armitage by Depth Class

Depth	Sessile predators		Suspension feeders		Mobile predators		Spongivores		Mobile grazers		Deposit feeders		Mobile scavengers	
class (m)	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
15-29	1.75	1.15	18.25	3.99	0.13	0.13	0.13	0.13	0	0	0	0	0.25	0.25
30-44	0.57	0.2	22.14	3.67	0.07	0.07	0	0	0	0	0	0	0	0
45-59	0.22	0.22	45.33	8.02	0	0	0	0	0	0	0	0	0.11	0.11
60-74	0	0	27.71	4.69	0.43	0.2	0.43	0.3	0	0	0	0	0	0
75-89	0	0	15	3.01	1	0.44	0.14	0.14	0	0	0	0	0	0
90-104	0	0	21.38	6.37	0.38	0.18	0	0	0	0	0	0	0	0
105-119	2.09	2.09	17.18	2.78	0.27	0.14	0.27	0.19	0	0	0	0	0	0

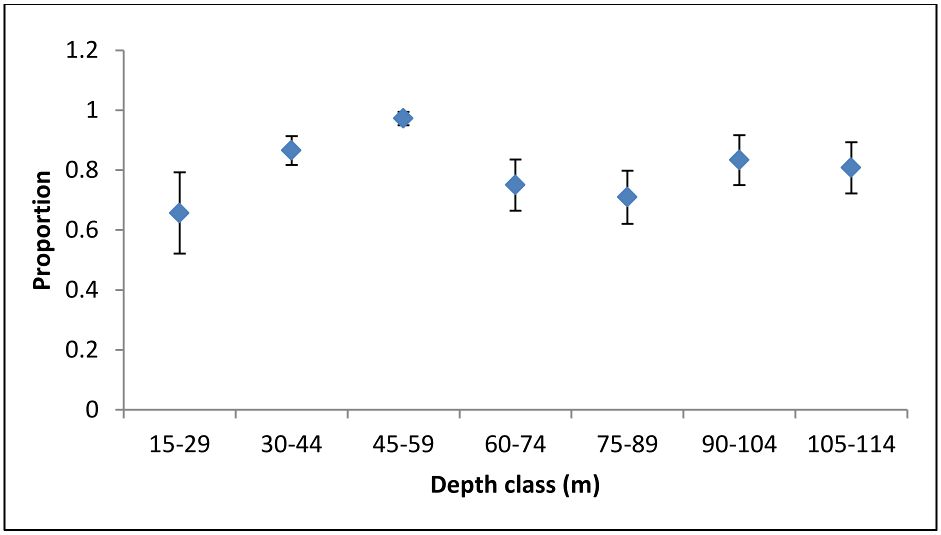


Figure 20. Proportion of suspension feeders and standard error with depth at Cape Armitage.

Diversity was not found to have any correlation with depth at Cape Armitage (Table 20) (Shannon-Wiener index $r^2 = 0.036$, $p = 0.68$; Species richness $r^2 = 0.000083$, $p = 0.98$), however lower image resolution at this site potentially impeded precise species designations, and diversity values may not be accurate.

Table 20

Average and Standard Error of Shannon-Wiener Index and Species Richness Values by Depth Class at Cape Armitage

Depth class (m)	Shannon-Weiner		Species richness	
	M	SE	M	SE
15-29	1.06	0.20	4.13	0.81
30-44	1.30	0.05	4.86	0.21
45-59	1.16	0.10	5.33	0.33
60-74	1.35	0.25	6.29	0.92
75-89	1.24	0.04	4.29	0.18
90-104	1.05	0.14	4.25	0.45
105-119	1.29	0.11	4.91	0.50

Sea Ice and Ice Shelf Comparisons

An nMDS plot at the OTU level showed that sites grouped fairly well with regards to type of ice cover, that is “ice shelf” or “sea ice” (Figure 21). A reduced PERMANOVA at depths that co-occurred at the sites Knob Point, Becker Point, and Cape Armitage, 30-119 m, showed that abundances were different between sites and depth classes, but a significant interaction term was still present (Table 21). Because of the interaction term of “Site x Depth” identified in the PERMANOVA analysis, sites could not be grouped by types of ice cover and rather, each site and depth class were compared individually in co-occurring depth zones to assess whether abundance of species, species diversity, and proportion of suspension feeders varied across type of ice cover. Knob Point, Becker Point, and Cape Armitage all were sampled at depths of 30-119 m, and these depths were used to compare these three sites. The narrow depth interval present at Heald Island, 180-209 m, was also sampled at Knob Point, and these depths and sites were compared as well. P-values were adjusted for multiple comparisons using sequential Bonferroni corrections by six for Knob Point, Becker Point, and Cape Armitage comparisons, and by two for Heald Island and Knob Point comparisons.

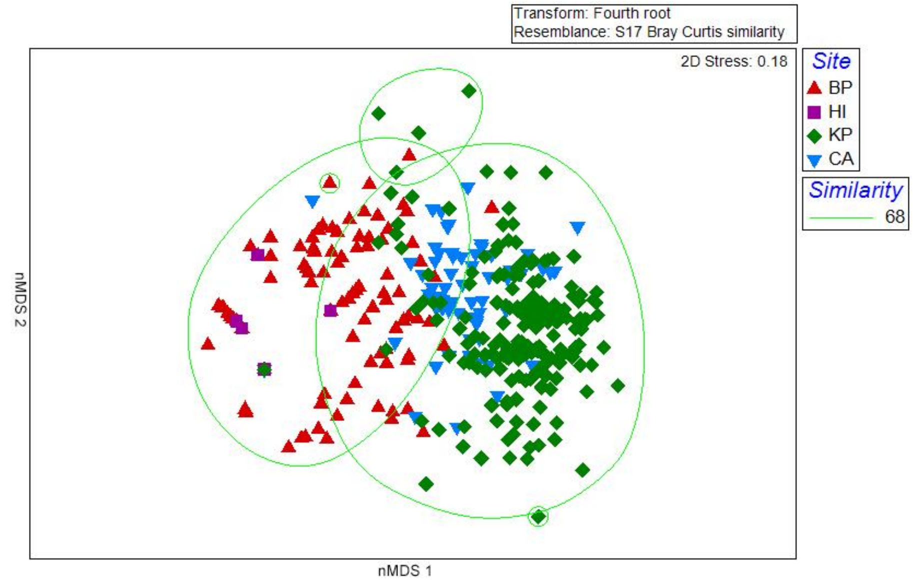


Figure 21. nMDS ordination of all 448 images analyzed at the operational taxonomic unit level, sorted by site. Based on fourth root transformed percent cover and Bray-Curtis similarities. Dark red triangles represent Becker Point, purple squares represent Heald Island, green diamonds represent Knob Point, blue triangles represent Cape Armitage. Warm colors represent ice shelf and cool colors represent seasonal sea ice. Similarity based on cluster analysis showing level of similarity between groups.

Table 21

Permutational Multivariate Analyses of Variance (PERMANOVA) of the Effects of Two Crossed, Fixed Factors, Depth and Site, on the Transformed Abundance Community Data

Source	df	SS	MS	Pseudo-F	P(perm)	Perms
Depth	5	5428.6	1085.7	0.491	0.841	998
Ice cover	1	45540	45540	21.316	0.001*	3
Site (Ice cover)	1	1507.1	1507.1	4.990	0.005*	999
Depth x Ice Cover	5	3364.6	672.93	0.324	0.979	999
Depth x Site (Ice Cover)	5	8697.6	1739.5	5.76	0.001*	999
Res	240	72480	302			
Total	257	1.41E+05				

Note. Data were tested at the OTU level, with six levels of depth, 30-44 m, 45- 59 m, 60-74 m, 75-89 m, 90-104 m, and 105-119 m, and three levels of site, Knob Point, Cape Armitage, and Becker Point. Site was nested in ice cover (seasonal sea ice or ice shelf). df = degrees of freedom, SS = sum of squares, MS = mean squares, Pseudo-F = the pseudo F-value, P(perm) = the permutational probability value, and Perms = the number of permutations of residuals carried out. *p < 0.05.

Results from one-way nested ANOVAs indicated that total faunal cover was significantly different at sites under sea ice than under ice shelf at each of the six co-occurring depth zones at sites Knob Point, Cape Armitage, and Becker Point (Table 22). Comparison of the means of total cover between the sea ice and ice shelf samples shows that total cover was consistently higher under sea ice (Table 23).

Table 22

Summary of One-Way Nested ANOVAs Testing Differences in Total Faunal Cover at Co-Occurring Depths at Knob Point, Cape Armitage, and Becker Point

Depth class (m)	df	SS	F-ratio	p-value	Bonferroni adjusted p-value
30-44	1	3038.8869	16.0128	0.0004	0.0004*
45-59	1	11384.161	62.8695	<.0001	0.0006*
60-74	1	8648.1304	94.9803	<.0001	0.0005*
75-89	1	6367.5277	78.6830	<.0001	0.0004*
90-104	1	4860.1633	24.6191	<.0001	0.0003*
105-119	1	7512.6132	33.1956	<.0001	0.0002*

Note. Sequential Bonferroni adjusted p-values reflect a correction of 6. *p < 0.05.

Table 23

Means and Standard Errors of Total Cover of Sea Ice and Ice Shelf Sites at Co-Occurring Depth Strata at Knob Point, Cape Armitage, and Becker Point from One-Way Nested ANOVAs

	Under sea ice		Under ice shelf	
Depth class (m)	M	SE	M	SE
30-44	22.43	2.94	1.30	0.44
45-59	30.97	2.70	2.95	0.79
60-74	33.65	2.35	4.37	0.59
75-89	31.47	2.22	4.70	0.64
90-104	31.78	3.33	6.33	1.81
105-119	32.34	2.88	4.40	1.04

At the deeper depth intervals, 180-194 m and 195-209 m, results from two two-sample t-tests showed that the two sites, Heald Island and Knob Point, were significantly different with regards to total faunal cover (Table 24). Tukey post-hoc analysis revealed that the percent cover at Heald Island was significantly lower than that of Knob Point (p=<0.001) (Table 25).

Table 24

Summary of T-Tests Testing Differences in Total Faunal Cover at Co-Occurring Depths at Knob Point and Heald Island

Depth class (m)	df	t-ratio	p-value	Bonferroni adjusted p-value
180-194	9.053	14.447	<0.0001	0.002*
195-209	9.000	10.283	<0.0001	0.001*

Note. Sequential Bonferroni adjusted p-values reflect a correction of 2. *p < 0.05.

Table 25

Mean Percent Cover and Standard Error at Heald Island and Knob Point at Co-Occurring Depth Classes

Depth class (m)	Site	Mean total cover	SE
180-194	Heald Island	1.0	0.246
180-194	Knob Point	66.5	4.527
195-209	Heald Island	0.0	0.000
195-209	Knob Point	53.3	5.183

Species richness and Shannon-Wiener diversity indices were calculated for Knob Point (sea ice) and Becker Point (ice shelf) within each depth class, and depth classes were compared to examine the difference in diversity of communities under ice shelf and under sea ice. Only these two sites were used because the resolution of images at these sites was much higher, and designations to species were rarely made at sites Heald Island and Cape Armitage. Results from a series of two-sample t-tests showed that the sites Becker Point and Knob Point were significantly different with regards to species richness at each of the six depth classes (Table 26), as well as at three of the six depth classes with regards to Shannon-Weiner diversity indices (Table 27). Tukey post-hoc analysis showed diversity indices to be greater at Knob Point than at Becker Point at each of the significantly different depth strata (p<0.001).

Table 26

Summary of Two-Sample T-Tests Testing Differences in Species Richness at Co-Occurring Depths at Knob Point and Becker Point

Depth class (m)	t-ratio	df	p-value	Bonferroni adjusted p-value
30-44	4.307	9.12	0.0019	0.0038*
45-59	6.192	29.035	<0.0001	0.0006*
60-74	4.492	15.148	0.0004	0.0016*
75-89	3.622	17.126	0.0021	0.0021*
90-104	3.774	22.755	0.0010	0.0030*
105-119	5.774	28.478	<0.0001	0.0005*

Note. Sequential Bonferroni adjusted p-values reflect a correction of six. *p < 0.05.

Table 27

Summary of Two-Sample T-Tests Testing Differences in Shannon-Weiner Diversity Indices at Co-Occurring Depths at Knob Point and Becker Point

Depth class (m)	t-ratio	df	p-value	Bonferroni adjusted p-value
30-44	4.062	10.631	0.0020	0.0100*
45-59	4.809	35.934	<.0001	0.0006*
60-74	2.334	23.296	0.0286	0.0858
75-89	1.215	25.356	0.2360	0.2360
90-104	2.294	22.845	0.0313	0.0626
105-119	2.727	31.359	0.0104	0.0416*

Note. Sequential Bonferroni adjusted p-values reflect a correction of six. *p < 0.05.

To test differences in proportions of suspension feeders among types of ice cover, a series of one-way ANOVAs was conducted, with site nested in type of ice cover. Only at two of six depth strata was the proportion of suspension feeders different at sites nested in ice cover type (Table 28). Comparing the means at these depth strata, 90-104 m and

105-119 m, shows the proportion of suspension feeders was significantly higher under sea ice than under ice shelves (p=0.0064, p=0.0001) (Table 29).

Table 28

Summary of One-Way Nested ANOVAs Testing Differences in the Proportion of Suspension Feeders at Co-Occurring Depths at Knob Point, Cape Armitage, and Becker Point

Depth class (m)	df	SS	F	p-value	Bonferroni adjusted p-value
30-44	1	0.0639	0.7158	0.4060	0.4060
45-59	1	0.647	7.3197	0.0100	0.0300*
60-74	1	0.712	7.6571	0.0084	0.0336*
75-89	1	0.386	3.7633	0.0590	0.1180
90-104	1	0.870	8.7228	0.0064	0.0320*
105-119	1	1.698	18.048	0.0001	0.0006*

Note. Sequential Bonferroni adjusted p-values reflect a correction of 6. *p < 0.05.

Table 29

Means and Standard Errosr of the Proportion of Suspension Feeders under Sea Ice and Ice Shelf Sites at Co-Occurring Depth Strata at Knob Point, Cape Armitage, and Becker Point from One-Way Nested ANOVAs

	Under sea ice		Under ice shelf	
Depth class (m)	M	SE	M	SE
30-44	0.70	0.070	0.50	0.12
45-59	0.88	0.06	0.64	0.08
60-74	0.89	0.08	0.60	0.06
75-89	0.88	0.08	0.66	0.06
90-104	0.81	0.07	0.46	0.09
105-119	0.82	0.06	0.42	0.07

Sites Heald Island and Knob Point could only be compared at the depth interval of 180-194 m with regards to proportion of suspension feeders because living fauna was only found at that single depth zone at Heald Island. There was not found to be any significant difference in the proportion of suspension feeders at the two sites in this depth class ((t_{16}) = 0.769, p = 0.452).

Discussion

Comparing Benthic Communities to Previous Studies and Extending Known Zonation

When comparing present benthic assemblages along a depth gradient to those described by Dayton et al. (1970, 1974), communities at comparable depth strata were similar but had experienced change over time. At Cape Armitage, changes in substrate composition along the depth gradient were consistent with Dayton's findings, with the zone between 15-29 m having a primarily cobble substratum, and the subsequent zone of 30-60 m having a dominant substrate of spicule mat and bivalve shells. In the present study, the substrate of spicule mat was found to extend to the deepest depth class surveyed, 105-199 m, with a higher proportion of bivalve shells mixed in at shallower depths. At the depth class of 15-29 m, where Dayton studies had found almost exclusively coelenterates, specifically anemones and octocorals, with "a few clumps of sponges" (Dayton et al., 1970), the benthos of the present study was dominated by sponges. Anemones were present, though low in abundance compared to sponges and colonial invertebrates. Octocorals were absent in this depth class. It is possible that anchor ice has removed the coelenterates over time and sponges have recruited in their place (Dayton et al., 2013; Dayton et al., 2016). In Dayton's depth class of 30-60 m, sponges dominated the community, and actinarians and asteroids were also common. (Dayton et al., 1974) Whereas sponges were common in the present study, actinarians and asteroids were fairly rare. In the present study, colonial invertebrates and sponges were most common at all depth classes, with little clear zonation. On the whole, differences in community composition appeared to be continuous rather than discrete, in contrast to the findings of Dayton et al. (1970, 1974).

Surveying at Knob Point began at 30 m, effectively picking up in the zone where Dayton et al. (1970, 1974) left off. The epifaunal community at Knob Point was similar to that described by Dayton et al. (1970, 1974) in that it was dominated by sponges, most commonly *Dendrilla antarctica, Polymastia invaginata*, and *Rosella podagrosa*. However, the anemones found in studies by Dayton et al. (1970, 1974) were largely absent in comparable depth zones of the current study. Also found in this depth strata in the present study were the seastar *Odontaster validus,* the hydroid *Hydrodendron arboretum,* unidentified bryozoans, and the polychaete *Perkinsiana* sp. Slightly deeper at 75 m, there appeared to be another break in community structure, beyond which point the community was dominated by bryozoans such as *Cellaria* sp, the polychaete *Perkinsiana* sp., various species of tunicates, and sponges. As depth increased, the proportion of colonial invertebrates increased, though gradually as opposed to in discrete bands of community change.

One possible explanation for these changes in community assemblages over time is a change in plankton composition due to a series of large grounded icebergs in the southwestern Ross Sea in the early-to-mid 2000s (Dayton et al., 2016; Thrush & Cummings, 2011). The icebergs, present for nearly a decade, blocked currents and interfered with the growth of the large phytoplankters that are typically advected from the north, reducing primary production in the southwestern Ross Sea by 40-95% compared to previous years (Arrigo et al., 2002; Thrush & Cummings, 2011). It is likely that this sudden reduction of primary production reaching the seafloor changed the benthic communities in the time between the Dayton studies (1970, 1974) and the present study (2008, 2009), as was observed in a nearby benthic study over a large time-scale (Dayton et al., 2013). A large-scale shift in community structure was observed in a nearby infaunal study as well, hypothesized to be due to the changes in sea-ice regime and phytoplankton transport by the same grounded icebergs (Conlan et al., 2010). These changes would explain the increase in suspension feeders over time; the high proportion of sponges found at the sites under sea ice are known to specialize on consuming very small plankton (Bell 2008), in contrast to the other taxa that were missing (i.e. actinians, asteroids) and that feed by direct predation. Furthermore, Antarctic sponges are known to have extremely episodic recruitment, with decades of little recruitment or growth at a time, as was observed by Dayton et al. (2016) during the 1960s through the mid-1990s. It is possible that other fauna such as actinians and asteroids are currently experiencing large scale shifts in recruitment, as has been observed in Antarctic sponges.

Faunal abundance was highest at Knob Point at a depth of 180-194 m, which appeared to be a zone of optimal distributions for multiple species. In this zone, sponges were decreasing in abundance but were still relatively common, and colonial organisms were beginning to increase to a greater abundance, resulting in overall higher cover of living fauna in general. Between 210-314 m, the benthic communities at Knob Point more closely resemble those of Becker Point than they do the shallower communities at Knob Point (Figure 4). It is possible that at these depths, the communities at Knob Point are increasingly food-limited, thus resembling assemblages under an ice shelf.

Under the ice shelf, community assemblages in the present study were comparable to those under the Amery Ice Shelf described by Riddle et al. (2007) at over 700 m depth. Various species of sponges, hydroids, polychaetes, echinoids, bryozoans, a bivalve, a gastropod, a holothurian, and a solitary tunicate were identified in the Riddle et al. (2007) study, all of which, except the gastropod and holothurian, were found at Becker Point in the present study. Many of the fauna described by Riddle et al. (2007) were only identified to higher taxonomic levels, though several taxa of sponges, polychaetes, and bivalves were identified to the genus and species level, and matched those found in the present study. In addition, anemones, soft corals, ophiuroids, and a chiton were present at Becker Point. The similarity between the community described here under the McMurdo Ice Shelf and that described by Riddle et al. (2007) under the Amery Ice Shelf can be attributed to Antarctic Circumpolar Current (ACC) and the Polar Front, which physically and thermally isolate Antarctic biota and contribute to the high endemism seen in marine Antarctic fauna (Arntz et al., 1994). Though it was unclear what proportion of the fauna were suspension feeders in the Riddle et al. (2007) study, they were found to dominate the community. In the present study under the McMurdo Ice Shelf at Becker Point, suspension feeders and sessile predators were both found to be common, with suspension feeders decreasing proportionally with depth, and sessile predators increasing proportionally with depth.

Differences in Community Structure with Depth

The abundance of fauna was expected to decrease with depth, and this prediction was partially supported, with the relationship generally found to be unimodal rather than linear. At two of the three sites exhibiting depth gradients, Knob Point and Becker Point, abundance followed a unimodal distribution with depth, with a peak in the cover of sessile invertebrates at Knob Point at 180-194 m depth and at Becker Point at 90-104 m. Abundances at Cape Armitage followed a similar trend, with abundance peaking at 45-59 m, though this was not of statistical significance. Species richness and Shannon-Weiner diversity followed a similar pattern though at slightly different depths, with quadratic distributions peaking at 75-89 m depth at Becker Point, and at 240-254 m depth at Knob Point for Shannon-Weiner index values. Species richness at Knob Point followed a unimodal trend, though AICc models were not significantly different in comparison to a linear model. Cape Armitage was not tested for species diversity because identifications were usually to higher taxonomic levels. Maximum total faunal cover varied in depth from site to site, but at all sites with depth gradients mid-depth peaks in cover were observed (two of three of statistical significance). The most dramatic patterns with depth were found at Knob Point, at which the greatest range of depths was sampled. It is possible that if depth ranges were extended in either direction at the other three sites, patterns in faunal cover would be strengthened.

These data imply that there are limitations for seafloor fauna on both the shallow and deep ends of the sampled ranges. A possible explanation for the observed lower abundance and diversity at shallow depths at the sites under seasonal ice is the inverse relationship of depth and frequency of ice disturbance. Though iceberg scours occur most commonly in shallow depths, scours have been found as deep as 500 m and have the potential to significantly reduce species abundances and diversity (Collins, 2015;

Dowdeswell et al., 1993). Reduced frequencies and intensities of physical disturbance at greater depths likely facilitate larger populations of sessile fauna such as bryozoans and other colonial organisms, which then increase habitat complexity and provide more space for epifaunal organisms (Dayton et al., 1974; Gutt, 2000). In contrast, the low organismal abundances observed at the greatest depths could be explained by food limitation. Benthic fauna are known to decrease in abundance with depth as a result of decreased particulate organic carbon, which they require for survival (Gage & Tyler, 1991; Gibson et al., 2005). Whereas diversity is often found to increase with depth as you move from the shelf to intermediate depths in many parts of the world's oceans (Rex et al., 1997), this is not thought to be the case in the Antarctic (Jones et al., 2007). Heavy ice impact during the last glacial maximum eradicated benthic shelf fauna, and the continental shelf was subsequently recolonized by deep-water organisms (Thatje et al., 2005).

At the sites under sea ice, mid-depth peaks in total cover occur at different depths, 45-59 m at Cape Armitage and 180-194 m at Knob Point (Figure 5). This difference in depth of peak cover could be due to the fact that Knob Point is more exposed to icebergs so disturbance may extend deeper, as well as slightly closer to productive open water than Cape Armitage. The difference in the depths of diversity peaks under sea ice at Knob Point (240-254 m) and under the ice shelf at Becker Point (75-89 m) could be due to differences in food availability. Diversity is known to increase with greater food availability (Chase, 2010; Tittensor et al., 2010), and the absolute amount of food available at Becker Point is lower than that at the same depths at Knob Point due to advection over a greater distance. Interestingly, Becker Point, a site under the ice shelf that is shielded from icebergs, exhibits a relatively deep (90-104 m) mid-depth peak in faunal cover despite low food availability. This could be due to under-ice currents concentrating food at this depth stratum. Further work on seafloor bathymetry and under-ice currents could elucidate the observed differences in peaks of abundance and diversity.

The proportion of suspension feeders was predicted to increase with depth, but this was never found at a statistically significant level. Knob Point was the only site with a trend of suspension feeders increasing proportionally with depth, though results were not significant (r^2=0.116, p=0.181). At Becker Point the proportion of suspension feeders dropped from 80% of the total faunal cover at 15-29 m to 29% at 135-149 m, and at Cape Armitage the proportion of suspension feeders was not found to have any relationship with depth (r^2=0.031, p=0.706). Rather, sessile predators, namely several species of anemones, were found to dominate under the ice shelf with abundance increasing with depth to a maximum of 61.56% of the fauna (2.6% total cover) at 90-104 m at Becker Point. In the past, the predatory anemones have been known to feed primarily on species of urchins, sea stars, and jellies (Amsler et al., 1999; Brueggeman, 1998; Dayton et al., 1970). However, Antarctic anemones are known to inhabit unique Antarctic habitats such as burrowed in sea ice (Daly et al., 2013) and are able to change feeding strategy when necessary (Orejas et al., 2001). This feeding plasticity may make them better adapted to habitats under an ice shelf, catching larger prey items when available and utilizing suspension feeding otherwise.

Differences in Community Structure between Types of Ice Cover

The benthic assemblages under the ice shelf, described here for the first time, were generally depauperate compared to sites under seasonal sea ice at the same depths. Populations at Knob Point and Cape Armitage, the sites under sea ice, were an order of magnitude more abundant and considerably more diverse than those under the ice shelf (Table 30, Table 31). This is consistent with the premise that communities at Becker Point and Heald Island do not have an *in situ* food source, only having access to primary production that is laterally advected under the ice shelf from nearly 100 km away, and thus are food limited, as opposed to Knob Point and Cape Armitage, where communities have access to local primary production during times of open water and are much closer to the ice edge otherwise.

The assumption of minimal *in situ* productivity at Becker Point and Heald Island is supported by measurements made by Dayton et al. (1986). They estimated *in situ* primary productivity at several sites in McMurdo Sound, including three of the sites in the present study: Knob Point (Cinder Cones in Dayton), Cape Armitage, and Heald Island. Measurements were also made at Garwood Valley, a site only 2.4 km away from Becker Point (Table 32). Estimates were made in chl α mg/m^2, which was used as a proxy for productivity. The chl α mg/m^2 values are four orders of magnitude greater at sites under the sea ice. These measured productivity values generally tally with the overall abundance (for the case of sea ice sites) or sparseness (in ice shelf sites) in benthic communities described. When using physical distance from the ice edge as a numerical proxy for *in situ* primary productivity, we see total faunal cover reflects the food availability (Table 30, Table 31).

Table 30

Distance from Open Water, Average Total Percent Cover, and Standard Error at Depth Classes that Occur at Becker Point, Knob Point, and Cape Armitage

		Total % cover	
Site	Distance from open water (km)	M	SE
Knob Point	52.9	31.56%	2.13%
Cape Armitage	59.7	25.78%	2.50%
Becker Point	91.6	4.01%	0.37%

Note. Distance from open water is distance to edge of sea ice. Co-occuring depth classes are 30-119 m.

Table 31

Distance from Open Water, Average Total Percent Cover, and Standard Error at Depth Classes that Occur at Heald Island and Knob Point

		Total % cover	
Site	Distance from open water (km)	M	SE
Knob Point	52.9	59.90%	2.83%
Heald Island	98.7	0.50%	0.50%

Note. Distance from open water is distance to edge of sea ice. Co-occuring depth classes are 180-209 m.

Table 32

In Situ Primary Productivity Values and Distance from Ice Edge

Site	Distance from ice edge in km	chl α mg/m^2
Knob Point	52.9	241-360
Cape Armitage	59.7	265-960
Garwood Valley[a]	91.6	0.02
Heald Island	98.7	0

Note. In situ primary productivity values in chl α mg/m^2 as measured by Dayton et al. (1986).

[a] Garwood Valley is 2.4 km from Becker Point

The differences in current patterns between the eastern and western coasts of McMurdo Sound further exacerbate the differences seen in the structure of the benthic communities due to types of ice cover. Cape Armitage and Knob Point lie on the eastern coast of McMurdo Sound, and are bathed by plankton-rich water in the summer. This coast, dominated by sponges (Dayton et al., 1970; 1974), is known to have high species diversity and abundance in shallow water. Conversely, the west coast of the McMurdo Sound is bathed year-round by plankton-poor water from under the ice shelf, where sites Becker Point and Heald Island lie, and has been found to have much less abundant and diverse benthic communities (Dayton et al., 1986).

Sites under the sea ice differed from those under the ice shelf in terms of dominant fauna. Under the ice shelf at Becker Point, budding sponges and the anemone *Artemidactis vitrix* were most common, as were unidentified species of sea whips and anemones at Heald Island. At both these sites, suspension feeders were the dominant functional group, followed closely by sessile predators. The high abundance of anemones under the ice shelf could be explained by the range of feeding strategies exhibited by anemones, namely capturing solid food, absorbing dissolved organic matter, and using assimilates of symbiotic algae (Schlichter, 1978). In this case where algae are not present, it is possible that there are symbioses occurring with other taxa such as bacteria or microbes, as has been described in marine invertebrates of nearly all phyla, but most commonly in sponges (Imhoff & Stöhr, 2003; Webster et al., 2008; Webster & Taylor, 2012). Though Antarctic anemones are typically described as predatory, they could be exhibiting feeding type plasticity or utilizing these feeding strategies simultaneously, as is likely the case in a newly described species of anemone that lives burrowed in the sea ice (Daly et al., 2013), making them well suited for the sparsely populated sub-ice-shelf sea floor. Under the sea ice at Knob Point, suspension feeders such as bryozoans and the sabellid polychaete *Perkinsiana* sp. were most common, as were bryozoans and demosponges at Cape Armitage. Antarctic bryozoans are varied in their suspension feeding, from feeding year-round at a low metabolic cost to an intensely seasonal feeding strategy consisting of a brief period of activity and growth, both well suited to the Antarctic seafloor (Barnes, 1995b). Furthermore, erect Antarctic bryozoans, are known to reproduce asexually via fragmentation in addition to sexually, making them able to spread in cover relatively quickly (Barnes, 1995b; Winston, 1983). *Perkinsiana* sp., common at Knob Point, is a large polychaete with a big tentacular crown, unlikely to have its feeding apparatus clogged by suspended matter, as is a common occurrence in smaller sabellids and filter feeders. This adaptation perhaps in part explains *Perkinsiana* sp.'s dominance on the Ross Sea benthos (Pabis & Sicienski, 2010).

Substrate was found to vary depending on type of ice cover. Knob Point and Cape Armitage, the sites under seasonal sea ice, were characterized by primarily a fine substrate, but both had relatively high abundances of spicule mat, shell, and a diatomaceous film. This largely biogenic substrate indicates that the conditions at these sites under the fast ice have been similar to the current conditions long enough for the present substrate to form. Specifically, siliceous spicules experience little degradation over time, and spicule mats build up where numerous sponges have lived and died. (Cattaneo-Vietti et al., 2000b). In contrast, the substrate at Becker Point was characterized by fine sediment, gravel, and scattered echinoderm ossicles, with a diatom film growing on the fine sediment in shallow depths of 30-44 m. Echinoderm ossicles in the substrate are consistent with the fairly low but present abundances of ophiuroids and asteroids at Becker Point. At Heald Island, the substrate was almost exclusively fine sediment. Aside from the scattered echinoderm ossicles and diatom film at shallow depths, these primarily geologic substrates are a reflection of the low-food conditions at these sites, and suggest that these communities have been low in biomass for a long time.

Suggestions for Improvement with SCINI

Because of the inherent difficulty of working under thick ice, few studies have examined life on the seafloor under ice shelves. The narrow torpedo shape of SCINI makes it ideal for putting it through a small ice hole to survey the underlying seafloor. However, despite its small size and ease of control, slight modifications could improve future ROV data collection. I would recommend using the downward-facing camera strictly for data analysis and using the forward-facing camera for navigation. Using forward-facing images in the analysis for two sites in the present study may have introduced biases, as images were on an angle and precise image area was impossible to determine. Furthermore, lighting with the forward-facing camera was inconsistent, and images had to be cropped at different sizes. Along those lines, the ROV was flown at inconsistent heights, resulting in images of varying areas from both cameras. Automation that kept the ROV flying at a consistent height using the distance of the lasers would be an ideal solution to this problem.

Climate Change in the Ross Sea

While some parts of the Antarctic region have been suffering rapid change due to changing climate patterns, other areas have as of yet been minimally affected. Surface temperature trends on the West Antarctic Peninsula (WAP) are on par with rates of increase recorded in the Arctic, and two long-standing ice shelves off the coast of the WAP have collapsed in the past 20 years (Turner et al., 2009). Much like melting ice sheets in the Arctic, collapse of Antarctic ice shelves opens the marine ecosystem to new species and rapid change. To a lesser degree, surface temperatures in West Antarctica have been steadily increasing over the past 50 years (Turner et al., 2009). Large climate patterns such as El Nino-Southern Oscillation and the Southern Annual Mode have varying effects around Antarctica and in contrast to the West Antarctic, the Ross Sea has experienced decreases in surface temperature and increases in sea ice extent. However, this regional cooling is not expected to last, and models predict that if greenhouse gas concentrations continue to increase at the current rate, one third of Antarctica’s sea ice will be lost within the next century (Turner et al., 2009). Because ice cover in the Ross Sea region has not yet been adversely affected by these large climate patterns, there is a brief window of opportunity to study the marine environment in an undisturbed state, establishing a baseline against which future changes can be evaluated. The present study has provided the first descriptions of under ice shelf communities in this region, in addition to extending the previously known zonation of the sub-sea ice Ross Sea benthos—a significant contribution to building the baseline. Further studies of benthic communities in the Ross Sea now can help us understand the ecosystems of which these fauna are a part before potentially devastating changes in sea ice cover and duration or ice shelf collapse permanently alter these communities.

Conclusions

Overall, several patterns were seen over multiple environmental gradients in Antarctic benthic communities. Species abundance typically exhibited a unimodal distribution with depth, which did not agree with the predicted decrease with depth (Table 33, Table 34). The observed unimodal distribution reflects limitations on both ends of the depth range. At the deep end, food availability, as predicted, appears to be the limiting factor. At the shallow end of the depth range the limiting factor is not clear, but physical stability is one possibility, specifically increased ice disturbance in the shallowest ranges or less consistency in conditions. Further sampling in both directions could help elucidate these community drivers.

Diversity varied from site to site in regards to patterns with depth. Shannon-Wiener index values followed a quadratic pattern at Becker Point and Knob Point, and no observable pattern at Cape Armitage. This initial increase of diversity with depth at two of the sites could be due to increased habitat complexity with depth, driven by sessile branching colonial fauna creating more complex substrate for other fauna to attach to, creating somewhat of a feedback loop. Shallow depths were largely found to have bare substrates of fine sediment or spicule mat, sometimes with a diatomaceous film growing atop the substrate, but as depth increased various species of colonial invertebrates were found to be growing in a mass atop each other. Making collections of these fauna would aid in making proper species designations and thus more accurate diversity measurements to better understand the true patterns in diversity under ice.

Table 33

Summary Table of Relationships of Abundance, Diversity, and Proportion of Suspension Feeders with Depth by Site, ΔAICc, r^2 Values, and P-Values

	Becker Point				Knob Point				Cape Armitage			
Factor	Best-fit relationship	ΔAICc	r^2	p-value	Best-fit relationship	ΔAICc	r^2	p-value	Best-fit relationship	ΔAICc	r^2	p-value
Abundance	Quadratic	11.71	0.95	0.0008*	Quadratic	3.96	0.729	0.0001*	Linear	12.33	0.0696	0.57
Shannon-Weiner index	Quadratic	8.73	0.838	0.0043*	Quadratic	3.88	0.618	<0.0001*	Linear	13.27	0.0362	0.68
Species richness	Quadratic	9.72	0.867	0.0024*	Quadratic	1.87	0.695	<0.0001	Linear	11.79	0.0000833	0.98
Prop. of suspension feeders	Linear (↓)	6.84	0.66	0.0076*	Linear	3.39	0.116	0.18	Linear	7	0.0308	0.71

Note. ΔAICc represents the difference in AICc values of the best-fit and second best-fit relationships, with values of 2 or greater indicating significance of models. * $p<0.05$.

Table 34

Summary Table of Patterns with Depth at Sites under Sea Ice Compared to Sites under the Ice Shelf

Site	Ice cover	Distance from sea ice edge (km)	Abundance	Shannon-Wiener diversity index	Proportion of suspension feeders
Knob Point	Sea ice	52.9	↗↘	↗↘	--
Cape Armitage	Sea ice	59.7	--	--	--
Becker Point	Ice shelf	91.6	↗↘	↗↘	↓
Heald Island	Ice shelf	98.7	N/A	N/A	N/A

Note. ↓ represent a decrease, ↗↘ represents a quadratic distribution.

The proportion of suspension feeders relative to other functional groups at Becker Point decreased with depth, but no pattern was found at other sites. It is possible that Antarctic fauna typically described as sessile predators use a wide range of feeding strategies, including suspension feeding, and this breadth of strategies allows them to succeed on the food-limited sub-ice sea floor.

Benthic communities under seasonal ice were different than those under permanent ice shelves, with higher overall species diversity, a greater proportion of suspension feeders, and were a degree of magnitude more abundant (Table 35), which agreed with original hypotheses based on food availability, though causality was not proven.

Table 35

Summary Table of Benthic Assemblages at Sites under Sea Ice Compared to Sites under the Ice Shelf

Site	Depth range sampled (m)	Dominant species	Dominant functional group	M % cover	Species count
Sea ice					
Knob Point	30-314	Unknown sp. bryozoa, *Cellaria* sp., *Perkinsiana* sp.	Suspension feeders	37.80 %	72
Cape Armitage	15-119	Unknown sp. bryozoa, Unknown sp. demosponge	Suspension feeders	25.03 %	37
Ice shelf					
Becker Point	15-149	Unknown sp. budding sponge, *Artemidactis vitrix*	Suspension feeders, Sessile predators	3.99%	43
Heald Island	180-209	Unknown sp. sea whip, Unknown sp. anemone	Suspension feeders, Sessile predators	0.50%	6

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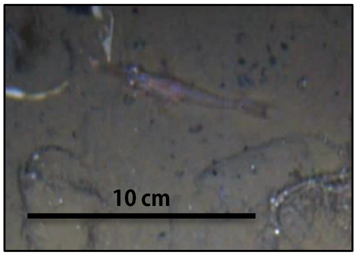
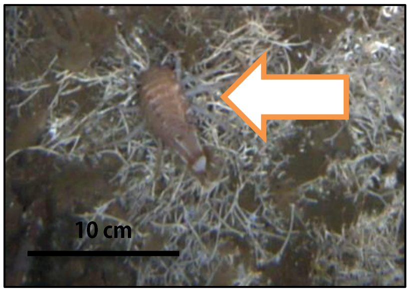
Appendix A: List and sample images of identified species

*species names in quotes refer to common names assigned in Supplement B of Dayton *et al.* 2016.

I. Arthropoda



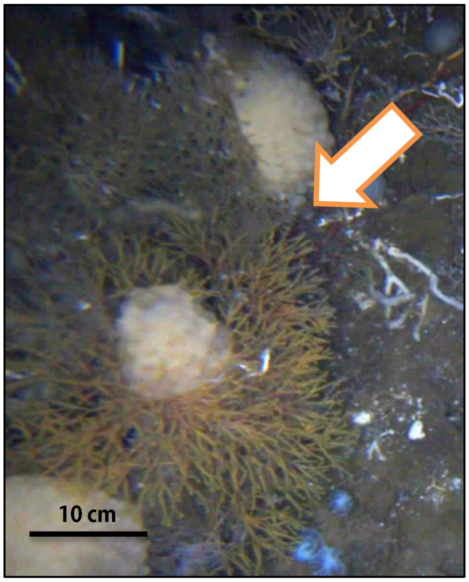
Decapoda- Shrimp



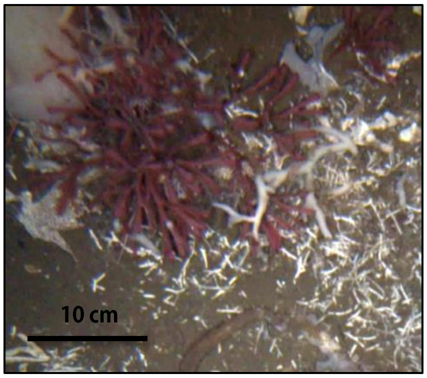
Glyptonotus antarcticus

Pycnogonida

I. Bryozoa

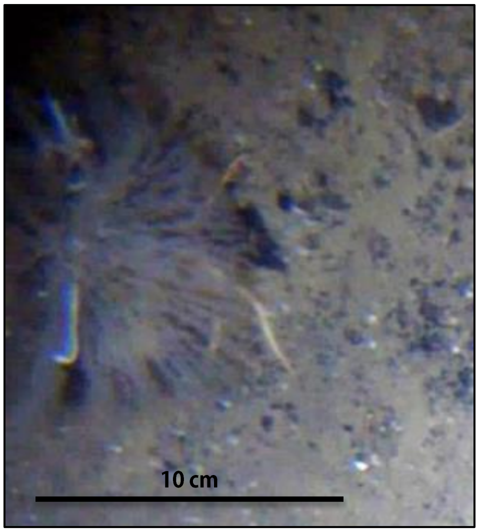


Bryozoan sp. A

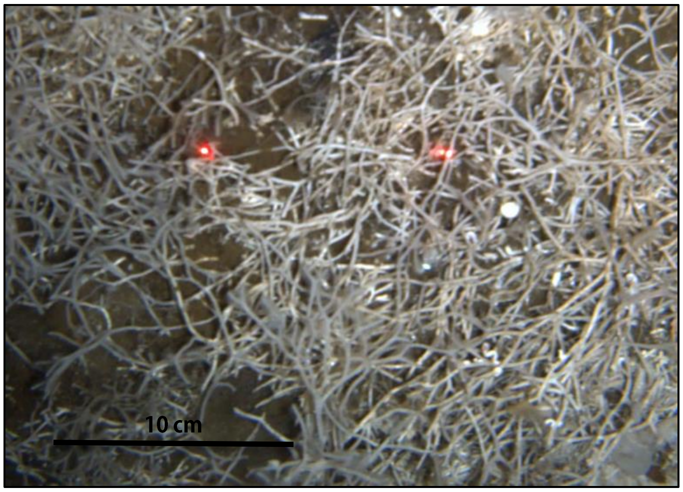


Bryozoan sp. B

Bryozoan sp. C

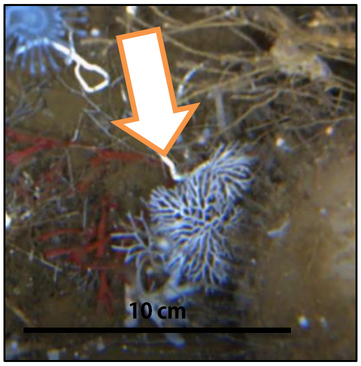


Camptoplites sp.

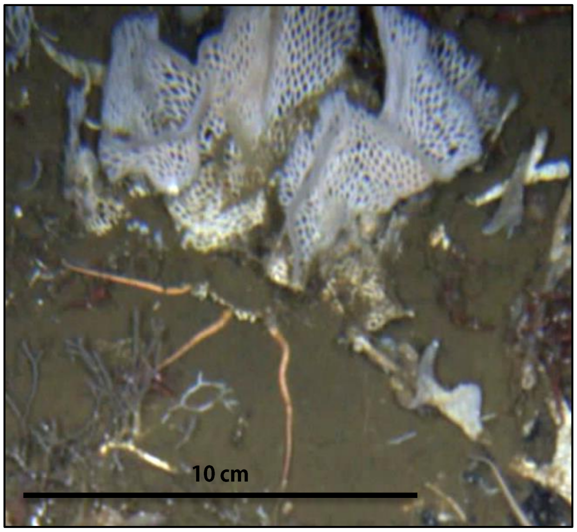


Cellaria sp.

Cellarinella sp.

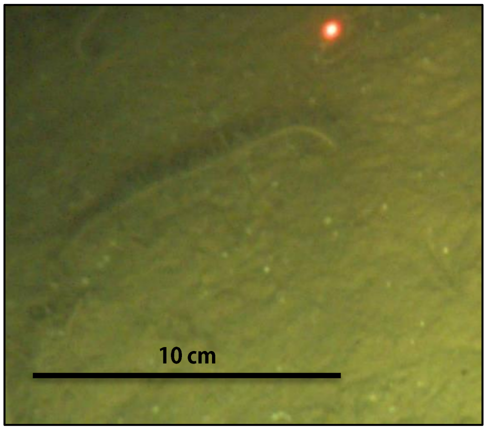


Hornera sp.

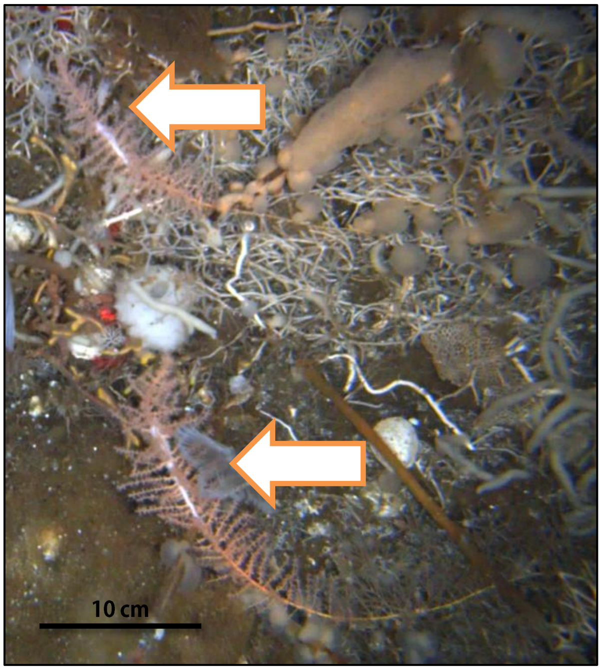


Reteporella sp.

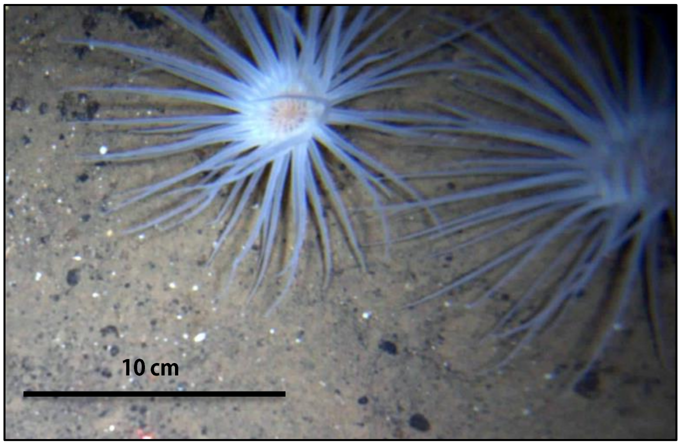
II. Cnidaria- Anthozoa



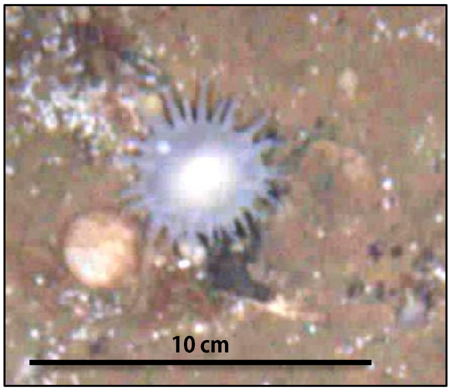
Alcyonaceae- Sea whip



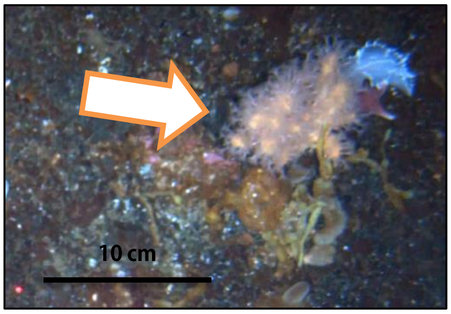
Alcyonaceae- Soft coral



Artemidactis victrix

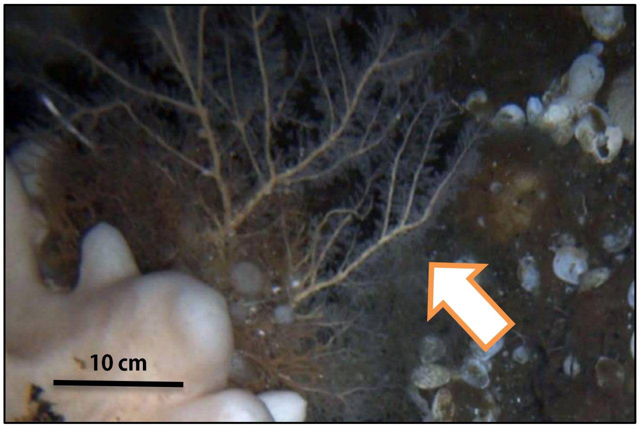


Isotealia antarctica



Gersemia Antarctica

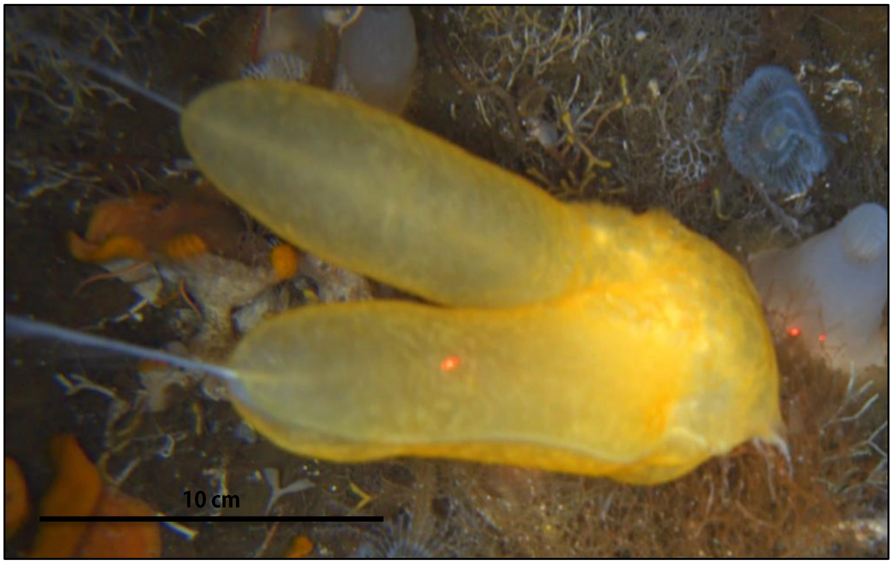
III. Cnidaria – Hydrozoa



Hydrodendron arboreum

Zyzzyzus parvula

IV. Ctenophora

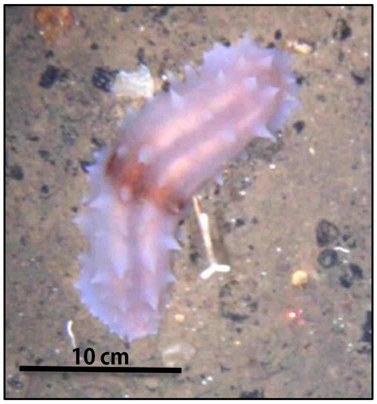


Lyrocteis flavopallidus

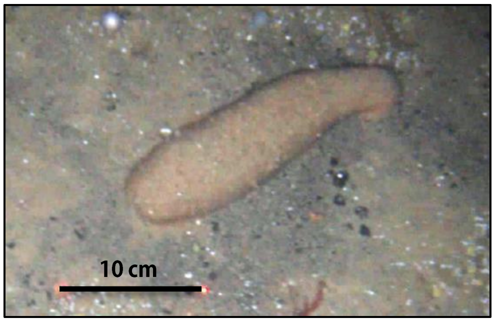
V. Echinodermata

Acondontaster sp.

Diplasterias brucei

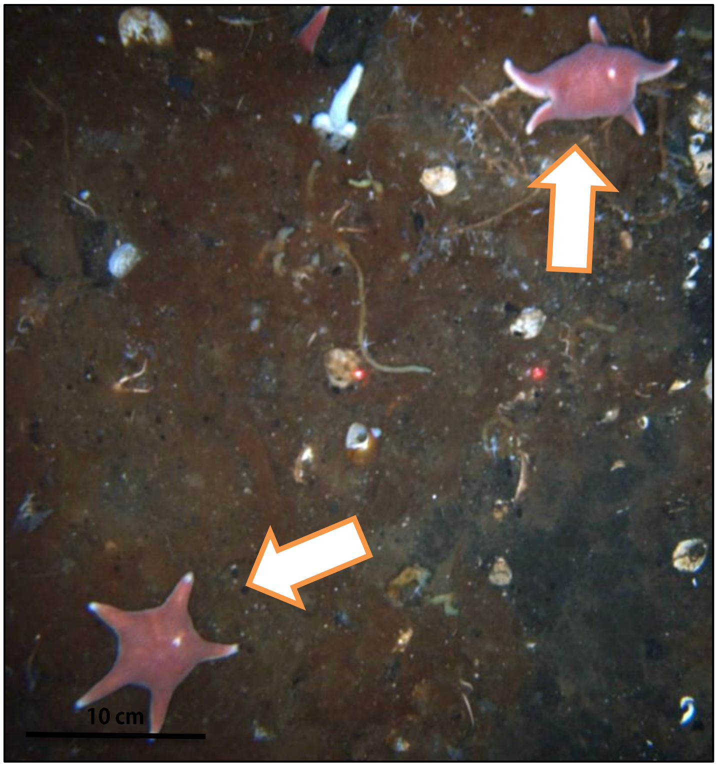


Bathyplotes bongraini

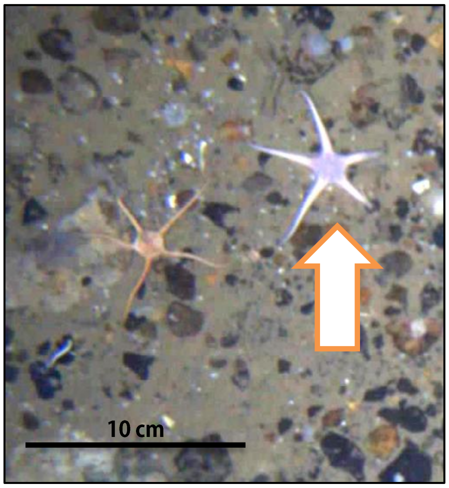


Holothuroidea (unknown sp.)

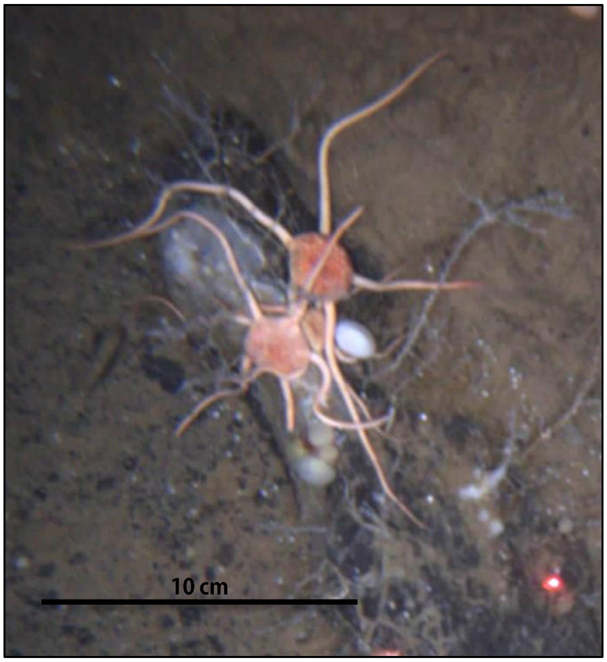
Macroptychaster accrescens



Odontaster validus



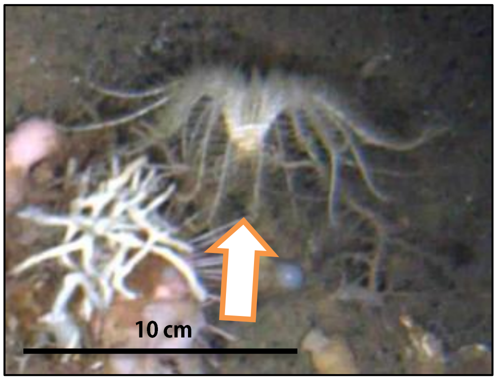
Ophionotus victoriae



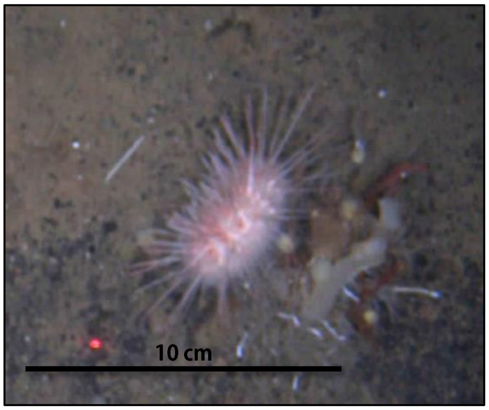
Ophiosparte gigas

Perknaster aurorae

Perknaster fuscus antarcticus

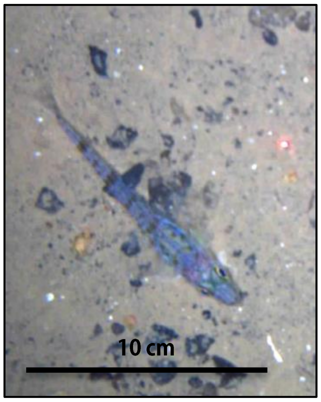


Promachocrinus kerguelensis



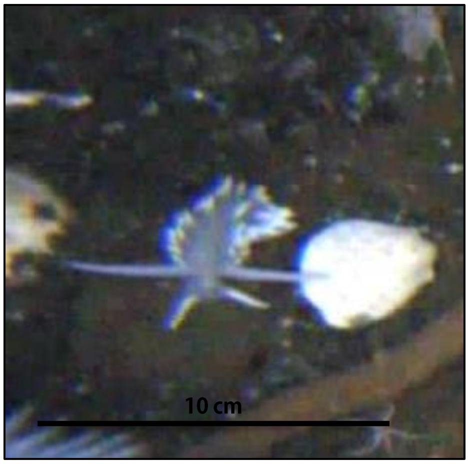
Sterechinus neumayeri

VI. Chordata

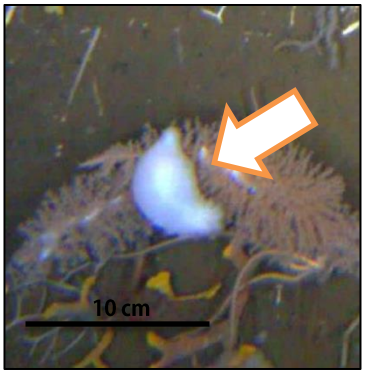


Fish (unknown sp.)

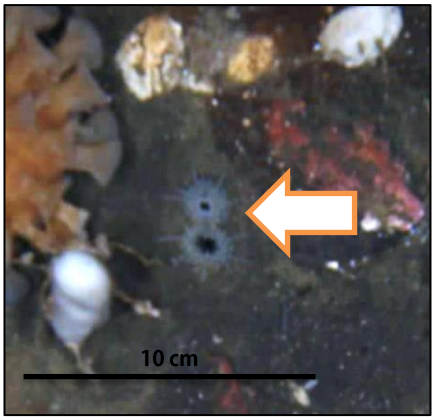
VII. Mollusca



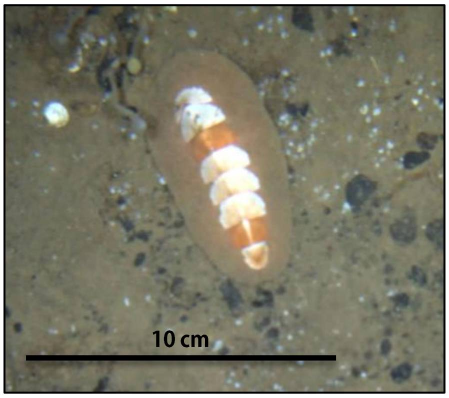
Cuthona crinita



Doris kerguelensis

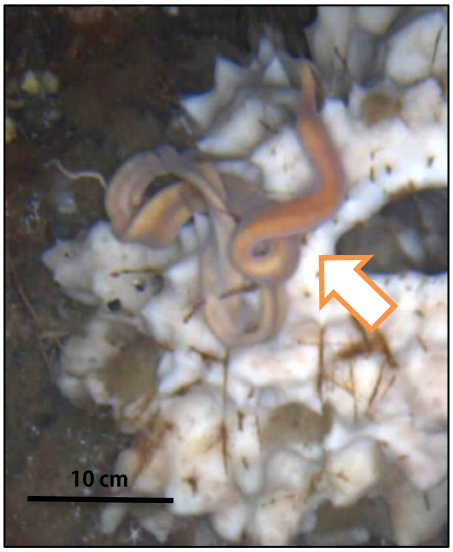


Laternula elliptica



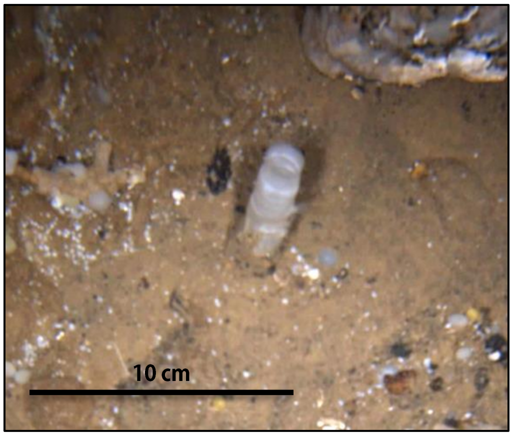
Nuttallochiton mirandus

VIII. Nemertea

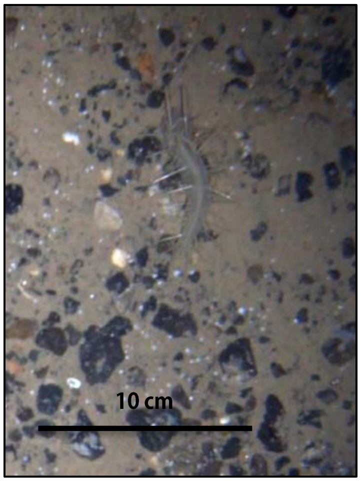


Parborlasia corrugatus

IX. Polychaeta

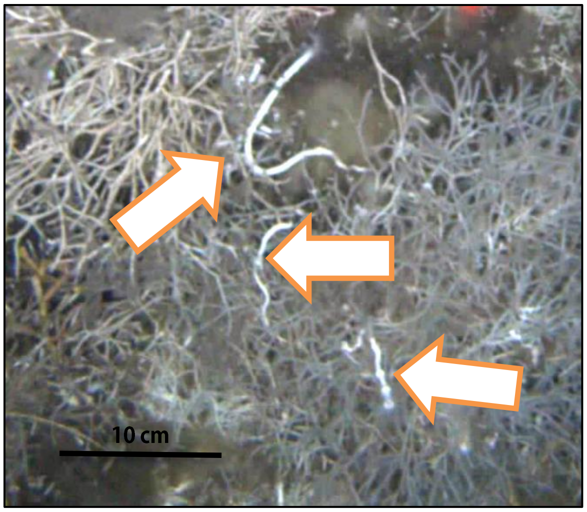


Chaetopterus variopedatus



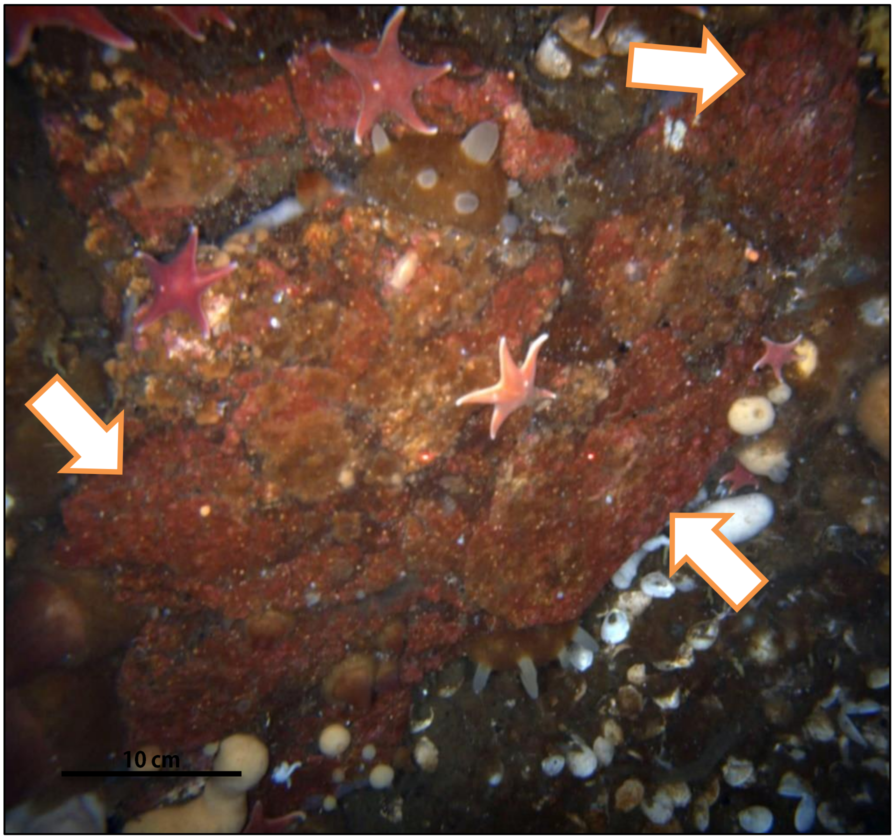
Flabelligera mundata

Perkinsiana sp.



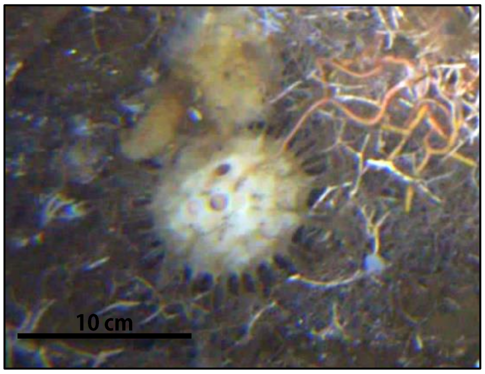
Serpula narconensis

X. Rhodophyta (algae)

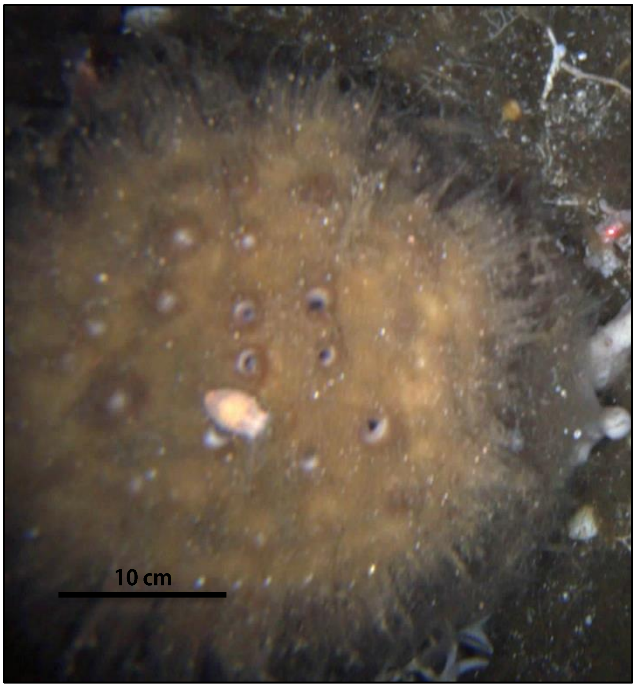


Phymatolithon foecundum

XI. Porifera

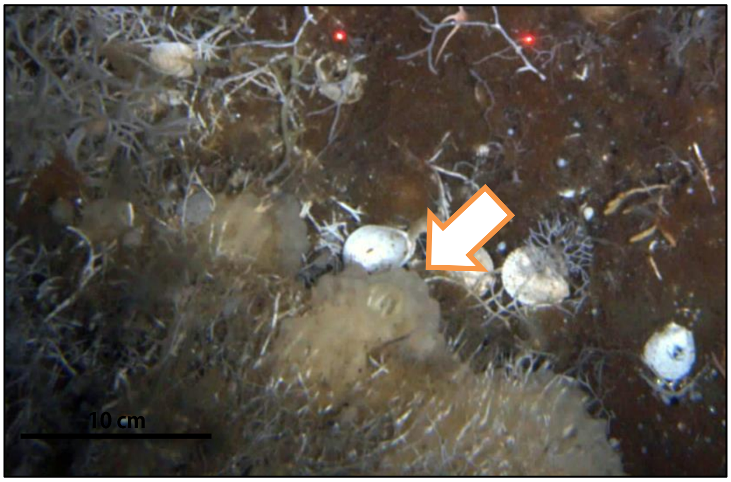


Cinachyra antarctica

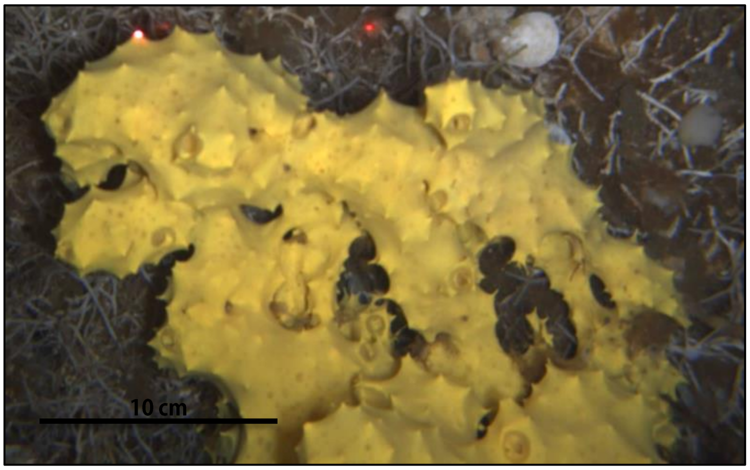


Cinachyra barbata

Cladocroce gaussiana



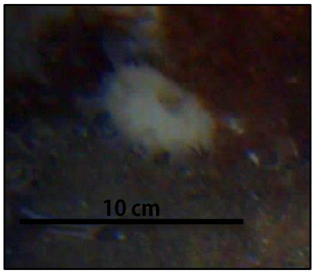
Clathria nidificata



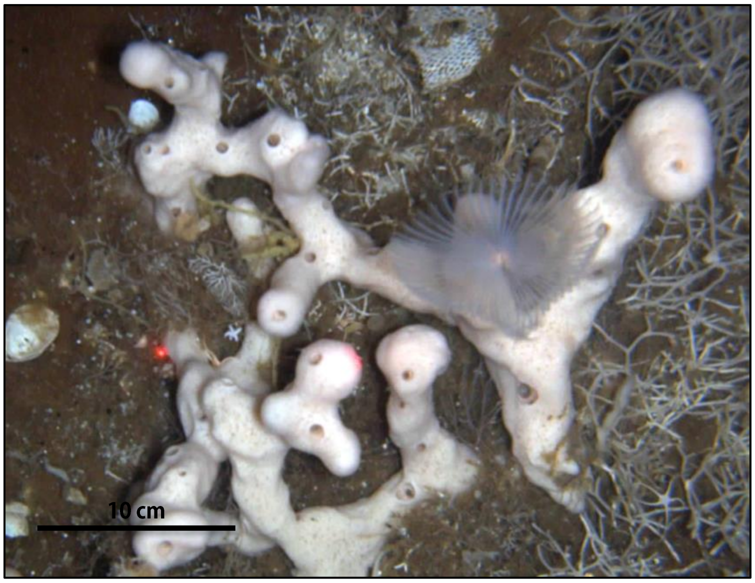
Dendrilla antarctica

Guitarra antarctica

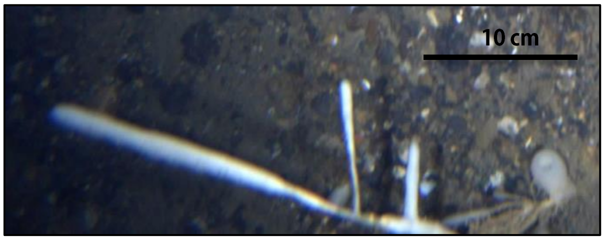
Haliclona scotti



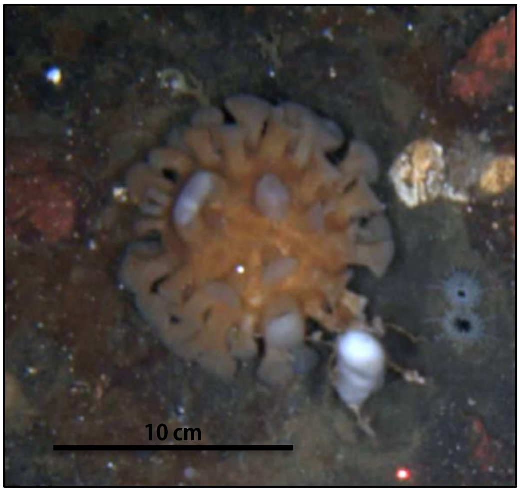
Haliclona sp.



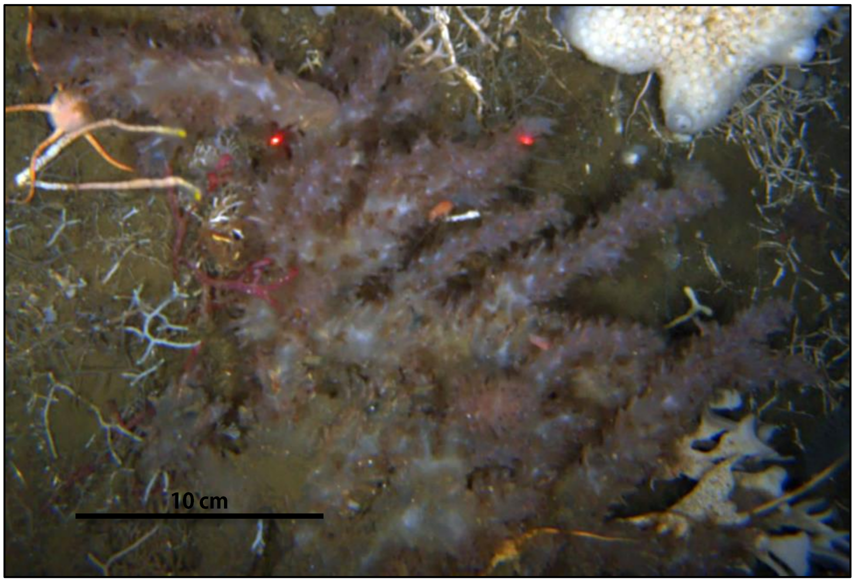
Hemigellius fimbriatus



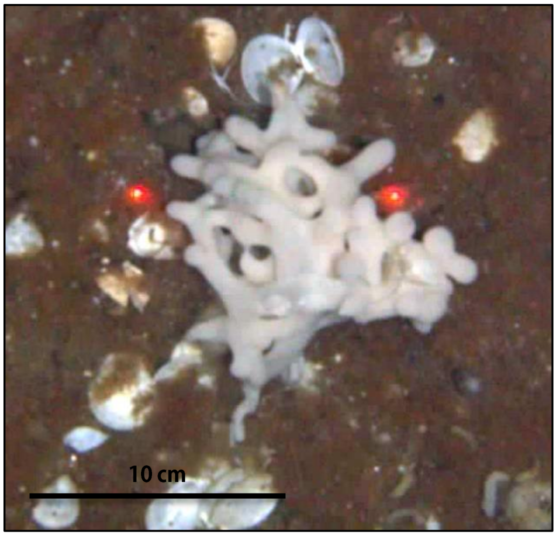
Homaxinella balfourensis



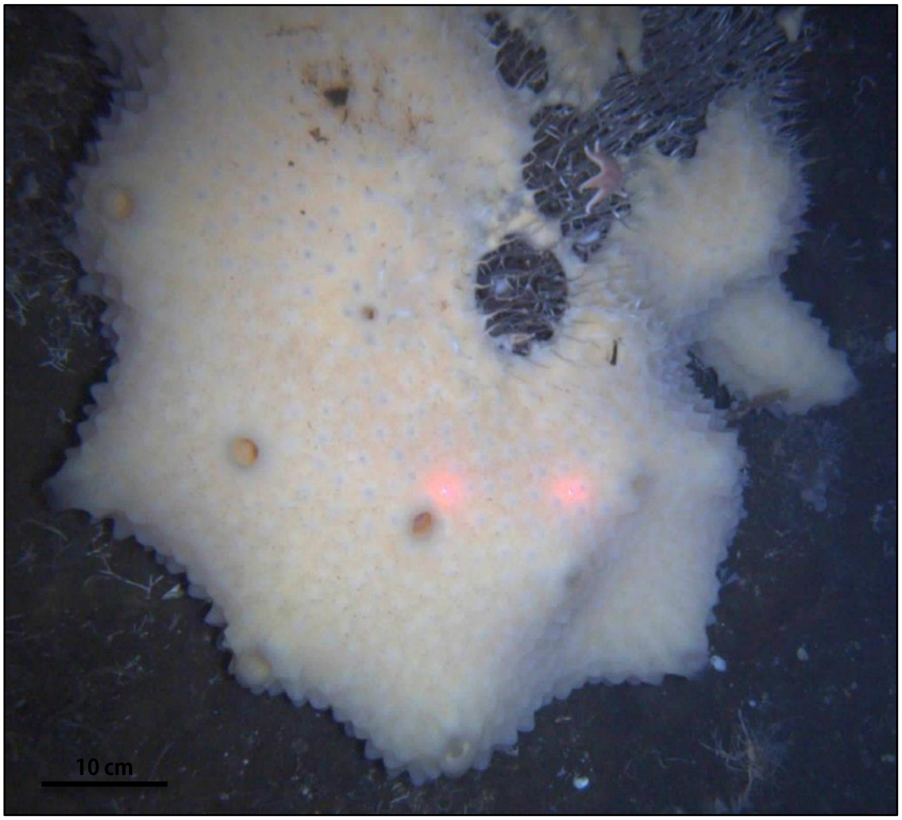
Inflatella belli



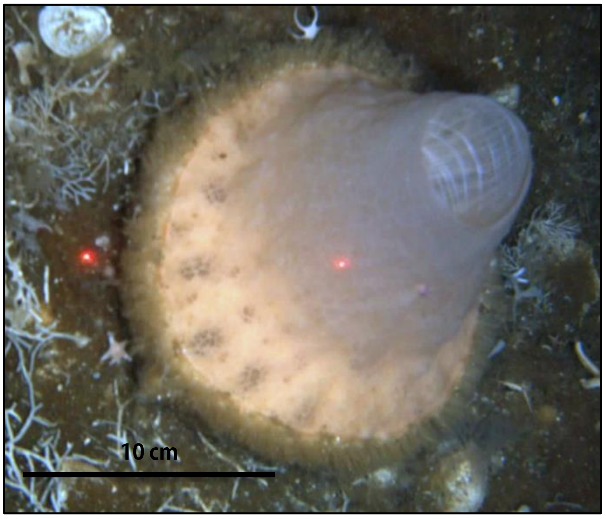
Isodictya setifera



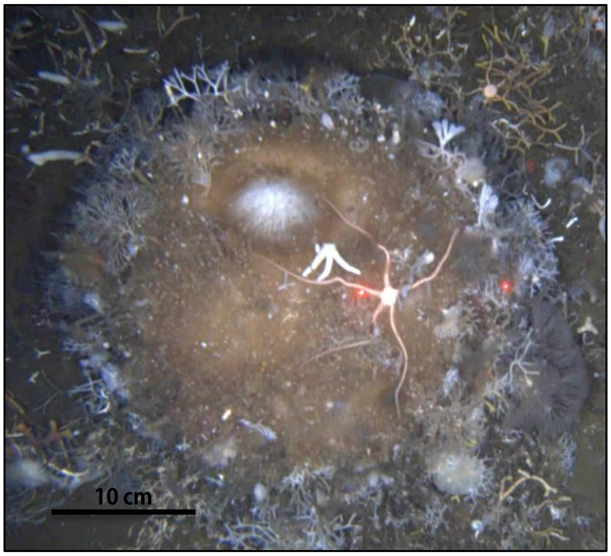
Leucascus leptoraphis



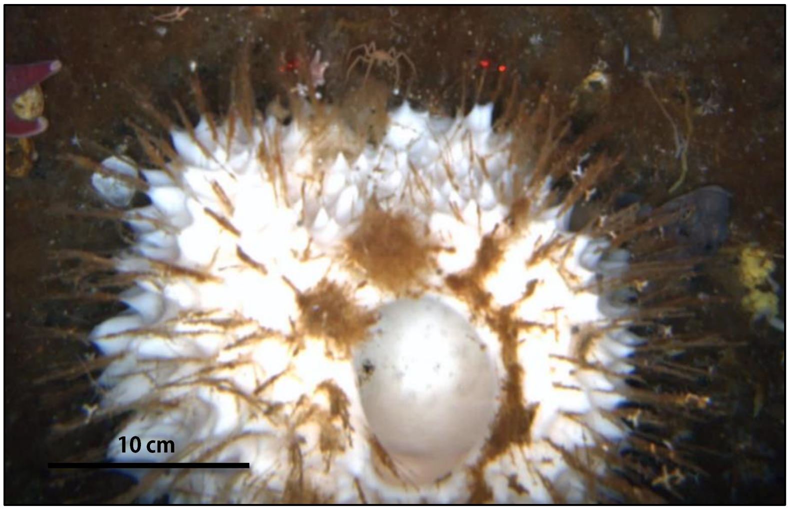
Mycale (Oxymycale) acerata



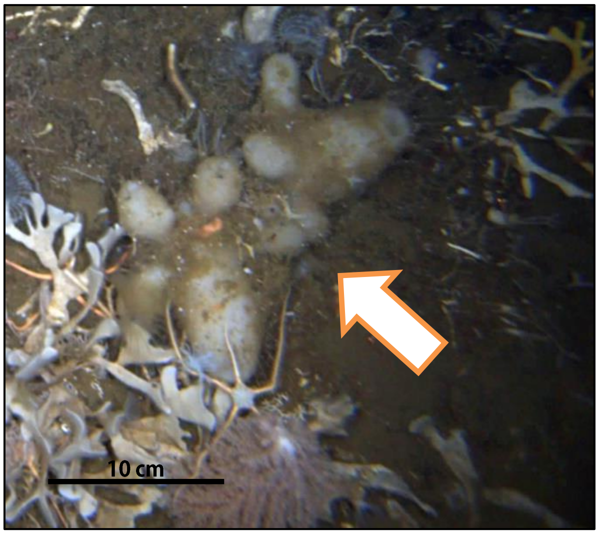
Polymastia invaginata



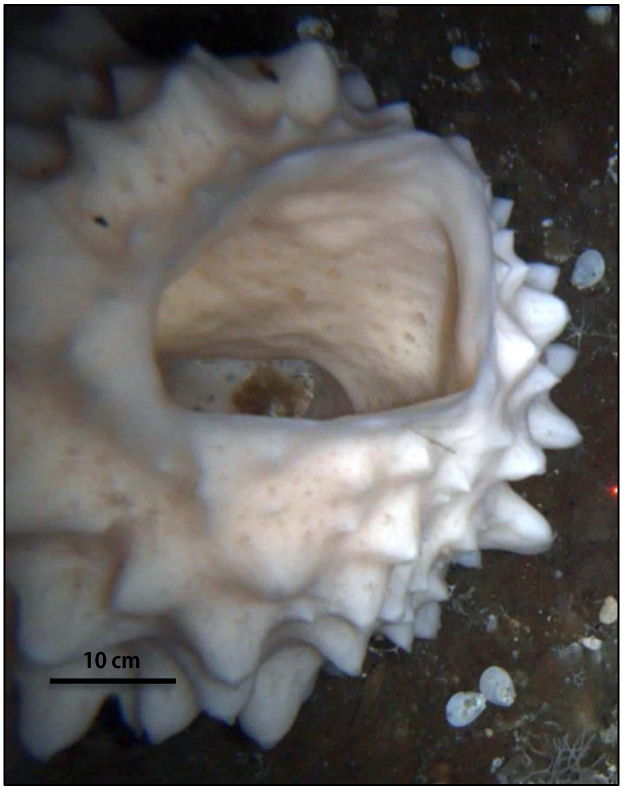
Rossella antarctica



Rossella levis

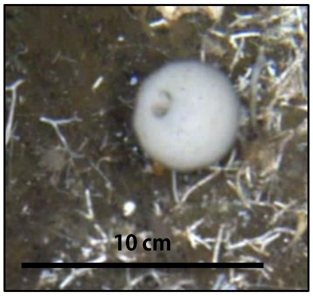


Rossella podagrosa

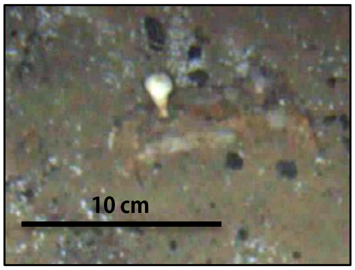


Rossella sp.

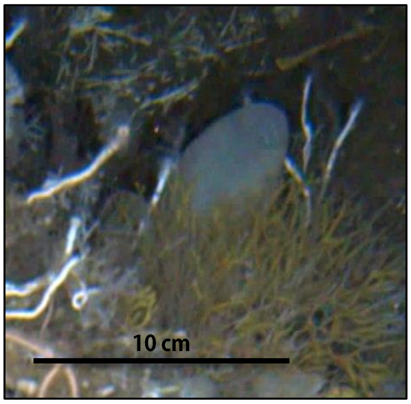
Sphaerotylus antarcticus



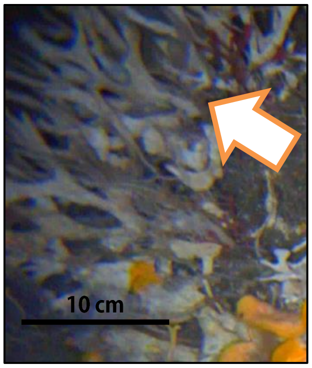
Sponge sp. A – “Eyeball sponge”



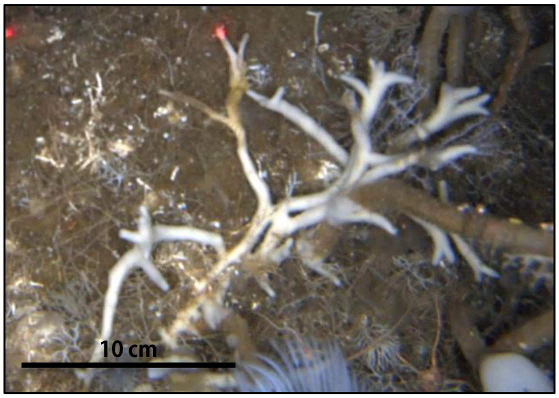
Sponge sp. B – “Golf tee sponge”



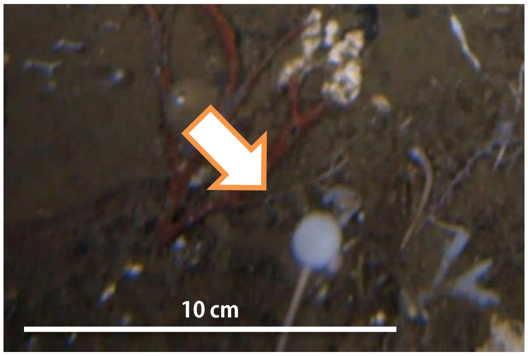
Sponge sp. C – “Pipe sponge”



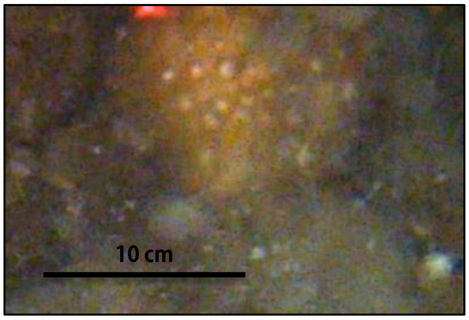
Sponge sp. D



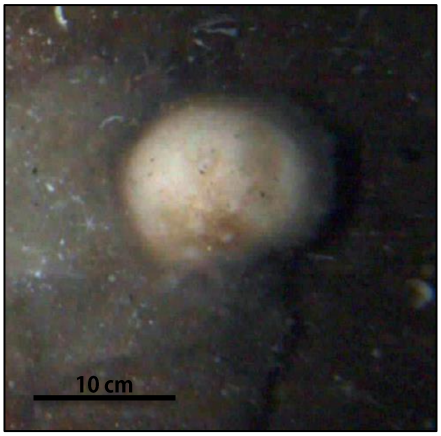
Sponge sp. E



Stylochordata chupachups

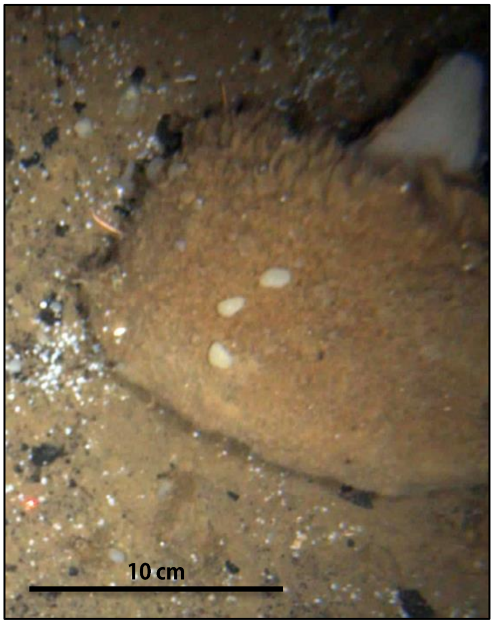


Suberites sp.



Tetilla leptoderma

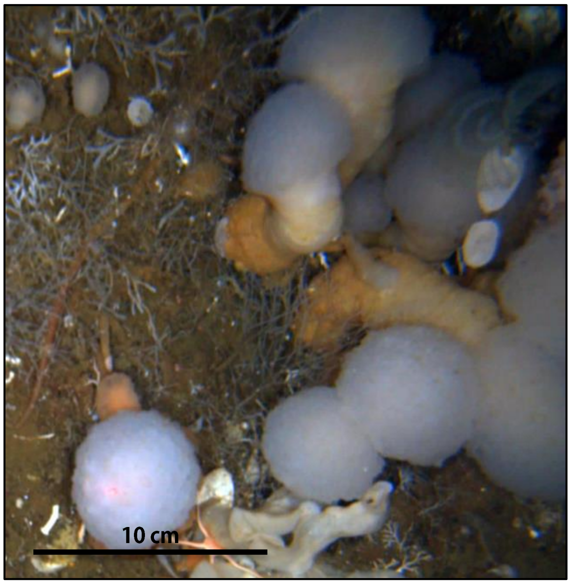
XII. Tunicata



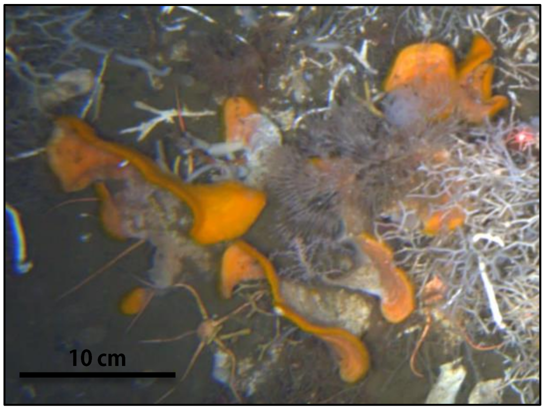
Cnemidocarpa verrucosa (solitary)

Distaplia cylindrical (colonial)

Tunicate sp. A (colonial)



Tunicate sp. B (colonial)



Tunicate sp. C (colonial)

Tunicate sp. D (colonial)

Appendix B: ANOSIM pairwise comparisons of depth classes per site

Table 1. *ANOSIM Pairwise Tests for Differences in Community Assemblage by Depth Classes at Becker Point*

Depth Groups (m)	R statistic	P-value	Number of permutations	Number > Observed
15-29, 30-44	0.738	**0.001**	999	0
15-29, 45-59	0.277	**0.005**	999	4
15-29, 60-74	0.744	**0.001**	999	0
15-29, 75-89	0.473	**0.001**	999	0
15-29, 90-104	0.440	**0.001**	999	0
15-29, 105-119	0.118	0.072	999	71
15-29, 120-134	0.238	**0.003**	999	2
15-29, 135-149	0.664	**0.001**	999	0
30-44, 45-59	0.736	**0.001**	999	0
30-44, 60-74	0.850	**0.001**	999	0
30-44, 75-89	0.822	**0.001**	999	0
30-44, 90-104	0.752	**0.001**	999	0
30-44, 105-119	0.795	**0.001**	999	0
30-44, 120-134	0.824	**0.001**	999	0
30-44, 135-149	0.709	**0.001**	999	0
45-59, 60-74,	0.117	**0.011**	999	10
45-59, 120-134	0.116	0.016	999	15
45-59, 135-149	0.144	0.053	999	52
60-74, 75-89	0.024	0.108	999	107
60-74, 90-104	0.122	0.032	999	31
60-74, 105-119	0.354	**0.001**	999	0
60-74, 120-134	0.32	**0.001**	999	0
60-74, 135-149	0.420	**0.001**	999	0
75-89, 45-59	0.051	0.112	999	111
75-89, 90-104	-0.049	0.777	999	776
75-89, 105-119	0.177	**0.002**	999	1
75-89, 120-134	0.201	**0.001**	999	0
75-89, 135-149	0.144	0.054	999	53
90-104, 45-59	0.038	0.174	999	173
90-104, 105-119	0.058	0.096	999	95
90-104, 120-134	0.141	0.024	999	23
90-104, 135-149	0.070	0.144	999	143
105-119, 45-59	0.069	0.023	999	22
105-119, 120-134	0.087	0.038	999	37
105-119, 135-149	0.039	0.267	999	266

120-134, 135-149	0.057	0.236	999	235

Note. Bold p-values indicate significance at p<0.05.

Table 2. *ANOSIM Pairwise Tests for Differences in Community Assemblage by Depth Classes at Knob Point*

Depth Groups (m)	R statistic	P-value	Number of permutations	Number >= observed
30-44, 45-59	0.117	0.096	999	95
30-44, 60-74	0.480	**0.001**	999	0
30-44, 75-89	0.735	**0.001**	999	0
30-44, 90-104	0.984	**0.001**	999	0
30-44, 105-119	0.998	**0.001**	999	0
30-44, 120-134	0.996	**0.001**	999	0
30-44, 135-149	1.000	**0.001**	999	0
30-44, 150-164	1.000	**0.001**	999	0
30-44, 180-194	0.998	**0.001**	999	0
30-44, 195-209	1.000	**0.001**	999	0
30-44, 210-224	0.992	**0.001**	999	0
30-44, 225-239	1.000	**0.001**	999	0
30-44, 240-254	0.999	**0.001**	999	0
30-44, 270-284	1.000	**0.001**	999	0
30-44, 285-299	0.998	**0.001**	999	0
30-44, 300-314	0.999	**0.001**	999	0
45-59, 60-74	0.316	**0.003**	999	2
45-59, 75-89	0.431	**0.001**	999	0
45-59, 90-104	0.707	**0.001**	999	0
45-59, 105-119	0.872	**0.001**	999	0
45-59, 120-134	0.872	**0.001**	999	0
45-59, 135-149	0.849	**0.001**	999	0
45-59, 150-164	0.890	**0.001**	999	0
45-59, 180-194	0.932	**0.001**	999	0
45-59, 195-209	0.905	**0.001**	999	0
45-59, 210-224	0.923	**0.001**	999	0
45-59, 225-239	0.941	**0.001**	999	0
45-59, 240-254	0.937	**0.001**	999	0
45-59, 270-284	0.946	**0.001**	999	0
45-59, 285-299	0.925	**0.001**	999	0
45-59, 300-314	0.947	**0.001**	999	0
60-74, 75-89	0.744	**0.001**	999	0
60-74, 90-104	0.982	**0.001**	999	0
60-74, 105-119	0.988	**0.001**	999	0

60-74, 120-134	0.981	**0.001**	999	0
60-74, 135-149	0.963	**0.001**	999	0
60-74, 150-164	0.970	**0.001**	999	0
60-74, 180-194	0.966	**0.001**	999	0
60-74, 195-209	0.978	**0.001**	999	0
60-74, 210-224	0.897	**0.001**	999	0
60-74, 225-239	0.973	**0.001**	999	0
60-74, 240-254	0.945	**0.001**	999	0
60-74, 270-284	0.966	**0.001**	999	0
60-74, 285-299	0.904	**0.001**	999	0
60-74, 300-314	0.955	**0.001**	999	0
75-89, 90-104	0.094	0.074	999	73
75-89, 105-119	0.346	**0.001**	999	0
75-89, 120-134	0.399	**0.001**	999	0
75-89, 135-149	0.355	**0.002**	999	1
75-89, 150-164	0.511	**0.001**	999	0
75-89, 180-194	0.585	**0.001**	999	0
75-89, 195-209	0.566	**0.001**	999	0
75-89, 210-224	0.632	**0.001**	999	0
75-89, 225-239	0.826	**0.001**	999	0
75-89, 240-254	0.747	**0.001**	999	0
75-89, 270-284	0.870	**0.001**	999	0
75-89, 285-299	0.786	**0.001**	999	0
75-89, 300-314	0.865	**0.001**	999	0
90-104, 105-119	-0.021	0.597	999	596
90-104, 120-134	0.136	0.048	999	47
90-104, 135-149	0.469	**0.001**	999	0
90-104, 150-164	0.506	**0.001**	999	0
90-104, 180-194	0.721	**0.001**	999	0
90-104, 195-209	0.651	**0.002**	999	1
90-104, 210-224	0.721	**0.001**	999	0
90-104, 225-239	0.922	**0.001**	999	0
90-104, 240-254	0.800	**0.001**	999	0
90-104, 270-284	0.963	**0.001**	999	0
90-104, 285-299	0.869	**0.001**	999	0
90-104, 300-314	0.964	**0.001**	999	0
105-119, 120-134	0.031	0.192	999	191
105-119, 135-149	0.307	**0.001**	999	0
105-119, 150-164	0.420	**0.001**	999	0
105-119, 180-194	0.636	**0.001**	999	0

105-119, 195-209	0.630	**0.001**	999	0
105-119, 210-224	0.728	**0.001**	999	0
105-119, 225-239	0.892	**0.001**	999	0
105-119, 240-254	0.758	**0.001**	999	0
105-119, 270-284	0.944	**0.001**	999	0
105-119, 285-299	0.836	**0.001**	999	0
105-119, 300-314	0.975	**0.001**	999	0
120-134, 135-149	0.057	0.216	999	215
120-134, 150-164	0.226	**0.007**	999	6
120-134, 180-194	0.461	**0.001**	999	0
120-134, 195-209	0.465	**0.001**	999	0
120-134, 210-224	0.599	**0.001**	999	0
120-134, 225-239	0.779	**0.001**	999	0
120-134, 240-254	0.593	**0.001**	999	0
120-134, 270-284	0.889	**0.001**	999	0
120-134, 285-299	0.743	**0.001**	999	0
120-134, 300-314	0.891	**0.001**	999	0
135-149, 150-164	0.166	0.020	999	19
135-149, 180-194	0.255	**0.003**	999	2
135-149, 195-209	0.347	**0.001**	999	0
135-149, 210-224	0.287	**0.001**	999	0
135-149, 225-239	0.750	**0.001**	999	0
135-149, 240-254	0.554	**0.001**	999	0
135-149, 270-284	0.784	**0.001**	999	0
135-149, 285-299	0.457	**0.002**	999	1
135-149, 300-314	0.82	**0.001**	999	0
150-164, 180-194	0.182	**0.006**	999	5
150-164, 195-209	0.145	0.027	999	26
150-164, 210-224	0.316	**0.001**	999	0
150-164, 225-239	0.454	**0.001**	999	0
150-164, 240-254	0.420	**0.001**	999	0
150-164, 270-284	0.818	**0.001**	999	0
150-164, 285-299	0.534	**0.001**	999	0
150-164, 300-314	0.832	**0.001**	999	0
180-194, 195-209	0.054	0.205	999	204
180-194, 210-224	0.284	**0.001**	999	0
180-194, 225-239	0.558	**0.001**	999	0
180-194, 240-254	0.598	**0.001**	999	0
180-194, 270-284	0.798	**0.001**	999	0
180-194, 285-299	0.645	**0.001**	999	0

180-194, 300-314	0.867	**0.001**	999	0
195-209, 210-224	0.220	**0.004**	999	3
195-209, 225-239	0.393	**0.001**	999	0
195-209, 240-254	0.320	**0.002**	999	1
195-209, 270-284	0.710	**0.001**	999	0
195-209, 285-299	0.614	**0.001**	999	0
195-209, 300-314	0.802	**0.001**	999	0
210-224, 225-239	0.149	0.022	999	21
210-224, 240-254	0.119	0.063	999	62
210-224, 270-284	0.222	**0.001**	999	0
210-224, 285-299	0.247	**0.001**	999	0
210-224, 300-314	0.329	**0.001**	999	0
225-239, 240-254	0.245	**0.003**	999	2
225-239, 270-284	0.294	**0.003**	999	2
225-239, 285-299	0.282	**0.004**	999	3
225-239, 300-314	0.466	**0.001**	999	0
240-254, 270-284	0.262	**0.005**	999	4
240-254, 285-299	0.153	0.025	999	24
240-254, 300-314	0.357	**0.002**	999	1
270-284, 285-299	0.048	0.228	999	227
270-284, 300-314	0.111	0.082	999	81
285-299, 300-314	0.036	0.306	999	305

Note. Bold p-values indicate significance at p<0.05.

Table 3. *ANOSIM Pairwise Tests for Differences in Community Assemblage by Depth Classes at Cape Armitage*

Depth Groups (m)	R statistic	P-value	Number of permutations	Number >= observed
15-29, 30-44	0.199	0.042	999	41
15-29, 45-59	0.470	**0.001**	999	0
15-29, 60-74	0.582	**0.001**	999	0
15-29, 75-89	0.203	0.030	999	29
15-29, 90-104	0.325	**0.007**	999	6
15-29, 105-119	0.620	**0.001**	999	0
30-44, 45-59	0.427	**0.002**	999	1
30-44, 60-74	0.576	**0.001**	999	0
30-44, 75-89	0.492	**0.001**	999	0
30-44, 90-104	0.528	**0.001**	999	0
30-44, 105-119	0.509	**0.001**	999	0
45-59, 60-74	0.047	0.257	999	256
45-59, 75-89	0.313	**0.001**	999	0

45-59, 90-104	0.475	**0.002**	999	1
45-59, 105-119	0.427	**0.001**	999	0
60-74, 75-89	0.204	0.035	999	34
60-74, 90-104	0.391	**0.008**	999	7
60-74, 105-119	0.465	**0.001**	999	0
75-89, 90-104	0.071	0.178	999	177
75-89, 105-119	0.480	**0.001**	999	0
90-104, 105-119	0.343	**0.002**	999	1

Note. Bold p-values indicate significance at $p<0.05$.

Appendix C: SIMPER results by depth class per site

Table 1. *SIMPER Analysis of Fauna at Species Level at Becker Point*

Depth (m)	Species	Avg. % cov.	Av.Sim	Sim/SD	%Contrib	Cum.%
15-29	Fine sediment	3.10	50.35	6.43	66.73	66.73
15-29	Gravel	1.09	13.36	1.93	17.71	84.44
15-29	Shell	0.92	10.22	1.24	13.55	97.99
30-44	Diatomaceous film	2.50	39.69	1.20	81.91	81.91
30-44	Fine sediment	1.01	6.38	0.68	13.17	95.08
45-59	Fine sediment	2.75	31.01	2.55	49.43	49.43
45-59	Gravel	1.84	18.25	2.41	29.09	78.52
45-59	Echinoderm ossicles	1.17	9.06	1.08	14.45	92.97
60-74	Fine sediment	2.85	30.43	6.77	43.98	43.98
60-74	Gravel	1.98	18.78	3.02	27.14	71.12
60-74	Echinoderm ossicles	1.43	12.79	2.22	18.49	89.61
60-74	Budding sponge	0.79	4.99	0.86	7.21	96.82
75-89	Fine sediment	2.91	30.65	5.76	47.95	47.95
75-89	Gravel	1.86	17.25	3.12	26.99	74.93
75-89	Echinoderm ossicles	1.04	7.28	1.12	11.39	86.32
75-89	Budding sponge	0.70	4.25	0.79	6.65	92.97
90-104	Fine sediment	2.88	33.61	3.30	51.00	51.00
90-104	Gravel	1.96	21.08	4.57	31.99	82.99
90-104	Echinoderm ossicles	0.76	4.19	0.70	6.36	89.35
90-104	Budding sponge	0.73	3.92	0.70	5.94	95.29
105-119	Fine sediment	3.02	38.72	5.48	62.13	62.13
105-119	Gravel	1.46	15.06	2.17	24.17	86.3
105-119	*Artemidactis victrix*	0.62	3.15	0.55	5.05	91.34
120-134	Fine sediment	2.87	35.86	5.57	53.72	53.72
120-134	Gravel	1.93	20.92	2.57	31.35	85.08
120-134	Echinoderm ossicles	0.57	3.53	0.61	5.29	90.37
135-149	Fine sediment	2.84	38.50	6.86	52.15	52.15

135-149	Gravel	2.24	29.05	4.29	39.34	91.49

Note. Analysis performed on fourth root transformed percent cover data and Bray-Curtis similarities to yield Avg. % cov., Av. Sim, Sim/SD, % Contrib, and Cum. %. Only the species contributing to the first 90% of differences between groups are listed. Avg. Sim = the average similarity contribution of each functional group. Sim/SD = ratio of the average similarity contribution divided by the standard deviation. % Contrib. = Percentage of contribution to similarity within a site. Cum. %= Cumulative contribution.

Table 2. *SIMPER Analysis of fauna at species level at Knob Point*

Depth (m)	Species	Avg. % cover	Av. Sim	Sim/SD	% Contrib.	Cum.%
30-44	Diatomaceous film	2.58	21.84	3.60	36.62	36.62
30-44	Fine sediment	2.23	17.86	3.39	29.94	66.56
30-44	*Laternula elliptica* shell	1.62	12.84	3.68	21.53	88.10
30-44	*Odontaster validus*	0.61	2.20	0.61	3.69	91.78
45-59	Diatomaceous film	2.38	17.88	1.83	36.43	36.43
45-59	Fine sediment	2.00	14.68	2.60	29.89	66.32
45-59	Shell	0.89	3.47	0.55	7.06	73.38
45-59	*Laternula elliptica* shell	0.78	2.89	0.53	5.88	79.25
45-59	*Hydrodendron arboreum*	0.85	2.87	0.53	5.84	85.09
45-59	*Dendrilla antarctica*	0.65	2.43	0.63	4.95	90.04
60-74	Diatomaceous film	2.69	25.78	7.43	42.10	42.10
60-74	Bryozoa	1.71	12.39	1.71	20.23	62.33
60-74	Fine sediment	1.32	8.32	1.21	13.60	75.92
60-74	*Laternula elliptica* shell	1.18	7.91	1.23	12.93	88.85
60-74	*Perkinsiana* sp.	0.65	2.60	0.52	4.25	93.10
75-89	Fine sediment	2.05	14.71	1.74	32.18	32.18
75-89	*Cellaria* sp.	1.62	10.23	1.23	22.37	54.55
75-89	Shell	1.14	8.00	1.90	17.50	72.04
75-89	*Perkinsiana* sp.	0.89	3.56	0.67	7.79	79.84

75-89	Diatomaceous film	0.99	3.46	0.53	7.56	87.40
75-89	*Rossella podagrosa*	0.78	2.36	0.52	5.15	92.56
90-104	Fine sediment	2.65	22.57	5.60	40.89	40.89
90-104	*Cellaria* sp.	2.09	15.73	4.09	28.50	69.40
90-104	*Perkinsiana* sp.	1.06	6.37	1.22	11.54	80.94
90-104	Shell	0.93	4.94	0.88	8.95	89.89
90-104	*Hemigellius fimbriatus*	0.82	2.65	0.49	4.81	94.70
105-119	Fine sediment	2.58	21.18	7.15	39.02	39.02
105-119	*Cellaria* sp.	2.11	15.98	2.81	29.44	68.47
105-119	*Perkinsiana* sp.	0.96	6.10	1.42	11.25	79.71
105-119	Spicule mat	0.89	2.58	0.46	4.76	84.47
105-119	Dead bryozoan	0.64	1.97	0.46	3.62	88.10
105-119	Shell	0.48	1.23	0.39	2.28	90.37
120-134	Fine sediment	2.54	17.19	5.02	31.46	31.46
120-134	*Cellaria* sp.	2.00	11.81	2.22	21.61	53.06
120-134	*Perkinsiana* sp.	1.12	5.59	1.23	10.24	63.30
120-134	Spicule mat	1.18	4.55	0.82	8.33	71.63
120-134	Shell	0.81	3.53	0.93	6.45	78.09
120-134	Dead bryozoan	0.94	3.34	0.70	6.12	84.21
120-134	Unidentified demosponge	0.69	2.03	0.54	3.72	87.93
120-134	*Polymastia invaginata*	0.53	1.37	0.47	2.51	90.43
135-149	Fine sediment	2.32	14.62	6.99	24.43	24.43
135-149	Unidentified bryozoan	1.86	10.92	4.65	18.26	42.69
135-149	*Cellaria* sp.	1.76	8.89	1.54	14.87	57.56
135-149	*Perkinsiana* sp.	1.29	7.04	1.77	11.78	69.34
135-149	Spicule mat	1.57	6.71	1.1	11.22	80.56
135-149	Shell	0.78	2.86	0.82	4.78	85.33
135-149	Unidentified ophiuroid	0.69	2.79	0.83	4.66	90.00

135-149	Unidentified demosponge	0.70	2.08	0.61	3.48	93.48
150-164	Fine sediment	2.56	16.18	6.75	29.28	29.28
150-164	Bryozoa	1.71	9.50	3.06	17.20	46.48
150-164	*Cellaria* sp.	1.53	6.55	1.17	11.85	58.32
150-164	Dead bryozoan	1.10	5.65	1.88	10.23	68.55
150-164	*Perkinsiana* sp.	1.14	5.65	1.87	10.23	78.78
150-164	Spicule mat	0.91	2.07	0.51	3.75	82.52
150-164	*Serpula narconensis*	0.60	2.02	0.69	3.65	86.17
150-164	Sponge sp. E	0.63	1.54	0.52	2.79	88.96
150-164	Tunicate sp. A	0.6	1.47	0.52	2.66	91.62
180-194	Fine sediment	2.17	12.13	6.56	21.01	21.01
180-194	Unidentified bryozoan	1.85	9.79	6.56	16.97	37.98
180-194	*Cellaria* sp.	1.79	7.23	1.05	12.52	50.50
180-194	*Perkinsiana* sp.	1.38	5.82	1.76	10.09	60.59
180-194	Tunicate sp. A	1.09	5.22	1.91	9.04	69.62
180-194	Unidentified hydroid	1.02	3.25	0.90	5.63	75.26
180-194	Unidentified demosponge	0.84	2.97	0.92	5.14	80.40
180-194	*Serpula narconensis*	0.64	1.92	0.70	3.32	83.72
180-194	Shell	0.64	1.82	0.70	3.14	86.86
180-194	Spicule mat	0.84	1.59	0.39	2.75	89.61
180-194	Sponge sp. E	0.64	1.51	0.52	2.62	92.23
195-209	Fine sediment	2.55	15.99	6.81	27.67	27.67
195-209	Bryozoa	2.00	11.86	7.34	20.53	48.21
195-209	*Cellaria* sp.	1.79	8.88	1.63	15.36	63.57
195-209	Tunicate sp. A	0.97	4.70	1.24	8.14	71.71
195-209	*Perkinsiana* sp.	0.99	3.70	0.89	6.40	78.11
195-209	Shell	0.79	3.04	0.91	5.26	83.37
195-209	Unidentified ophiuroid	0.64	2.34	0.69	4.04	87.41
195-209	Sponge sp. E	0.65	2.12	0.69	3.67	91.08
210-224	Fine sediment	2.41	14.77	8.10	31.81	31.81

210-224	Unidentified bryozoan	2.00	11.84	6.43	25.49	57.30
210-224	Tunicate sp. D	1.07	3.44	0.88	7.42	64.71
210-224	*Perkinsiana* sp.	0.96	3.21	0.88	6.92	71.63
210-224	*Cellaria* sp.	1.08	2.95	0.68	6.35	77.98
210-224	Bryozoan sp. B	0.69	1.71	0.53	3.67	81.66
210-224	Unidentified demosponge	0.64	1.64	0.51	3.53	85.18
210-224	Tunicate sp. C	0.67	1.52	0.51	3.28	88.46
210-224	Sponge sp. D	0.42	0.80	0.39	1.73	90.19
225-239	Fine sediment	2.73	17.71	5.65	30.83	30.83
225-239	Bryozoa	2.01	12.26	4.47	21.34	52.17
225-239	Tunicate sp. A	0.92	4.49	1.22	7.82	59.99
225-239	*Perkinsiana* sp.	0.99	4.42	1.21	7.70	67.69
225-239	Bryozoan sp. B	0.96	4.20	1.21	7.31	75.00
225-239	Tunicate sp. D	0.75	2.36	0.69	4.11	79.11
225-239	Dead bryozoan	0.75	2.34	0.67	4.07	83.18
225-239	Unidentified ophiuroid	0.64	1.97	0.69	3.43	86.61
225-239	Tunicate sp. C	0.59	1.36	0.52	2.38	88.99
225-239	Shell	0.50	1.35	0.52	2.35	91.34
240-254	Fine sediment	2.80	17.76	10.17	32.17	32.17
240-254	Unidentified bryozoan	1.90	11.52	7.73	20.87	53.04
240-254	Bryozoan sp. B	1.02	4.50	1.23	8.15	61.19
240-254	Unidentified ophiroid	0.87	3.89	1.26	7.04	68.23
240-254	*Perkinsiana* sp.	0.85	3.43	0.90	6.21	74.44
240-254	Sponge sp. E	0.65	2.00	0.70	3.62	78.05
240-254	Dead bryozoan	0.68	1.74	0.52	3.15	81.20
240-254	*Polymastia invaginata*	0.63	1.67	0.53	3.03	84.23
240-254	*Sphaerotylus antarcticus*	0.61	1.62	0.52	2.94	87.17

240-254	Unidentified demosponge	0.59	1.48	0.52	2.69	89.86
240-254	Tunicate sp. D	0.50	1.34	0.53	2.42	92.28
270-284	Fine sediment	2.76	19.09	7.49	31.85	31.85
270-284	Unidentified bryozoan	2.08	14.04	6.55	23.43	55.28
270-284	Bryozoan sp. B	1.20	5.89	1.18	9.83	65.11
270-284	Tunicate sp. D	1.07	4.90	1.25	8.18	73.29
270-284	*Perkinsiana* sp.	0.93	4.80	1.25	8.02	81.31
270-284	Unidentified ophiuroid	0.83	3.86	0.91	6.43	87.74
270-284	*Homaxinella balfourensis*	0.73	2.34	0.69	3.91	91.65
285-299	Fine sediment	2.79	21.90	5.64	42.62	42.62
285-299	Unidentified bryozoan	1.98	14.47	5.15	28.15	70.76
285-299	*Perkinsiana* sp.	0.88	3.95	0.90	7.68	78.44
285-299	Unidentified demosponge	0.71	2.70	0.69	5.25	83.69
285-299	Unidentified ophiuroid	0.55	1.66	0.53	3.22	86.91
285-299	Bryozoan sp. B	0.58	1.59	0.38	3.10	90.01
300-314	Fine sediment	2.88	22.88	4.12	39.37	39.37
300-314	Unidentified bryozoan	2.03	15.76	5.13	27.12	66.49
300-314	Tunicate sp. D	0.94	5.04	1.13	8.68	75.17
300-314	*Perkinsiana* sp.	0.74	3.02	0.83	5.20	80.37
300-314	*Homaxinella balfourensis*	0.63	2.29	0.60	3.94	84.31
300-314	Gravel	0.66	1.92	0.61	3.30	87.6
300-314	Unidentified ophiuroid	0.47	1.37	0.44	2.35	89.95
300-314	Tunicate sp. C	0.61	1.26	0.43	2.17	92.12

Note. Analysis performed on fourth root transformed percent cover and Bray-Curtis similarities to yield Avg. % cov., Av. Sim, Sim/SD, % Contrib, and Cum. %. Only the species contributing to the first 90% of differences between groups are listed. Avg. Sim =

the average similarity contribution of each functional group. Sim/SD = ratio of the average similarity contribution divided by the standard deviation. % Contrib. = Percentage of contribution to similarity within a site. Cum. %= Cumulative contribution.

Table 3. *SIMPER Analysis of Fauna at Species Level at Cape Armitage*

Depth (m)	Species	Avg. % cov.	Av. Sim	Sim/SD	% Contrib.	Cum.%
15-29	Spicule mat	2.13	13.42	1.05	32.10	32.1
15-29	*Polymastia invaginata*	1.41	9.67	1.64	23.13	55.22
15-29	Shell	1.23	8.48	1.58	20.27	75.49
15-29	Fine sediment	1.00	2.75	0.33	6.57	82.07
15-29	*Tetilla leptoderma*	0.62	2.37	0.51	5.67	87.74
15-29	Unidentified demosponge	0.67	2.17	0.51	5.19	92.93
30-44	Spicule mat	2.90	26.25	10.27	42.85	42.85
30-44	*Polymastia invaginata*	1.22	8.27	1.5	13.49	56.35
30-44	Shell	1.18	7.98	1.55	13.03	69.37
30-44	*Tetilla leptoderma*	1.05	5.81	0.95	9.49	78.87
30-44	Unidentified bryozoan	1.01	5.67	0.97	9.25	88.12
30-44	Unidentified demosponge	0.86	4.46	0.79	7.29	95.41
45-59	Spicule mat	2.66	23.34	5.72	47.00	47.00
45-59	*Tetilla leptoderma*	1.17	7.57	1.15	15.24	62.24
45-59	*Cellaria* sp.	1.50	7.06	0.80	14.22	76.46
45-59	Unidentified bryozoan	0.89	3.98	0.60	8.02	84.48
45-59	Unidentified demosponge	0.59	1.87	0.43	3.77	88.26
45-59	*Cinachyra antarctica*	0.55	1.82	0.44	3.67	91.92
60-74	Spicule mat	2.89	25.54	5.39	51.62	51.62
60-74	*Cellaria* sp.	1.40	7.78	0.85	15.72	67.34
60-74	*Hemigellius fimbriatus*	0.83	4.52	0.90	9.13	76.47
60-74	Unidentified	0.87	4.29	0.90	8.68	85.15

	bryozoan					
60-74	*Tetilla leptoderma*	0.55	1.51	0.40	3.05	88.20
60-74	*Perkinsiana* sp.	0.54	1.35	0.39	2.73	90.92
75-89	Spicule mat	2.49	20.91	1.47	54.50	54.50
75-89	*Tetilla leptoderma*	0.89	5.40	0.92	14.08	68.57
75-89	Fine sediment	1.05	2.73	0.39	7.13	75.70
75-89	*Hydrodendron arboreum*	0.74	2.2	0.39	5.75	81.45
75-89	Unidentified demosponge	0.56	1.86	0.40	4.84	86.29
75-89	Unidentified ophiuroid	0.50	1.49	0.40	3.89	90.18
90-104	Spicule mat	2.15	16.85	1.39	36.75	36.75
90-104	Fine sediment	1.79	10.3	0.94	22.47	59.22
90-104	Unidentified bryozoan	1.16	6.73	0.99	14.67	73.89
90-104	Unidentified demosponge	0.89	5.17	0.72	11.28	85.18
90-104	*Tetilla leptoderma*	0.52	2.14	0.51	4.68	89.85
90-104	*Perkinsiana* sp.	0.45	1.35	0.34	2.94	92.79
105-114	Spicule mat	2.99	31.64	6.03	59.31	59.31
105-114	Unidentified bryozoan	1.10	8.44	1.30	15.83	75.14
105-114	Unidentified demosponge	0.97	6.20	0.97	11.62	86.76
105-114	*Rossella* sp.	0.68	2.51	0.46	4.70	91.46

Note. Analysis performed on fourth root transformed percent cover and Bray-Curtis similarities to yield Avg. % cov., Av. Sim, Sim/SD, % Contrib, and Cum. %. Only the species contributing to the first 90% of differences between groups are listed. Avg. Sim = the average similarity contribution of each functional group. Sim/SD = ratio of the average similarity contribution divided by the standard deviation. % Contrib. = Percentage of contribution to similarity within a site. Cum. %= Cumulative contribution.