Spatial and temporal variation of coastal Ross Sea macrozoobenthos

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Abstract

Antarctic shallow-water communities are projected to undergo considerable changes in the coming decades due to the impacts of climate change on the prevailing environmental conditions. A clear understanding of these communities' vulnerability to change requires that the current relationships between environmental conditions and species assemblages be well understood. The benthic environment of the Ross Sea is subject to constant changes, including but not limited to changes in ice formations, salinity, light intensity, food types and food availability. The aim of this study was to quantify the temporal and spatial differences in macrozoobenthos between four coastal sites within the Ross Sea and determine the impact these abiotic factors could have on macrozoobenthic ecology.

The macrozoobenthic communities in four Ross Sea coastal sites (Cape Armitage and Cape Evans within the McMurdo Sound, and two sites within Terra Nova Bay, designated as Gondwana and Mario Zucchelli) were investigated, with multiple video transects taken from each site over the space of several years. Transects were taken at depths of 19 to 23 m, between late December and early January. 15 quadrats were selected at random for each of the transects, scaled to a size of 0.25 m^2.

Cape Armitage had the highest species diversity (Simpson's Diversity Index), while Mario Zucchelli had the lowest. Cape Evans and Gondwana shared a similar diversity. Cape Armitage was the most ecologically diverse, with most macrozoobenthos visible through the *Cinachyra barbata* spicule mat in evenly spaced clusters of diverse species. Cnidaria was the dominant phylum at Cape Armitage, while the remaining three sites were dominated numerically by two Echinoderms *Odantaster validus* and *Sterechinus neumayeri*, which were mainly observed on gravel and cobble substrates.

Macrozoobenthos species composition varied significantly between all four locations (One-way PERMANOVA *p* >0.001). A SIMPER analysis showed that Echinodermata (*S. neumayeri* and *O. validus*) and Cnidaria (*Alcyonium antarcticum* and *Artemidactis victrix*) were the main drivers of these differences. Only the Mario Zucchelli site showed a significant temporal difference over time, and there the change was marginal (*p* = 0.048). The change was largely due to an increase/decrease in the density of the main urchin species (*S. neumayeri*) between sequential year sampling. When data from all sites were combined, the species composition varied significantly across substrates (Two-way PERMANOVA, *p* >0.001), though it was hard to determine the underlying substrate in Cape Armitage due to spicule mats.

This research highlights the diverse benthic biota within the Ross Sea, and supports previous conclusions that assemblages are site-specific but rather stable over time. In terms of ongoing conservation and monitoring of the Ross Sea benthic environment, it points to the need for increased understanding of ecology in the Ross Sea for maintaining the diverse faunal communities found within the Southern Ocean.

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1 Introduction

1.1 The Ross Sea within the Southern Ocean

The Southern Ocean constitutes approximately 9.6% of the world's oceans, making it the fourth largest in the world (Kidawa & Janecki, 2011). The waters of the Southern Ocean outside of the intertidal zone are characterized by low and stable temperatures (Kidawa & Janecki, 2011). At latitudes greater than 74°S, which was where my study sites were located, the variation in water temperature is around ±1.8°C at depths of approximately 10-20 m (Convey et al., 2014; Kidawa & Janecki, 2011).

The oceanographic history of the Southern Ocean is complex. It took on its circumpolar structure following the separation of the Antarctic and Australian continental plates approximately 30 million years ago, and with the establishment of the circumpolar winds and currents, became increasingly isolated from its northern neighbours (Orsi, Whitworth, & Nowlin, 1995; Scher et al., 2015). Since then the location of the circumpolar front has been impacted by multiple variables, including climate change and glacial cycles, which have helped to shape the communities of marine benthic organisms residing south of the front by influencing salinity, sea ice dynamics, light levels and habitat availability (Convey et al., 2014; Thatje, Hillenbrand, & Larter, 2005).

The Ross Sea lies to the south of the Southern Ocean and is the southernmost sea in the world; it is also one of the most productive areas in the Southern Ocean in terms of biomass (Arrigo, & van Dijken, 2008). The Ross Sea varies over spatial (north-south) and temporal (seasonal, inter-annual and longer) scales, including ice cover, physical forcing from currents, wind, meltwater runoff, and biological processes such as phytoplankton blooms (Convey et al., 2014; Smith, Ainley, Arrigo, & Dinniman, 2014). Substantial meltwater inputs enter the

Ross Sea from the Amundsen Sea to the east, and are then transferred to the northern regions that are off the shelf via the Ross Gyre, a clockwise circulation of surface water, while outlet glaciers along the coast also contribute surface meltwater (Smith et al., 2014). Currents are predicted to change within the Ross Sea, likely due to changes in ice formation and northerly boundary conditions, with fluctuating abiotic (nutrients, temperature, ice cover etc.) and biotic (plankton recruitment and food) factors ultimately having a flow-on impact on the species composition throughout the region (Iriarte, Gómez, González, Nahuelhual, & Navarro, 2019; Smith, Sedwick, Arrigo, Ainley, & Orsi, 2012). Understanding the potential impacts of these changes on macrozoobenthos can be enhanced by a better appreciation of the current dynamics of species assemblages, and the factors that drive such variability.

1.2 Benthic Structure

The diversity of macrozoobenthos are frequently influenced by physical characteristics of the seabed, such as the complexity of seabed topography as well as the substrate type (Gutt et al., 2019; Rimondino, Torre, Sahade, & Tatián, 2015; Torre, Tabares, Mono, Meyer, & Sahade, 2017). This holds true especially for sessile organisms. Variations in faunal distribution tend to occur across environmental gradients, meaning that distinct clusters of benthic species can be sorted by their preferred substrate (Cummings, Thrush, Chiantore, Hewitt, & Cattaneo-Vietti, 2010; Gutt, 2007; Smith et al., 2014).

Soft substrate includes a wide range of particle sizes, including sand (0.0625 to 2 mm), silt (0.0039 to 0.0625 mm) and clay (less than 0.0039 mm) (Blair & McPherson, 1999; Blott & Pye, 2012). Conversely, hard substrate is larger, including scour-protective layers and large rocks such as bedrock and cobble (64 mm to 256 mm) (Blair & McPherson, 1999; Blott & Pye, 2012). Sedimentary processes can gradually change the seabed substrate composition to contain a greater ratio of soft sediment, thereby reshaping the benthic structure and favouring different species over time. The substrates found within the coastal regions of the Ross Sea range from fine particles such as silt and clay through to bedrock (Cattaneo-Vietti, Chiantore, Schiaparelli, & Albertelli, 2000b; Cummings et al., 2018; Kern, Rodrigues, & Absher, 2014; McClintock, Pearse, & Bosch, 1988b; Thrush et al., 2006). The sites investigated in this study have clearly distinct sediment types, with either large stones and bedrock, large gravel, or sand and smaller particles, making them easy to distinguish. The large stones originate from nearby land masses, and are known as drop stones (Gambi, Castelli, & Guizzardi, 1997; Post et al., 2017). The shifting of drop stones into benthic environments is caused by ice melt, and results in a patchwork of soft and hard substrates in a given area, therefore increasing the benthic species diversity on a small scale (Gambi et al., 1997; Post et al., 2017).

Benthic habitats can also consist of biogenic habitats, which are usually three-dimensional structures generated by ecosystem engineers (Rimondino et al., 2015). Jones et al. (1994) define ecosystem engineers as species that “directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain, and create habitats” (Jones, Lawton, & Shachak, 1994; Meadows, Meadows, & Murray, 2012). Organisms which alter the environment through the development of physical structures (shells, corals etc.) are known as autogenic engineers (Meadows et al., 2012). Biogenic structures can consist of organic matter as produced by autogenic engineers, such as coral and sponges. They can also consist of non-living structures, such as hardened substrate generated by allogenic engineers (Boström, Pittman, Simenstad, & Kneib, 2011; Ingall et al., 2013).

Biogenic habitats fulfil a range of functions, including protection of the sediment from erosion, increased nutrient recycling and benthic-pelagic coupling, supply of food and shelter and an overall increase in biodiversity (Boström et al., 2011; Ingall et al., 2013). The magnitude of an ecosystem engineer's impact varies depending on the organism itself and the surrounding biotic and abiotic factors (Jones, Lawton, & Shachak, 1997). The modification of the environment by ecosystem engineers can have varying spatial and temporal scales, often resulting in long cyclical changes (Jones et al., 1997; Meadows et al., 2012). Understanding these temporal changes are important, as there can be a follow-on effect to other species which depend on these structures for survival.

1.3 Environmental Drivers

The central focus of benthic ecology is in determining the relevance and roles of biological and physical factors in influencing spatial variation of the community. Habitat mapping is a useful tool in determining the spatial variation of different zones, and includes factors such as substrate type, bathymetry, species diversity and habitat distribution within a region (Kröger & Rowden, 2008; Lecours et al., 2015). Due to multiple interactions between various factors, linking these factors can be a challenging task, therefore it is useful to have an easily isolated study area such as Antarctica where external influences are limited (Smith et al., 2014). An improved understanding on how organisms respond to changes in environmental factors is important to facilitate the protection of rare and threatened species, and also to assess the state of the environment over time using indicator species as a proxy (Micallef et al., 2012; Post et al., 2017).

The structure of benthic communities can be strongly correlated with seabed topography, hydrodynamic processes, and sedimentary processes resulting from waves and ice scour (Clark, Stark, Palmer, Riddle, & Johnston, 2017; Cummings et al., 2018; Gutt et al., 2016; Gutt et al., 2019). A variable topography can provide shelter for a range of organisms with different needs, and an increased surface area to which sessile species can attach to (Gutt et al., 2016; Rimondino et al., 2015). On the other hand, hydrodynamic processes have a role in benthic community structuring by facilitating larval dispersal, transporting sediment and supplying nutrients (Cummings et al., 2018; Gutt et al., 2016; Passaelli, Oliver, Paterson, & Hubas, 2012; Shields et al., 2011). Dispersal of species is largely regulated by the Antarctic Circumpolar Current (ACC), which is a strong current that moves around the Antarctic continent (Iriarte et al., 2019; Janosik & Halanych, 2010; Kidawa & Janecki, 2011; Moles et al., 2015). The presence of the ACC limits the movement of species between the Southern Ocean and the surrounding waters (Iriarte et al., 2019; Janosik & Halanych, 2010).

Depth is also an important feature within the Ross Sea, with shallower habitats experiencing a greater degree of physical disturbance in the form of wind, waves and ice sedimentation compared to deeper habitats (Vause et al., 2019). This is a likely cause of the vertical zonation observed in the Ross Sea, as many organisms may not be able to survive or effectively compete within these more variable areas (Angulo-Preckler, Leiva, Avila, & Taboada, 2017). The greatest productivity and species diversity are found to occur in shallower depths, as there is an increase in light penetration driving primary production (Bowden, Clarke, Peck, & Barnes, 2006; Campana et al., 2018). Other important environmental variables include availability of food, richness of nutrients, temperature, light and salinity (Convey et al., 2014; Iriarte et al., 2019; Post et al., 2017), as well as glacial retreat (Gutt et al., 2016) and geomorphic variability (Post et al., 2017). These variations in environmental conditions may impact the diversity and composition of organisms by inducing selective pressure, resulting in spatial heterogeneity over time (Post et al., 2017). As of 2017, many driving factors of the community change are not well understood (Post et al., 2017; Rowden, Kröger, & Clark, 2015).

Due to the low temperatures and many changes in environmental conditions, the sublittoral zone of the Southern Ocean is a highly demanding habitat for benthic organisms (Krzeminska & Kuklinski, 2018). It has been found that the effect of some environmental drivers on benthic communities varies greatly between geographical regions (Krzeminska & Kuklinski, 2018; Post et al., 2017). Such variation could be due to water depth (where deeper waters have less variability and reduced impact from ice) and the resilience of the organisms present (Post et al., 2017). Seasonal changes such as the melting and freezing of surface water changes water salinity, sedimentation and ice scour (Gutt et al., 2016; Krzeminska & Kuklinski, 2018; Vause et al., 2019), which can then drive changes in biodiversity throughout the year, especially with mobile species that may migrate to more suitable environments (Krzeminska & Kuklinski, 2018). These effects are most prevalent in shallow waters close to land masses, as the ice can have a greater impact on the sediment below it (Angulo-Preckler et al., 2017). In these areas, hard benthic substrates can offer important support to sessile/rock encrusting organisms and limit the change in community structure (Krzeminska & Kuklinski, 2018).

1.4 Macrozoobenthos

Initially it was predicted that benthic diversity would be low within the Southern Ocean, and by extension the Ross Sea (Lagger, Servetto, Torre, & Sahade, 2017). However, following extensive research, it has been found that this hypothesis was incorrect (Lagger et al., 2017). Over 8800 described species were found within the Southern Ocean (including invertebrates and fish), 400 of which were found in the Ross Sea, with 40 of these being endemic to the Ross Sea (Moles et al., 2015; Smith et al., 2012). The Ross Sea is thus one of the most species-rich regions of the Southern Ocean, potentially due to the physical heterogeneity of habitats in the area (Moles et al., 2015; Smith et al., 2014).

Within the Ross Sea, the richness of benthic species varies between the major taxonomical groups (Kidawa & Janecki, 2011). Of the major groups, amphipods, ascidians, polychaetes, pycnogonids and certain groups of Echinodermata are well represented (Convey et al., 2014; Kidawa & Janecki, 2011). In comparison, the bivalves, gastropods, isopods and sponges are poorly represented (Convey et al., 2014; Kidawa & Janecki, 2011). Additionally, the Southern Ocean lacks any decapods (Convey et al., 2014; Kidawa & Janecki, 2011). When compared to similar species occurring in the lower latitudes, it was found that the growth and development of species in the Southern Ocean is approximately five times slower than their warm-water counterparts (Convey et al., 2014; Kang et al., 2019; Kidawa & Janecki, 2011), with subsequently lower rates of population turnover (Convey et al., 2014; Lagger et al., 2017). This is important as a slow rate of growth and population turnover results in a longer recovery time following any ecological disturbances (Bowden et al., 2006; Kim, Hammerstom, Conlan, & Thurber, 2010). The impacts from this lag in recovery time can be exacerbated in areas where disturbances are frequent, as the ecosystem will be unlikely to achieve a stable state even after a long timeframe, potentially contributing to the loss of certain species and therefore the loss of biodiversity (Kim et al., 2010).

Variations in biodiversity have historically been determined using regional species collections, thus existing knowledge is the most extensive in areas around established research centres, close to Ross Island and the Antarctic Peninsula (Dayton et al., 2019; Janosik & Halanych, 2010). When habitats are in spatial proximity to one another, a shared species distribution can often be observed (Carrea, Burridge, King, & Miller, 2016; Krzeminska & Kuklinski, 2018). However, this shared species distribution is not well understood within the Ross Sea (Boström et al., 2011; Carrea et al., 2016; Krzeminska & Kuklinski, 2018).

Benthic communities in the shallower waters of the Ross Sea are characterized by mobile species such as Echinoderms, while sessile species become more prevalent as the water becomes deeper, from depths of 15 m onwards (Smale, 2008). It was also noted by Smale (2008) that the abundance of mollusc species decreases with depth. The dominant phylum in McMurdo Sound is the Echinodermata, which show an increase in abundance going from 5 m to 20 m depth (Smale, 2008). Porifera and Cnidaria are the second most dominant taxa within McMurdo Sound (Cummings et al., 2018; Norkko et al., 2002; Thrush et al., 2006; Vause et al., 2019). A similar trend for Porifera and Cnidaria is observed in Terra Nova Bay; additionally, molluscs are also more common here compared to McMurdo Sound (Cummings et al., 2018; Gambi, Lorenti, Russo, & Scipione, 1994; Peña Cantero, Boero, & Piraino, 2013; Smale, 2008). Both McMurdo Sound and Terra Nova Bay are dominated by three species of rhodophytes, of which one is an encrusting coralline (Cattaneo-Vietti et al., 2000a; Gambi et al., 1994; Norkko et al., 2002; Thrush et al., 2006).

A decrease in the abundance of long-lived species within the Southern Ocean is a cause for concern – this has an impact on overall ecosystem functioning as some of these species have a role in forming habitats for other species (Angulo-Preckler et al., 2017). Gorgonians are one of the main structural benthic species within the Ross Sea, and this trend persists across both depth and latitude (Ambroso et al., 2017). Additionally, a reduction in water clarity and increase in turbidity as a result of suspended sediments has been linked to a reduction in biodiversity of benthic marine ecosystems (Angulo-Preckler et al., 2017). Exceedingly fine-grained sediments can smother certain infauna and clog gills (Lohrer, Hewitt, & Thrush, 2006; Vause et al., 2019).

1.5 Anthropogenic Influences

Antarctic marine habitats are greatly affected by changes in the climate, but less so by direct anthropogenic impacts (Smith, et al., 2014). An increase in trawling and other methods of industrial fishing have been found to have an adverse impact on other cold-water continental shelves, therefore there is a concern that this could eventually occur within the Ross Sea (Ambroso et al., 2017; Iriarte et al., 2019). However, while industrial fishing activity is present within the Ross Sea, it has been found to have little impact on the macrozoobenthos within this area (Ambroso et al., 2017). The food web and diversity in the Ross Sea is considered pristine, as industrial fishing in the area is limited, especially in areas with extended ice cover (Smith, et al., 2014). However, climate change has introduced seawater acidification due to an increase in dissolved carbon dioxide, which can ultimately shape the species composition of the years to come (Smith et al., 2014).

Changing climate is also expected to affect the Ross Sea due its impact on the ice cover (Smith et al., 2014). Compared to the rest of the Southern Ocean, this section has seen an increase in ice extent (Smith et al., 2014) and duration (Smith et al., 2014) in recent decades, resulting in a net increase in the Southern Ocean's ice cover since 1979 (Sansiviero et al., 2017; Smith et al., 2014). Models for future ice and atmospheric conditions (Smith et al., 2014) predict that this increase in ice cover will revert to substantial ice loss within the next 50 years (Smith et al., 2014). A reduction in ice cover and formation due to a warming climate can impact shallow water coastal communities (Gutt et al., 2016; Lagger et al., 2017) and expose more substrate that can be colonised, potentially driving seasonal and long-term changes (Gutt et al., 2016; Lagger et al., 2017).

The relative isolation of Ross Island from human activity makes it a useful testing location for hypotheses covering the effect of abiotic processes and species interactions in absence of anthropogenic effects (Smith et al., 2014). By performing studies in isolated habitats, a baseline can be obtained as a reference for studies involving habitats more prone to anthropogenic effects (Ambroso et al., 2017). This makes Ross Island an ideal location for setting up sentinel sites – sites where long-term monitoring can be used to assess slow changes within the area – to study the specific effect of climate change on benthic communities in the Ross Sea, with minimal confounding variables present (Ambroso et al., 2017).

1.6 Aims and Objectives

This study focuses on the changes in the Ross Sea benthic community assemblage over time. It is part of an extended research project across four locations in the Ross Sea, Antarctica; occurring from 1990 to the present, using video analysis and building off previous surveys. The motivation behind this study is to determine whether long-term changes and trends in macrozoobenthos community structure can be understood well enough to link these to fluctuations in abiotic factors (such as climate change and ice cover). These changes and trends may then provide further indicators of changing ecosystem functioning in the area.

The specific aims of the study were to investigate the following questions regarding variation in species diversity:

- How does the community structure vary between McMurdo Sound and Terra Nova Bay? Additionally, how did the community structure vary between the two sites in each of the two locations?

- How stable is the community structure over short time scales?
- Do certain sites exhibit more change over time when compared to other sites?
- What are potential causes resulting in the observed spatial and temporal variability? Were there physical differences at the site (depth, proximity to land, changes etc.) that could explain the changes?
- How does the substrate type (cobble, gravel, sand, undetermined) impact community structure? What visual trends in species type and size were observed based on substrate?

It was predicted that the overall species composition would vary between sites but not temporally. Between-site variance was expected to manifest as a dominance of certain species, and the presence of unique species in certain sites. Substrates, and therefore their encrusting species, was known to vary between sites, and the prevalence of taxa can be strongly linked to the availability of suitable substrate.

2 Methods

2.1 Study Area

Two distinct areas of the Ross Sea were examined in this study: The western side of Ross Island in McMurdo Sound (Southern Ross Sea), and Terra Nova Bay (Western Ross Sea) (Emslie, Polito, Brasso, P., & Sun, 2014). These areas fall within the Ross Sea Marine Protected Area, which was established by the CCAMLR (Committee for the Conservation of Antarctic Marine Living Resources) in December 2017 following international collaboration by New Zealand and the United States, meaning that the local fauna is currently under no threat of commercial fishing (New Zealand Foreign Affairs & Trade, 2020).

Two study sites were selected for each of the two areas. Cape Armitage and Cape Evans were selected within McMurdo Sound, while an unnamed site close to the Korean base at Jang Bogo Station (termed Gondwana) and a site close to the Italian Mario Zuchelli Station (termed Mario Zucchelli) were selected within Terra Nova Bay (Figure 1). The benthic environments of these locations consist of both soft and hard sediment substrates, with ratios of each varying greatly between the sites. Cape Evans and Cape Armitage consist mainly of volcanic gravel and large drop stones from the volcanic Ross Island (Cummings et al., 2018; Kiest, 1993; McClintock et al., 1988b). Gondwana and Mario Zucchelli are more variable, containing sections of solid rock with patches of sand scattered in-between, large sections of gravel, and mixtures of sand, rocks and boulders (Cattaneo-Vietti et al., 2000b; Gambi et al., 1997).

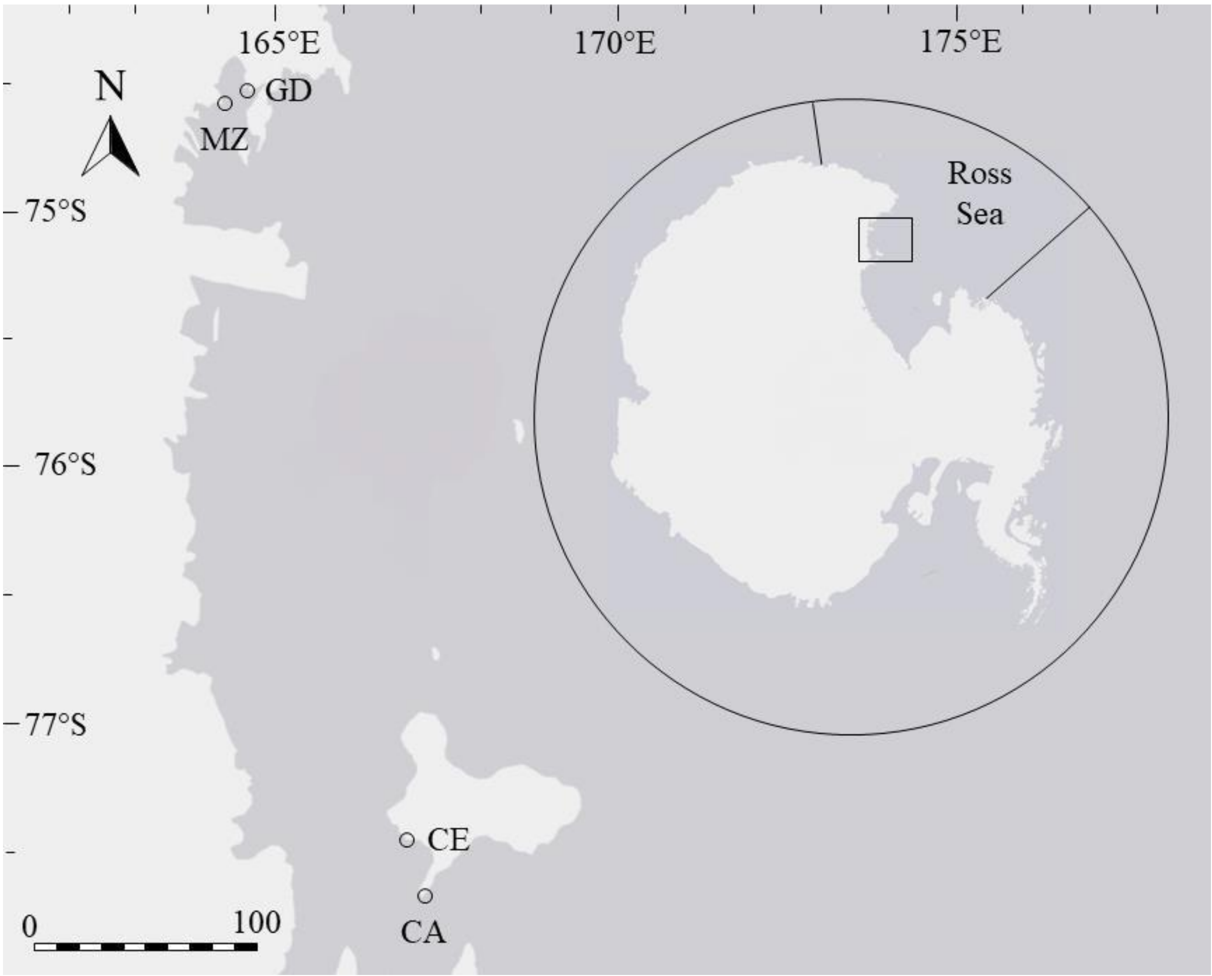


Figure 1. Map of the south western Ross Sea indicating the locations of study sites: CA = Cape Armitage (77° 51' 37"S 166° 41' 00"E), CE = Cape Evans (77° 38' 8"S 166° 24' 46"E), GD = Gondwana (74° 38' 15"S 164° 13' 47"E) and MZ = Mario Zucchelli (74° 41' 30"S 164° 5' 38"E).The inset shows the position of the expanded area. ArcMAP version 10.8.1 (ESRI, Redlands, CA).

2.2 Study Design

The study is part of an extended research project spanning 30 years, to determine changes in the macrozoobenthos community structure in the coastal regions of the Ross sea. Most of the data were obtained between years 2017 and 2019, with Cape Armitage having the oldest data dating back to 1990. Study sites were selected primarily for their proximity to resources. To avoid seasonal disturbance of the study sites due to ice formation and movement, all selected sites were situated below fast ice and anchor ice depths, while maintaining similar depths between all sites where possible (Dayton, Robilliard, & DeVries, 1969; Mager, Smith, Kempema, Thomson, & Leonard, 2011). The Mario Zucchelli site had a depth of 23m, with two of the 2017 transects taken at shallower depths, while the remaining sites had depths ranging between 18-20m. The primary data source was video records of the benthos taken via SCUBA diving along fixed transects, set up using a soft measuring tape or line anchored at each end. Where feasible, videos were taken not only from directly above, but also at 45-degree angles from the left and right of the transects. This allows for previously unidentified organisms found along the periphery of the transect to be better determined, as underwater videography tends to blur at the edges (Norkko et al., 2002). This was especially beneficial for sedentary organisms which would remain in approximately the same area over time. Two to three transects were set in each of the four locations, with each transect remaining in a fixed location. An additional point with two transects was taken for Mario Zucchelli in 2017.

Videos were taken using a mirrorless digital camera - a Sony A7IIs, equipped with a Sony FE 16-35mm f/4 ZA OSS Vario-Tessar T* Lens (fixed at 16mm), housed in a Nauticam Housing NA-A7II with a dome port. The camera was also equipped with two LED video dive lights (Keldan 4X Compact), held approximately 50 cm apart. The lens was held at approximately 0.75 m above the sea floor, determined using a weighted line attached to the camera. Despite best efforts, the depth of the lens varied slightly throughout the videos due to changes in topography and tension of the measuring line.

Throughout the project, data from each of the four sites were always taken during late spring to early summer (December to early January), as ice, water and clarity conditions during this time were the most favourable for conducting research. Older data from Cape Armitage precedes the video era and was recorded as on-site counts. From 2017 onwards, videos were used instead in the study for counting and checking purposes. These data were compared to historical data when possible.

2.3 Macrozoobenthos diversity

A total of eight videos, with two from each location, were counted to generate a complete macrozoobenthos list. Only macrozoobenthos which were large enough to identify from the videos were included, which effectively eliminated organisms of small size, any animals that fled the camera, and any infauna except where feeding organs were extended above the surface (i.e. some terebellid annelids and bivalves) (Meadows et al., 2012). Species observed in the videos were primarily identified using the Underwater Field Guide to Ross Island & McMurdo Sound, Antarctica by Bruenggeman (1998) and was mostly to species level. Chelicerata were not determined to species level as there are great similarities in appearance between species, making them challenging to distinguish in video frames. Highly mobile species were not counted to avoid counting the same organism more than once. This was especially important with fish, as they could be easily disturbed by the presence of the divers and were attracted to the lighting equipment used. Five species were observed to consistently obscure underlying substrate when they are present, four of which are algae. These include two types of seaweed (*Phyllophora antarctica* and *Iridaea cordata*), a pink coralline alga (*Leptophytum coulmanicum*) and a red coralline alga (*Hildenbrandia lecannellieri* Hariot). The fifth species is a sponge (*Cinachyra barbata*) which produces spicule mats.

2.4 Video Analyses

Two transects from each location were split into equal and non-overlapping quadrats, then counted for species richness. For the purposes of this study, species richness refers to the number of unique taxa encountered in the sampling site. These data were combined with counts performed in 1990 to compile a comprehensive species list for each site. For each consecutive quadrat, a count of any new species that were not found in previous quadrats was performed, to determine the point at which the number of new species found approaches zero (Figure 2). For Gondwana and Mario Zucchelli, the graph of new species found flattened out at no more than 11 quadrats (Figure 2. c and d), while for Cape Armitage and Cape Evans, the value at which the graph flattened out was between 10-15 quadrats (Figure 2. a and b). Therefore, 15 was selected as the upper limit for the number of quadrats to be counted for each transect.

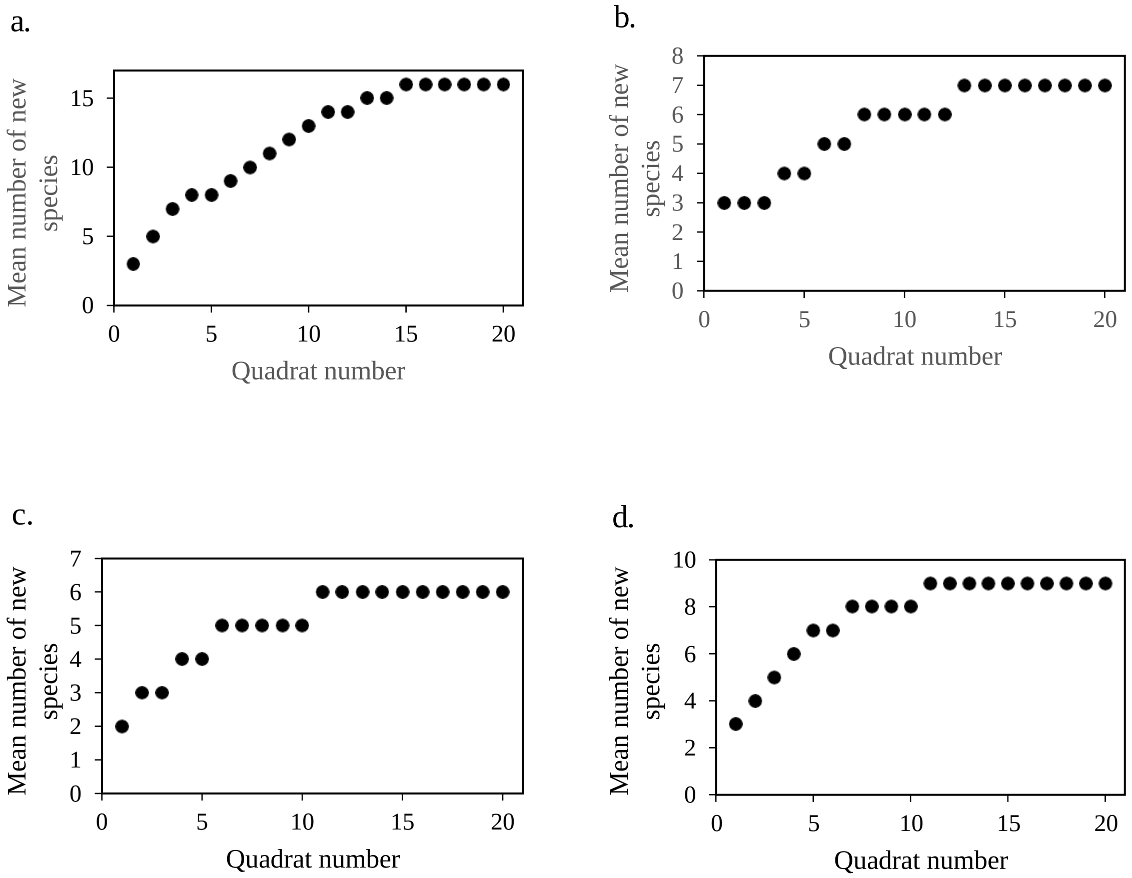


Figure 2. Scatterplot of cumulative species count by number of quadrats counted for Cape Armitage (a), Cape Evans (b), Gondwana (c) and Mario Zucchelli (d). The number of required quadrats for a species number estimate were determined using the value at which the line flattens out.

Once this guideline had been established, 15 quadrats were selected at random for each transect using a random number generator, with video timestamps a minimum of 4 seconds apart to prevent any overlap of quadrats. Quadrat size was set at 0.25 m^2, determined using the measuring tape. If the tape measure values were not visible, or if anthropogenic objects such as the positional tracking cards were present, another quadrat was selected instead. Quadrats were not taken where the topography was varied, as it would impact the total quadrat surface area; or if the tape measure was not level, as the varied distance of the tape measure from the camera lens would impact estimations of quadrat size.

Species density, defined as the number of individuals for each species, was determined for each quadrat, and summary statistics for these (mean and standard deviation) were calculated. Frequency was defined as the number of quadrats each species was found in. Organisms were only counted if more than half of their body was within the quadrat.

The percentage of area occupied by each substrate type, algae and spicule mats respectively was determined for the selected quadrats using ImageJ (version 1.52t) (Schneider, Rasband, & Eliceiri, 2012). Substrate patches were categorised manually into sand, gravel, cobble and undetermined, differentiated by size as follows: Sand (<2 mm), gravel (2-64 mm), cobble (>64 mm) (Blair & McPherson, 1999; Blott & Pye, 2012; Norkko et al., 2002), delimited as areas of interest and the area estimated. If the underlying substrate could not be determined due to obstruction, the substrate type was designated as undetermined.

2.5 Statistical analysis

Spirorbids (likely *Spirorbis antarctica* but video quality did not permit confirmation), *Clavularia frankliniana* and *C. barbata* were removed from the species list when performing statistical analyses. This was because the first two species were small in size and occurred in clusters, making them difficult to count accurately, and the last species had hair-like protrusions and occurred in dense spicule mats, making it difficult to determine the number of individuals present. However, it was possible to measure the frequency of these species. All statistical tests were conducted using R version 3.6.3 (Vienna, Austria), using the vegan version 2.5-6 package, unless stated otherwise.

Simpson's Diversity Index (SDI) was used to estimate level of diversity. SDI provides a metric that includes diversity as the number of species and the relative abundance of each species within a given area, with zero being a low diversity and one being high (Xu, Böttcher, & Chou, 2020).

It is often difficult to get a complete census in ecology, and the intensive effort involved to achieve a complete census can make it unviable (Chao, 1984). For this reason, estimators provide an acceptable level of data accuracy and greatly reduce the time investment required in generating a complete census. To provide an estimation of species richness in each of the study sites, the bias-corrected Chao-1 estimator was used (Chao, 1984; Silva, Ligeiro, Hughes, & Callisto, 2016). The Chao-1 estimator is known to be a suitable tool for determining the species richness of marine invertebrates, as it focuses on the abundance of rarer species rather than the species which are plentiful, to generate an upper and lower bound for species richness. A Chao-1 analysis was performed for the species data in R using the iNEXT version 2.0.20 package.

The assumptions for MANOVA were not met for my dataset, therefore a PERMANOVA based on a Bray-Curtis dissimilarity matrix of the species data was used instead. A non-parametric multivariate PERMANOVA test was used to determine whether there were significant differences when comparing substrate categories and sites. Spatial and temporal changes in species composition were tested using a PERMANOVA generated by the adonis function. For temporal changes, a Tukey post-hoc pairwise test was generated using agricolae version 1.3-2 to compare significant differences between the sites. The assumption of multivariate dispersion homogenous dispersion was tested. A two-way PERMANOVA, generated with the adonis function in R, was used to determine the interaction between species diversity and substrate type across sites.

The Bray-Curtis dissimilarity matrix was also used for a similarity percentages (SIMPER) analysis, to determine how much each species contributed to the overall dissimilarity observed between the sites.

A non-metric multidimensional scaling (nMDS) plot was used to visualise the species composition data. To reduce the impact of species that were sampled by chance on the overall data analysis, species were removed if they were present in two or fewer transects, and if the density of the species was less than 1 individual per 10 m^2. This reduced the number of species analysed from 51 to 22. A nMDS plot, derived from a Bray-Curtis dissimilarity matrix of the species density, was used to determine if differences in community density composition occurred between the four locations either spatially or temporally. A Tukey's post-hoc pairwise test was generated using agricolae version 1.3-2 to determine if there were significant differences between or within the sites.

3 Results

3.1 Environmental Variables

All sites were selected to have a depth just below the formation of anchor ice, as anchor ice can alter the sediment composition due to bulldozing of the sediment and can remove sessile and encrusting organisms. Therefore, selecting sites free from anchor ice and at approximately the same depths allowed for more comparable data on local species compositions over time. The transects for each site were also placed at a similar distance from land. Variations in ice cover throughout the year were observed across the different sites. All sites are covered in ice during the winter. Cape Armitage often maintains ice cover even during the summer, while ice surrounding the Cape Evans sites recedes only during mid to late summer (Lee, Lim, & Ewe, 2011; Miller & Pearse, 1991; Wing, McLeod, Leichter, Frew, & Lamare, 2012). In Gondwana, the ice cover is inconsistent as the ice formed is swept away from the site due to strong winds (Thrush & Cummings, 2011a). The Mario Zucchelli site is in a sheltered bay, allowing it to remain ice-locked for most of the year, similarly to Cape Evans (Lee et al., 2011; Vacchi, DeVries, & Evans, 2012; Wing et al., 2012).

A post-hoc pairwise test was performed, as substrate composition was found to vary significantly between all four sites (Pr(>F) >0.001 based on PERMANOVA). In terms of temporal variation, Cape Evans had no significant difference (Pr(>F) = 0.122), while Gondwana and Mario Zucchelli had a significant difference, with Pr(>F) = 0.024 and Pr(>F) = 0.031, respectively. Analysis of temporal variation could not be done for Cape Armitage as no substrate data was available for the older transects. Cobble or larger substrates was the most prevalent throughout the surveyed sites in terms of mean percentage coverage (30%), followed by undetermined substrate (27%), gravel (24%), and then sand or smaller (19%) (Table 1). A main point of interest lies in the distribution of this substrate and the thickness of the sandy sediment. Several of the species observed in this study were found to favour soft sediment, including the Antarctic scallop (*Adamussium colbecki*) and the Antarctic soft-shelled clam (*Laternula elliptica*). Neither were found in Gondwana, likely because the sandy sediment present was too thin to support their behaviours. An average of 71% of substrate in Gondwana consisted of cobble and rock, with much of it covered by a thin layer of sand that filled in the pits of the rock, giving it a patchy appearance (Figure 3; Table 1).

The substrate distribution of Mario Zucchelli consisted of large swathes of gravel, with small patches of sand and cobble in between (Figure 3; Table 1). The gravel occurring in Mario Zucchelli mainly consisted of the larger-grained variety, while the cobble consisted of several large drop stones and smaller cobble pieces. The main substrate found in Cape Evans was sand. The sand and smaller grains present in the area were covered by what appeared to be a fine, darker layer of unidentified “crust”, while cobble and gravel occurred in small clusters (Figure 3).

Cape Armitage consisted of thick *C. barbata* spicule mats, with small patches of sand observed where the mats were thinner (Figure 3). It is possible that the Porifera species generating these spicule mats may preferentially occur on larger substrate and not on sand, therefore obstructing any large substrate that may have been present under the spicule mat. Shell hash was most prevalent in Cape Armitage compared to the other sites and was found to occur on top of the mats. The presence of these spicule mats obscured the underlying substrate, making it difficult to determine during analyses. It may be pertinent to note that a *C. barbata* spicule mat was not recorded in the 1990 transect.

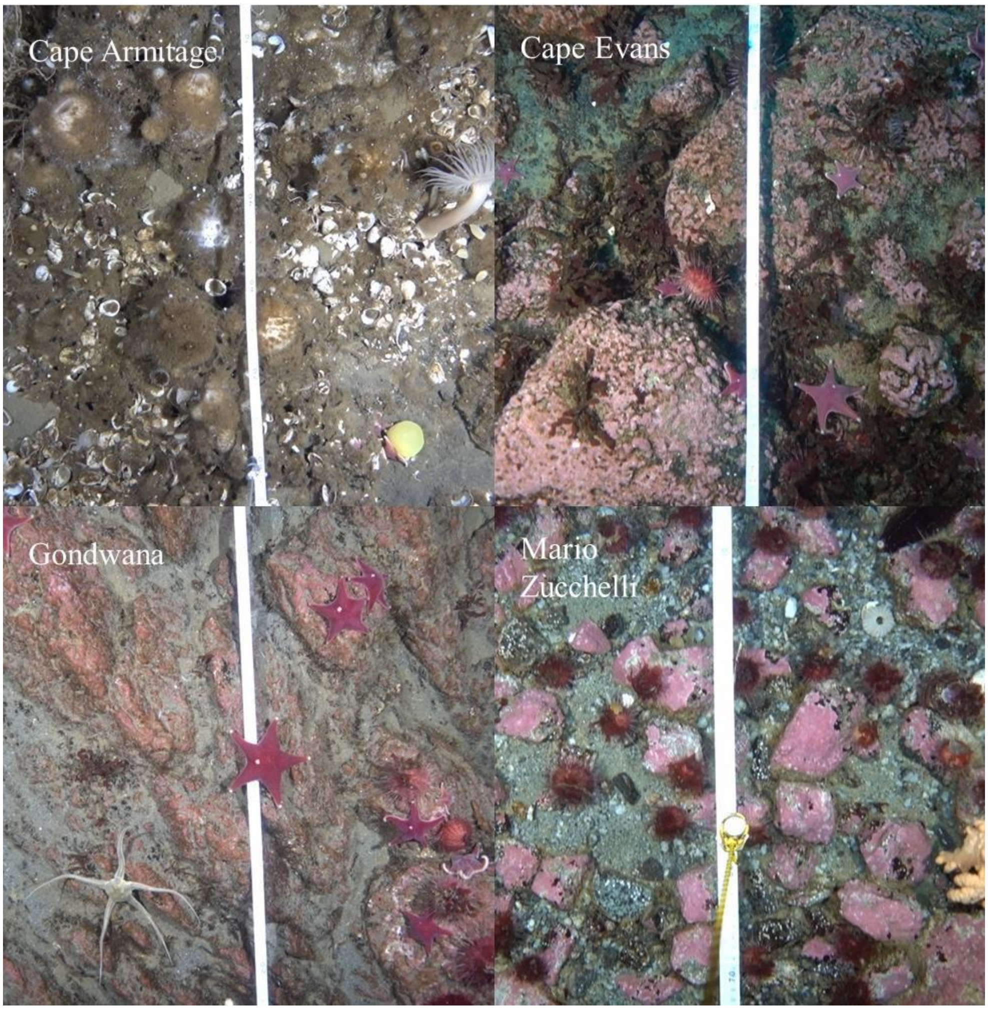


Figure 3. Image stills selected at random for each of the four study sites. The Cape Armitage image includes spicule mats, while seaweed can be observed in the Cape Evans image.

Table 1. Descriptive statistics of substrate category distribution for the study sites in terms of percentage coverage.

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Cobble (> 64 mm)	0	0	0	17	7	27	71	56	88	33	7	62
Gravel (2-64 mm)	0	0	0	23	12	32	11	0	29	63	35	89
Sand (< 2 mm)	9	4	15	44	30	57	18	12	25	4	2	5
Undetermined	91	85	96	16	5	24	0	0	0	0	0	1

3.2 Algae

The two dominant types of seaweed *P. antarctica* and *I. cordata* were combined into a single category, as the seaweed was sometimes attached to urchins, which makes it difficult to distinguish between the two species. Most of the seaweed resembled *P. antarctica*, while small pieces of what might be *I. cordata* were found attached to the sea urchins (*Sterechinus neumayeri*). This observation fits with research by Miller and Pearse (1991) finding that *I. cordata* occurred at depths around 3.5 m, while *P. antarctica* occurred around 12 m and deeper with a gradual transition to *L. coulmanicum*. This phenomenon was observed in sites which did not have a permanent ice cover. This same trend was observed for all transects in which seaweed was observed.

The seaweed was present at all sites apart from Cape Armitage (Figure 3; Table 2). Cape Evans was the only site where most of the seaweed observed was not attached to urchins, instead forming large clusters in between the surrounding cobble (Figure 3; Table 2). For the remaining two sites, the seaweed was either found attached to sea urchins or in small pieces along the substrate (Table 2). Shell hash was also observed in two of the sites: sparse clusters were found in one of the quadrats in Cape Evans 2017 PerTL1-R, and shell hash coverage occurred consistently in Cape Armitage, being found in every quadrat of the transects taken in 2018.

The two coralline species (*H. lecannellieri* Hariot and *L. coulmanicum*) were only observed on the larger gravel and cobble substrates. They were the most prevalent in Mario Zucchelli, and absent in Cape Armitage (Table 2). *L. coulmanicum* was the dominant species compared to *H. lecannellieri* Hariot (Table 2).

Table 2. Descriptive statistics of substrate-covering species distribution within the study sites in terms of mean percentage coverage.

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Hildenbrandia lecannellieri Hariot	0	0	0	0	0	0	0	0	1	4	0.	11
Leptophytum coulmanicum	0	0	0	2	0	8	1	0	2	37	8	53
Cinachyra barbata spicule mat	91	85	96	0	0	0	0	0	0	0	0	0
Phyllophora antarctica and *Iridaea cordata* total	0	0	0	18	9	24	1	0	2	3	1	6
Phyllophora antarctica and *Iridaea cordata* on substrate	0	0	0	17	7	23	0	0	2	0	0	0
Phyllophora antarctica and *Iridaea cordata* on urchins	0	0	0	1	1	2	1	0	1	3	1	6

3.3 Species Diversity and Density

A total of 56 taxa were recorded throughout the study, of which 18 were Porifera, nine were Cnidaria, nine were Mollusca, 10 were Echinodermata, one Nemertea, three were Annelida, four were from Rhodophyta, and two were Chordata (Table A1). All Arthropoda found were part of the sub-phylum Chelicerata. As it was difficult to distinguish between individual taxa, all Chelicerata species were combined into a single group called Chelicerata and considered as one taxon for the purposes of this study (Table A1). Thirty-seven taxa were found in Cape Armitage, 12 were found in Cape Evans, 13 were found in Gondwana and 23 were found in Mario Zucchelli (Figure 4). There was a significant difference in the number of taxa identified between each of the sites (*p*-value of >0.001) based on a one-way ANOVA, obtained from the mean diversity of each site.

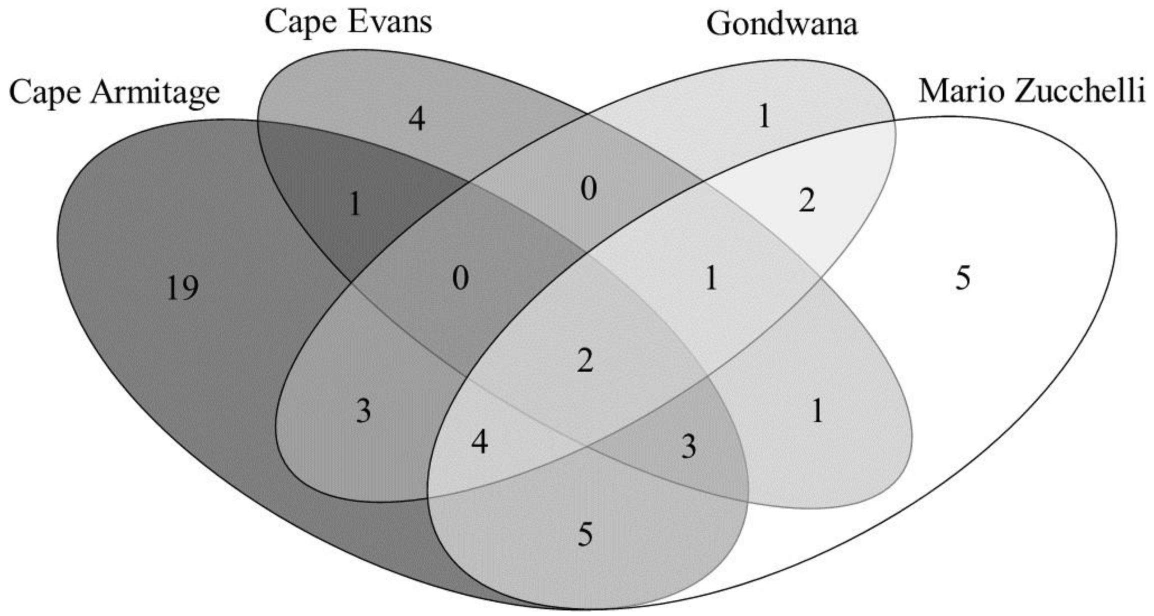
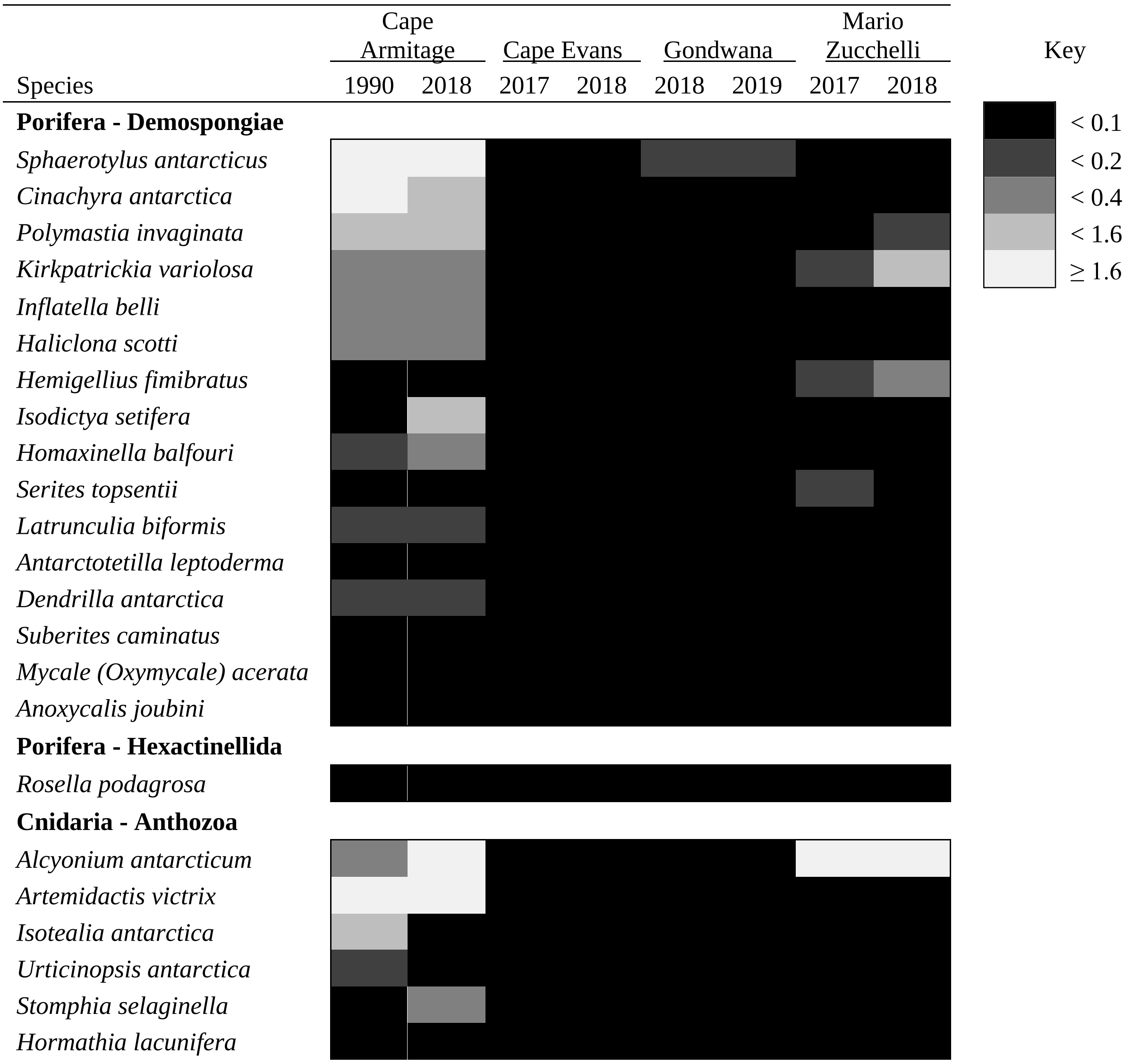


Figure 4. Venn diagram depicting the number of taxa across sites, and how these taxa are distributed.

Most organisms found in Cape Evans, Gondwana and Mario Zucchelli were Echinodermata, consisting mainly of *Odantaster validus* and *S. neumayeri* (Figure 5). The sea urchins (*S. neumayeri*) were found spread out evenly on the rocks and gravel, but appeared to avoid soft sandy sediment. *Odantaster validus*, the dominant species of starfish, was found to form 'trains' or clusters by sources of food; this was particularly evident in Gondwana 2019 Transect 3, where a single quadrat had approximately 9.5 times the average of the other quadrats (Figure 5; Table A1). This made it hard to determine the exact number of *O. validus* within this quadrat.



	Cape Armitage		Cape Evans		Gondwana		Mario Zucchelli	
Species	1990	2018	2017	2018	2018	2019	2017	2018
Porifera - Demospongiae								
Sphaerotylus antarcticus	□	□	■	■	▓	▓	■	■
Cinachyra antarctica	□	░	■	■	■	■	■	■
Polymastia invaginata	░	░	■	■	■	■	■	▓
Kirkpatrickia variolosa	▒	▒	■	■	■	■	▓	░
Inflatella belli	▒	▒	■	■	■	■	■	■
Haliclona scotti	▒	▒	■	■	■	■	■	■
Hemigellius fimibratus	■	■	■	■	■	■	▓	▒
Isodictya setifera	■	░	■	■	■	■	■	■
Homaxinella balfouri	▓	▒	■	■	■	■	■	■
Serites topsentii	■	■	■	■	■	■	▓	■
Latrunculia biformis	▓	▓	■	■	■	■	■	■
Antarctotetilla leptoderma	■	■	■	■	■	■	■	■
Dendrilla antarctica	▓	▓	■	■	■	■	■	■
Suberites caminatus	■	■	■	■	■	■	■	■
Mycale (Oxymycale) acerata	■	■	■	■	■	■	■	■
Anoxycalis joubini	■	■	■	■	■	■	■	■
Porifera - Hexactinellida								
Rosella podagrosa	■	■	■	■	■	■	■	■
Cnidaria - Anthozoa								
Alcyonium antarcticum	▒	□	■	■	■	■	□	□
Artemidactis victrix	□	□	■	■	■	■	■	■
Isotealia antarctica	░	■	■	■	■	■	■	■
Urticinopsis antarctica	▓	■	■	■	■	■	■	■
Stomphia selaginella	■	▒	■	■	■	■	■	■
Hormathia lacunifera	■	■	■	■	■	■	■	■

Key

■	< 0.1
▓	< 0.2
▒	< 0.4
░	< 1.6
□	≥ 1.6

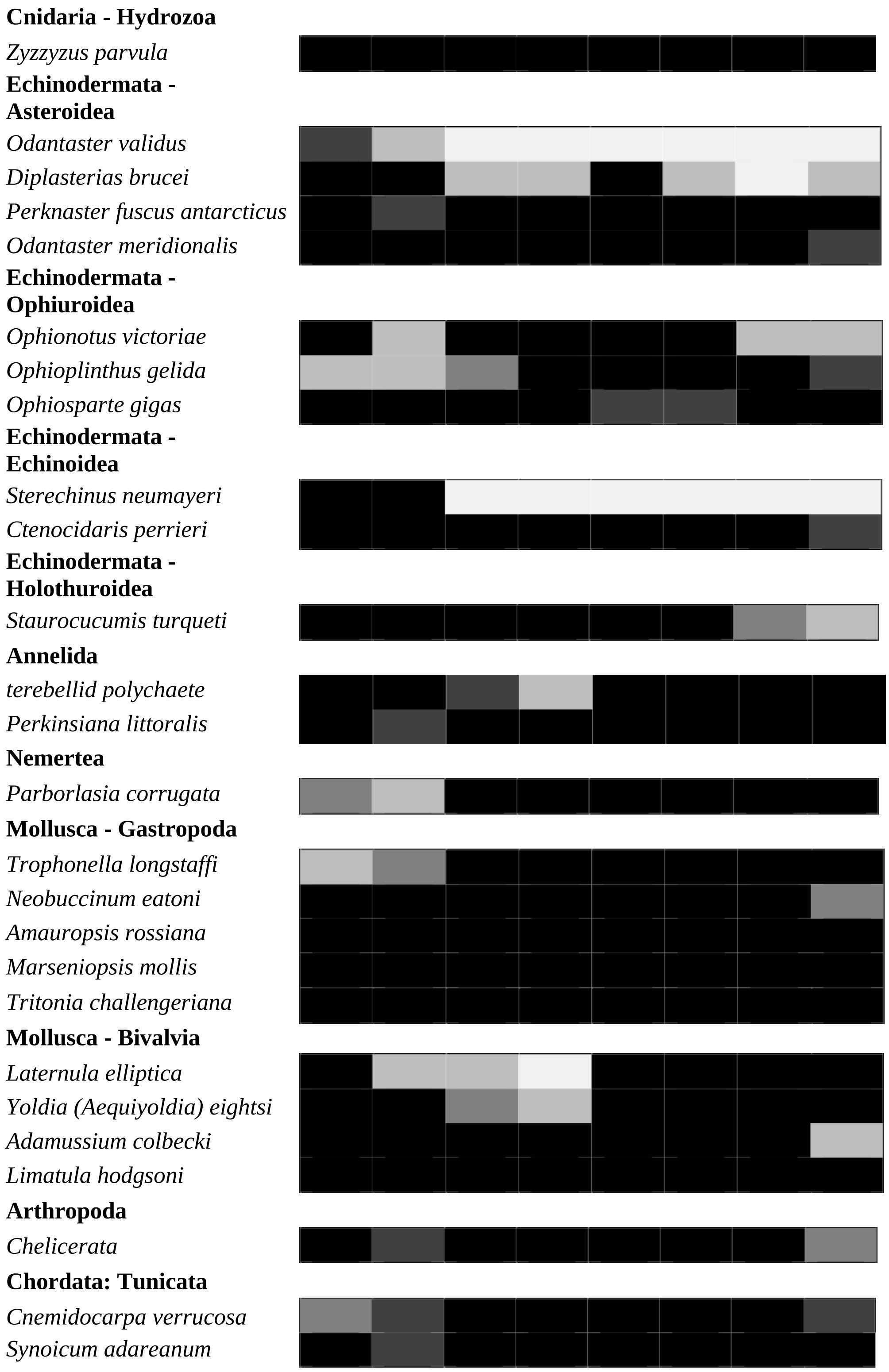


Figure 5. Heatmap depicting mean species density (#/m^2) across sites over time, based on video transect analyses. Species are divided into groups based on phylum, with certain phylum divided further based on class. Classes within each phylum are ordered from most to least diverse, and species within each class are ordered from highest to lowest density based on group. Figure key shows the cell colour representing each density category.

The frequency of species occurring on 75% or more transects in at least one study site was compared. Cape Armitage was dominated by Cnidaria (eight of the nine taxa) and Porifera (15 of the 18 taxa) (Figure 5; Figure 6). On average, Cape Armitage has the highest percentage of Porifera occurrence (88%), followed by Gondwana (13%) (Figure 6; Table A1). These two sites also had the greatest and second-greatest abundance of Cnidaria respectively (Figure 6; Table A1). The highest abundance of Echinodermata was observed in Mario Zucchelli (86%), followed by Cape Evans (63%), Gondwana (44%) and then Cape Armitage (40%) (Figure 6; Table A1). It is interesting to note that while Cape Armitage had the second highest species diversity for Echinodermata following Mario Zucchelli, it had the lowest population density out of all study sites (Table A1).

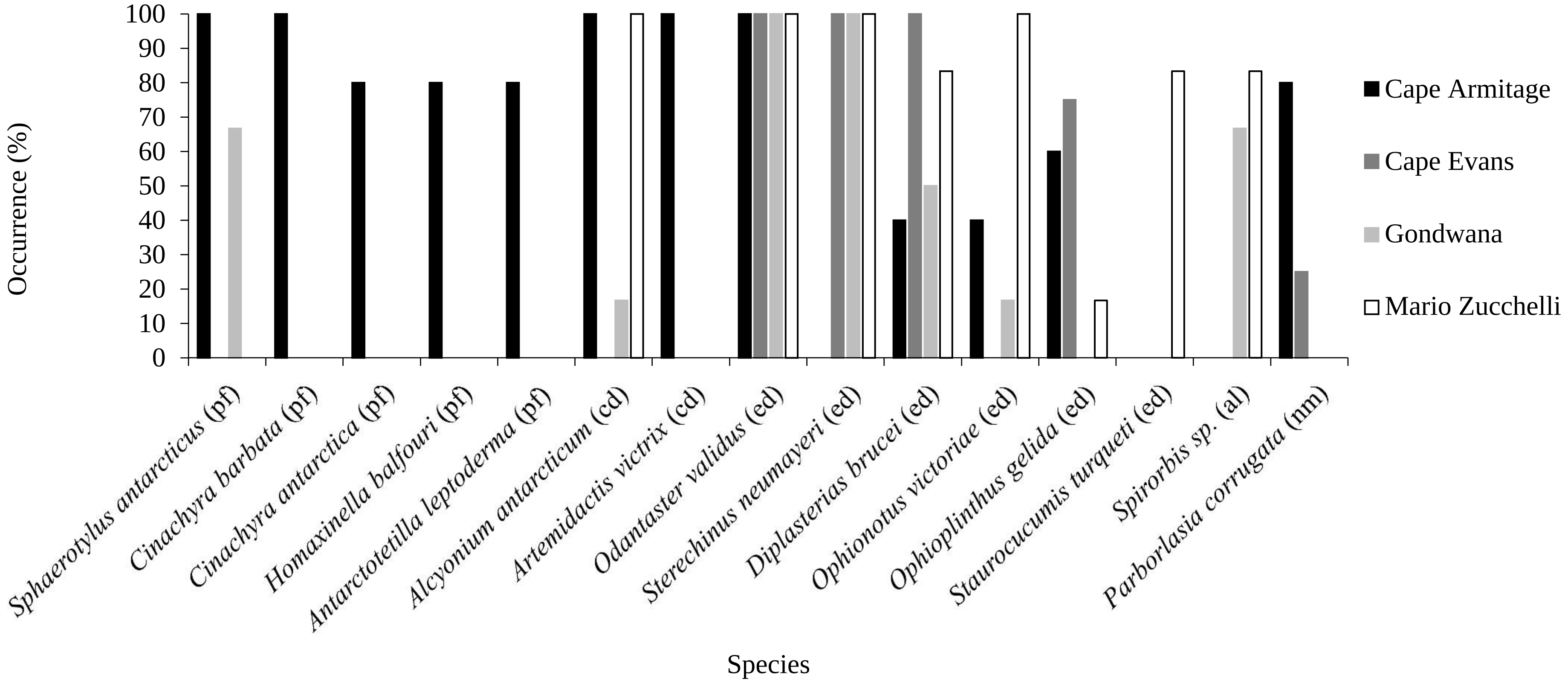


Figure 6. Percentage occurrence of macrozoobenthos species that are present on ≥75% of transects for at least one study site. Species are ordered by phylum, then from highest to lowest based on total percentage occurrence, with 100% occurrence indicating that the species was present in every transect for that study site. Figure key: al = Annelida, cd = Cnidaria, ed = Echinodermata, nm = Nemertea and pf = Porifera.

Direct comparisons were made between identical transects in sequential years; this was possible for Gondwana Transect 1 (2018 and 2019), Mario Zucchelli Transect 1 (2017 and 2018) and Mario Zucchelli Transect 2 (2017 and 2018). Under ideal circumstances, this would have been done for all the studied transects, especially for Cape Armitage which has a greater diversity of sessile organisms. Sessile species including *Sphaerotylus antarcticus*, *Kirkpatrickia variolosa*, *Hemigellius fimibratus*, *A. antarcticum*, *Urticinopsis antarctica*, *Cnemidocarpa verrucose*, *Mycale (Oxymycale) acerata* and *C. frankliniana* were counted for each paired transect. Of the eight species, the populations of four remained unchanged, three decreased and only one increased over time. Two new clusters of *C. frankliniana* were observed and one cluster was lost in Gondwana between years 2018 and 2019, resulting in an overall increase over time. One *S. antarcticus* organism was lost in Gondwana between years 2018 and 2019. *A. antarcticum* was found in both Mario Zucchelli transects, having an overall variation of less than 8% difference between years 2017 and 2018. Most of the variation in numbers of *A. antarcticum* in Mario Zucchelli were contributed by Transect 2. Only one *U. antarctica* organism was observed on Mario Zucchelli Transect 2 2017, and this individual was absent in 2018.

Simpson’s Diversity Index was used to quantify species diversity. Cape Armitage 1990 had the highest species diversity of all the transects, while Mario Zucchelli 2017 Transect 1 had the lowest (Figure 7). Cape Evans and Gondwana show a similar level of species diversity (Figure 7). Shallower transects in Mario Zucchelli showed a 9% higher diversity compared to deeper transects (0.35 in shallower transects compared to 0.26 in deeper transects). Cape Armitage and Cape Evans had a decrease in diversity over time when comparing the new to the old transects, with a 9% and 1.9% decrease, respectively. On the other hand, Gondwana and Mario Zucchelli showed a slight increase in diversity of 0.9% and 1.7% respectively.

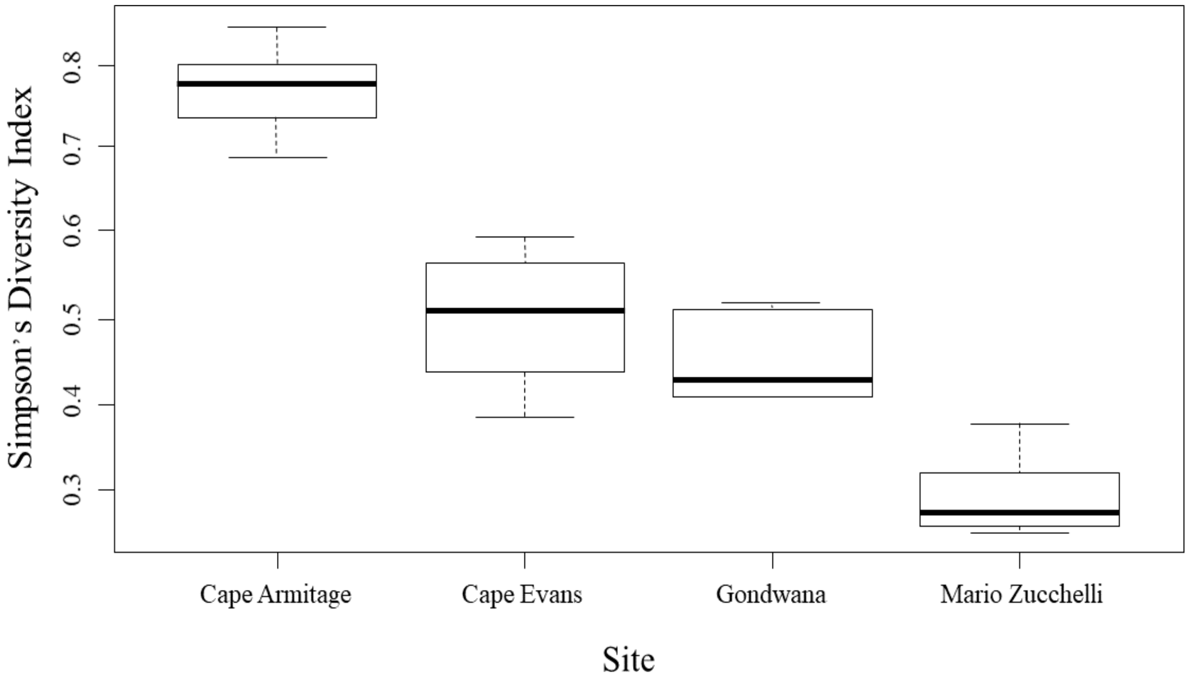


Figure 7. Box plot representing the median (±SD) Simpson's Diversity Index for macrozoobenthos for each of the four Ross Sea study sites.

Species richness for the four sites was extrapolated using the Chao-1 species richness estimator (Table 3). The lower limit values from the Chao-1 estimator matched those found during sampling (Table 3; Table A1). This trend did not occur for the upper limit as the estimation for Mario Zucchelli showed a higher value than sampling suggested (Table 3; Table A1). When comparing individual transects, Mario Zucchelli 2017 Transect 2 was an outlier with an upper limit of 136 (Table 3). This value is more than double that of the second highest transect within the site, resulting in a high variability for Mario Zucchelli. Cape Evans 2017 Transect PerT4 also stood out as an outlier, having an upper limit of 135, while the remainder of the transects in Cape Evans had a lower value than what was observed in Gondwana (Table 3). This outlier increased the upper limit in Cape Evans (mean of 46) compared to Gondwana (mean of 34), as Cape Evans would only have a mean upper limit of

16 with the outlier removed (Table 3). The estimated values for Cape Armitage were relatively consistent overall with what was observed during sampling.

Table 3. Chao-1 species richness estimator values for Ross Sea macrozoobenthos across four coastal benthic sites. Estimator = Estimated number of taxa, Est_s.e. = Estimated standard error, 95% Lower = Lowest number of taxa with 95% confidence and 95% Upper = highest number of taxa with 95% confidence.

Site	Year	Transect	Observed	Estimator	Est_s.e.	95% Lower	95% Upper
Cape Armitage	2018	A1	13	15	3	13	27
	2018	A2	18	26	7	20	55
	2018	B1	17	21	5	18	42
	2018	B2	19	21	2	19	32
Cape Evans	2017	ExT1	6	8	4	6	28
	2017	PerT4	10	28	23	12	135
	2017	PerT1	5	5	1	5	10
	2018	T1	6	6	1	6	11
Gondwana	2018	T1	5	6	2	5	18
	2018	T2	4	5	2	4	17
	2018	T3	6	10	7	6	46
	2019	T1	6	7	2	6	19
	2019	T2	7	10	4	7	31
	2019	T3	9	17	11	10	73
Mario Zucchelli	2017	L	8	8	1	8	13
	2017	R	9	13	7	9	49
	2017	T1	9	11	4	9	31
	2017	T2	11	29	23	13	136
	2018	T1	11	17	7	12	50
	2018	T2	14	23	10	15	66

3.4 Spatial Changes

A non-metric multidimensional scaling ordination (nMDS) was used to examine patterns in species density composition between sites and years (Figure 8). The stress value was <0.2, which provides a “potentially useful” picture, although closer to 0.2 little reliance should be placed on the fine structure of the plot, unless the course differences are compelling. The same trends and a slightly higher stress value were observed when no species were removed to minimize noise in the data.

Based on Figure 8, Cape Armitage was distinct from the other three sites across Coordinate 1, with the former being found to the far left of the graph. The Cape Armitage transects form a loose cluster, with the 1990 and A2 transects being the furthest from the rest of the cluster (Figure 8). While the remaining three sites were found to the far right of Figure 8, Mario Zucchelli was distinct from Cape Evans and Gondwana across Coordinate 2. The Mario Zucchelli transects formed a tight cluster with both years being similar; however, two of the transects from 2017 that were taken at a slightly shallower depth are slightly further away from the main cluster (Figure 8). Cape Evans and Gondwana were also highly similar, forming a tight cluster for all transects except the Gondwana 2019 Transect 1 (Figure 8). There was a significant difference between the sites based on the PERMANOVA (Table 4). A post-hoc test showed that all but one of the comparisons were significantly different; Cape Evans and Gondwana were the only pair that did not show significant differences.

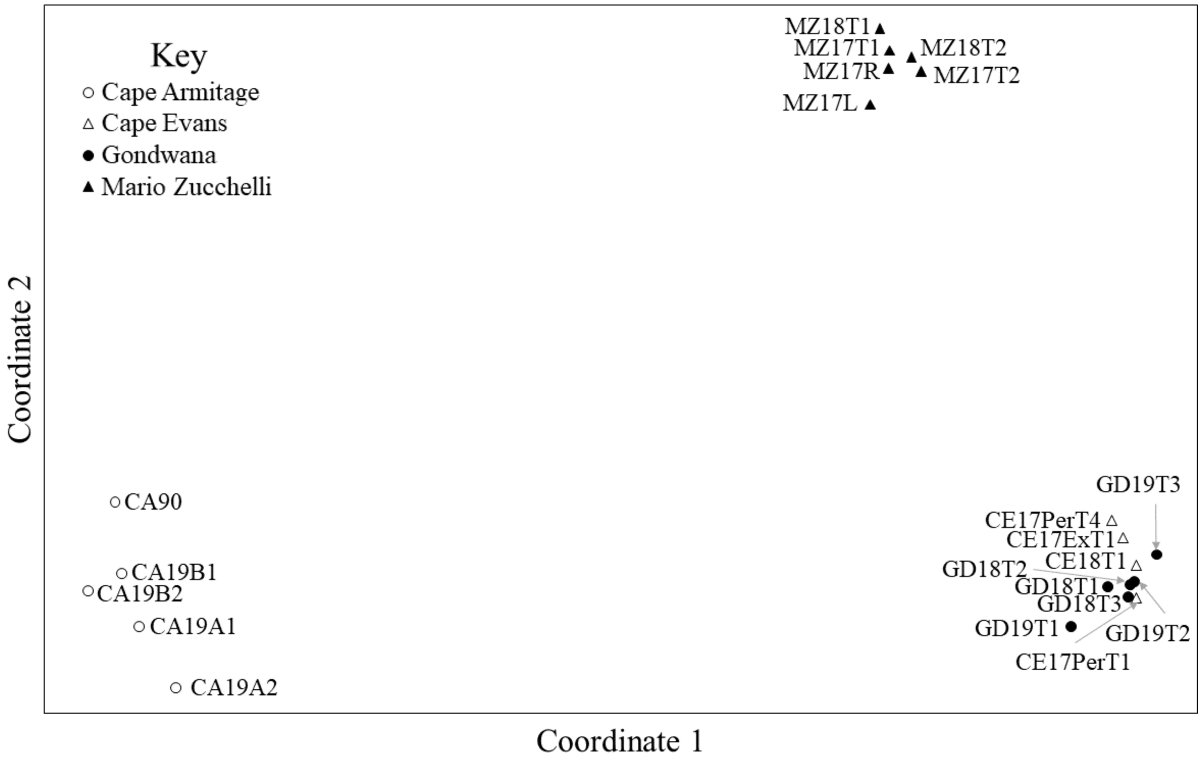


Figure 8. Non-metric multidimensional scaling ordination (nMDS), showing species density from each study site. Individual transects are identified using CA = Cape Armitage, CE = Cape Evans, GD = Gondwana and MZ = Mario Zucchelli, followed by the year (two digit) and the transect name. Stress value = 0.127.

Table 4. One-way PERMANOVA test (Bray-Curtis dissimilarity, 9999 permutations) performed on macrozoobenthos as a function of sites. Significance P(perm) <0.05 in bold.

	Source	df	MS	Pseudo-F	R^2	P(perm)
Macrozoobenthos	Site	3	14.294	87.728	0.476	**0.001**
	Residuals	290	0.163		0.524	

A similarity percentages (SIMPER) analysis was used to identify the contribution of each species to the observed dissimilarity between the four sites (Table 5). It was found that the highest dissimilarity was between Cape Armitage and Mario Zucchelli (98.349), and the lowest was between Cape Armitage and Gondwana (47.117). The greatest average dissimilarity was attributed to *S. neumayeri* (50.327%), occurring with the highest density in

Mario Zucchelli, which was 10 times greater than the next highest density, found in Cape Evans. *O. validus* (23.293%) contributed the second highest average dissimilarity and was found most abundantly in Cape Evans; followed by *A. victrix* (17.814%), which was only found at Cape Armitage (Table 5; Table A1). Only four species were found to have a greater than 4.5% variation; these were: *A. victrix* (Cnidaria), *O. validus* (Echinodermata), *S. antarcticus* (Porifera) and *S. neumayeri* (Echinodermata) (Table 5). *S. neumayeri* contributed greater than 4.5% variation in all comparisons (Table 5). Similar to the temporal comparisons, spatial comparisons involving Cape Armitage have the highest number of taxa showing a greater than 4.5% variation (Table 5).

Table 5. SIMPER analysis of species data from each of the study sites. Species were only included if the dissimilarity was greater than 4.5%.

Sites	Species	Average density comparison		Contribution (%)	Dissimilarity (%)
CA vs CE	*Odantaster validus*	0.643	21.200	35.050	97.399
	Sterechinus neumayeri	0.000	11.533	19.468	
	Artemidactis victrix	9.364	0.000	16.220	
	Sphaerotylus antarcticus	3.934	0.000	7.401	
CA vs GD	*Odantaster validus*	0.643	14.800	34.294	96.878
	Artemidactis victrix	9.364	0.000	19.407	
	Sterechinus neumayeri	0.000	5.889	15.211	
	Sphaerotylus antarcticus	3.934	0.178	9.000	
CA vs MZ	*Sterechinus neumayeri*	0.000	113.200	67.925	98.349
	Hormathia lacunifera	0.014	0.000	7.875	
	Odantaster validus	0.643	9.911	6.253	
	Alcyonium antarcticum	1.710	7.422	5.104	
CE vs GD	*Sterechinus neumayeri*	11.533	5.889	51.020	47.117
	Odantaster validus	21.200	14.800	34.463	
CE vs MZ	*Sterechinus neumayeri*	11.533	113.200	72.502	75.808
	Odantaster validus	21.200	9.911	15.641	
	Alcyonium antarcticum	0.000	7.422	5.463	
GD vs MZ	*Sterechinus neumayeri*	5.889	113.200	75.833	80.525
	Odantaster validus	14.800	9.911	14.055	
	Alcyonium antarcticum	0.044	7.422	5.466	

3.5 Temporal Changes

A one-way PERMANOVA and SIMPER analysis was conducted to determine the temporal variation at sites. No significant difference over time was found for three of the four study sites (P(perm) > 0.05) (Table 6). A significant difference was found using PERMANOVA for Mario Zucchelli, even when depth was controlled and accounted for (P(perm) = 0.048) (Table 6). A SIMPER analysis showed that this variation in Mario Zucchelli mainly reflected an increase in abundance of the mobile species *S. neumayeri* over time (Table 7). While PERMANOVA found no overall difference over time, *O. validus* contributed the most to the variation at Cape Evans and Gondwana (Table 7). *S. neumayeri* supplied the second largest contribution to the temporal variation for Cape Evans and Gondwana (Table 7). Cape Armitage had the highest number of unique taxa that contributed more than 4.5% of variation between the old and new transects; however, *O. validus* and *S. neumayeri* were not present amongst those taxa (Table 7). It was expected that mobile species such as these Echinodermata would contribute the most to short-term temporal variation, as they are able to relocate to the most favourable locations (Table 7). This was not the case for Cape Armitage where a far greater time gap was present between samplings, with variation in species composition largely involving sessile species (Table 7). It was found that Cape Armitage had the highest average dissimilarity, while Mario Zucchelli had the lowest average dissimilarity when comparing the old to the new transects (Table 7).

Table 6. One-way PERMANOVA tests (Bray-Curtis dissimilarity, 9999 permutations) performed on macrozoobenthos as a function of time. Significance P(perm) <0.05 in bold. *Shallower transects excluded from analysis.

Site	Source	df	MS	Pseudo-F	R^2	P(perm)
Cape Armitage	Year	1	0.236	0.739	0.013	0.657
	Residuals	58	0.320		0.987	
Cape Evans	Year	1	0.168	1.433	0.024	0.261
	Residuals	58	0.117		0.976	
Gondwana	Year	1	0.095	0.689	0.008	0.606
	Residuals	82	0.138		0.992	
Mario Zucchelli	Year	1	0.902	8.656	0.090	**0.001**
	Residuals	88	0.104		0.910	
Mario Zucchelli*	Year	1	0.205	2.8841	0.047	**0.048**
	Residuals	58	0.071		0.953	

Table 7. SIMPER analysis using species data from the four study sites, comparing older and newer transects. Species were included if the dissimilarity was greater than 4.5%.

Site	Species	Average density comparison		Contribution (%)	Dissimilarity (%)
Cape Armitage	*Cinachyra antarctica*	3.929	0.150	22.200	73.216
	Artemidactis victrix	4.956	2.567	21.243	
	Sphaerotylus antarcticus	1.805	1.117	8.400	
	Ophionotus victoriae	0.000	0.050	6.659	
	Polymastia invaginata	0.920	0.133	4.941	
	Trophonella longstaffi	0.814	0.050	4.787	
Cape Evans	*Odantaster validus*	4.844	6.667	51.251	46.045
	Sterechinus neumayeri	3.111	2.200	76.450	
	Laternula elliptica	0.267	0.667	4.593	
Gondwana	*Odantaster validus*	3.867	4.933	57.431	46.954
	Sterechinus neumayeri	1.667	1.778	34.137	
Mario Zucchelli	*Sterechinus neumayeri*	24.483	35.933	73.324	41.045
	Odantaster validus	2.200	3.033	10.071	
	Alcyonium antarcticum	1.683	2.200	9.357	

3.6 Species Communities Across Substrates

A two-way PERMANOVA was conducted to determine if species composition varied significantly between sites based on substrate composition. Species composition varied significantly for each substrate type across the four sites (P(perm) >0.001), apart from the undetermined type (P(perm) = 0.914) (Table 8). This is probably because the undetermined substrate was mainly observed in Cape Armitage and not the other sites, where it was primarily made up of sponge spicule mat, while the other substrate types were well distributed across all sites, allowing between-site differences to develop (Table 1). Based on the post-hoc pairwise test performed, Gondwana showed greater variation in species composition on cobble compared to all the other sites, while Cape Evans showed the least variation when compared to Mario Zucchelli (Table 8). Mario Zucchelli showed the greatest variation for species composition on gravel compared to all the other sites, while Gondwana showed the least variation when compared to Cape Evans (Table 8). Cape Armitage did not have any cobble or gravel, and therefore could not be used in those comparisons (Table 8). Species composition on undetermined substrate was significant for all comparisons apart from Gondwana and Mario Zucchelli (*p*-value of 0.996), likely due to the low occurrence or complete absence of this substrate category in those transects (Table 8). No significant difference was observed when comparing the same site over time for any of the substrate categories (Table 8).

Table 8. Two-way PERMANOVA test (Bray-Curtis dissimilarity, 999 permutations) performed on substrate composition as a function of community structure by site. Significance P(perm) <0.05 in bold. Post-hoc pairwise tests indicate significance between sites. SxSi: interaction between substrate and site.

Substrate category	Source	df	MS	Pseudo-F	R^2	P(perm)	Post-hoc pairwise tests
Cobble	SxSi	1	5.806	27.596	0.065	**<0.001**	GD≠CA GD≠CE GD≠MZ GD≠MZ
Gravel	SxSi	1	13.956	66.33	0.156	**<0.001**	MZ≠CA MZ≠CE MZ≠GD
Sand	SxSi	1	0.085	43.594	0.102	**<0.001**	CE≠CA CE≠GD CE≠MZ MZ≠GD
Undetermined	SxSi	1	0.210	0.406	0.001	0.914	MZ=GD
	Residuals	288			0.676		

Sessile taxa from the Cnidaria, Chordata and Rhodophyta were only found to occur on the very coarse gravel (32-64mm) and larger substrate sizes where the substrate was visible (Blair & McPherson, 1999; Blott & Pye, 2012). Mollusca favoured the smaller substrate sizes such as fine gravel (4-8mm) or smaller (Blair & McPherson, 1999; Blott & Pye, 2012), while Porifera favoured the larger substrate sizes. Echinodermata varied in their preference of substrate sizes, with the urchin *S. neumayeri* favouring coarser substrates, and the sea cucumber *Staurocucumis turqueti* found exclusively in Mario Zucchelli favouring smaller substrates. No trend was observed for the remaining taxa.

4 Discussion

4.1 Spatial and Temporal Variations in Macrozoobenthos

In this study, I investigated the spatial and temporal variations of Ross Sea macrozoobenthos at four sites, with two sites being in McMurdo Sound (Cape Evans and Cape Armitage) and the two in Terra Nova Bay (Gondwana and Mario Zucchelli). McMurdo Sound and Terra Nova Bay are both well-known, extensively studied regions in the Ross Sea. Previous studies involving Cape Armitage and Cape Evans can be reliably compared to my investigation, as the site locations are well defined and relatively small. On the other hand, Terra Nova Bay encompasses a large area, and relatively few of the studies describing “Terra Nova Bay” biota are likely to have occurred in the same location as my studies. Therefore, comparisons with historic Terra Nova Bay research need to be undertaken carefully. Based on the results of this study, there was a significant spatial difference overall between sites, but no significant temporal change.

It was expected that sites within the same region (McMurdo Sound and Terra Nova Bay) would be more comparable to each other than to those of the other region; however, the results paint a different picture. An overview of all four sites showed that Cape Armitage was the odd site out in terms of species composition, with all the other sites being equally dissimilar to it. The Terra Nova Bay sites also showed little similarity to each other, with Gondwana more closely resembling Cape Evans in McMurdo Sound. In fact, Cape Evans and Gondwana are so incredibly similar in terms of species diversity that they are almost indistinguishable from each other based on the MDS (Figure 8). This confirms that geography may play a smaller role in defining species compositions than initially expected.

To better understand why variations between sites occur, it is important to understand the feeding guilds present within this region. Each feeding guild is influenced differently by the environment and by other species around them based on their needs and role in the ecosystem. Environmental conditions and species interactions within each site can therefore impact the success of various feeding guilds, which in turn shapes the species diversity in that site. A wide range of observed taxa have more than one feeding method. Many macrozoobenthic taxa are filter feeders, including Mollusca – Bivalvia, Annelida, Porifera, and Chordata – Tunicata, the latter two of which are exclusively filter feeders (Table A1). Suspension feeders include the Cnidaria and Annelida, while deposit feeders were found in Echinodermata, Annelida, Mollusca – Gastropoda, and Arthropoda (Table A1). Many marine invertebrates are also predators, including Cnidaria, certain Echinodermata, Nemertea, Mollusca and Arthropoda, and all are also scavengers except for Mollusca. Other species of Arthropoda and Echinodermata prefer grazing on algae (Table A1).

Six main methods of feeding were found within this study. Based on the species densities obtained, the dominant feeding types are filter feeding, grazing, predation, and scavenging, while deposit and suspension feeding was less prevalent. Cape Armitage is dominated by filter feeders (Porifera), followed by suspension feeders (Cnidaria) and certain predators (Cnidaria and Echinodermata) (Table A1). This is consistent with research conducted by Conlan et al. (2004), which found that Porifera was the dominating phylum in Cape Armitage, especially at depths of 30 m or less. The remaining three sites were dominated by Echinodermata, with the two dominant species being *O. validus* and *S. neumayeri* (Cattaneo-Vietti et al., 2000a; Kang et al., 2019; Thrush & Cummings, 2011a). The former is part of all mentioned feeding guilds apart from suspension feeding, while the latter is predominantly a grazer and deposit feeder (McClintock, 1994; Obermüller, Morley, Barnes, & Peck, 2010; Peck, Webb, Miller, Clark, & Hill, 2008).

A notable distinction between the two McMurdo Sound sites is the different sizes of the dominant species *O. validus*, with specimens found in Cape Evans being larger overall. A study by Dayton et al. (1974) also found that *O. validus* has been declining in Cape Armitage. The most likely explanation for these observations is food availability – increased food productivity in Cape Evans could have led to higher growth rates and densities, while certain factors such as low productivity or competition in Cape Armitage may have induced their decline (Dayton et al., 1974). This finding would explain why there was an overall decline in the density of this species in Cape Armitage when comparing the old (0.8 $\#/m^2$) and the new (0.2 $\#/m^2$) transects.

No variation in feeding guilds was observed temporally, with the dominant feeding guilds remaining consistent, though some differences were observed in the species compositions (Figure 5). Cape Armitage showed the least temporal variation, even though the transects had the largest time interval between them; this was expected as Cape Armitage had the greatest diversity of sessile organisms. However, recent literature has suggested that Cape Armitage is highly variable both spatially and temporally (Kim, Hammerstom, & Dayton, 2019). It is important to note that Cape Armitage was only sampled across two points in time, and only in a small section of the site, therefore the results from my study may not be representative of the whole site. In contrast to Cape Armitage, Mario Zucchelli had a significant temporal difference between the old and new transects. The cause for this is unclear, though the greater density of mobile species within this site compared to the others is a likely explanation. Most of the variance was caused by *S. neumayeri* (Table 7) – based on existing knowledge of their feeding guilds, it is reasonable to conclude that individuals of this species were moving to areas with greater food availability to optimise grazing (Obermüller et al., 2010).

The data obtained from the Terra Nova Bay sites in this study was somewhat inconsistent with other studies performed in Terra Nova Bay, although this is to be expected as their selected study sites and sampling methods did not necessary overlap with mine. One such study sampled in 1990 found that *L. elliptica* and *Limopsis* sp. occurred in high densities of up to 300 individuals per m^2, while *Alcyonium* sp. and *U. antarcticus* were only observed occasionally (Cattaneo-Vietti et al., 2000a). A discrepancy arises with the *L. elliptica* and *Limopsis* sp. in my study – the former was found in lower densities while the latter was not found at all (Table A1). This is most likely due to sampling limitations in my study – while *L. elliptica* could be identified from their siphons which are visible at the surface of the sediment, it is unknown what proportion of the population was visible at the time this count was performed. Additionally, the pink coralline species *L. coulmanicum* was found in much higher densities in Mario Zucchelli compared to the remaining three sites, though the reasons for this is unknown, as the available literature on this subject is limited.

4.2 Environmental Controls on Macrozoobenthos

None of the environmental variables (depth, longitude, latitude, and substrate composition) appeared to be a significant predictor of the overall species composition. However, it was found that Mollusca species favoured soft substrate, with certain burrowing species such as the Antarctic soft-shelled clams occurring exclusively in this sediment type. While soft sediment was present in small amounts in Gondwana, the clams were notably absent there – this may be due to insufficient depth of the soft sediment. As the clams tend to burrow into the sediment, leaving only its feeding parts exposed, the thin layer of sand found in Gondwana is unsuitable for these organisms. Certain species such as *S. neumayeri* were more prevalent on hard substrate, though this may not be a direct causation – the increased presence of encrusting species (*H. lecannellieri* Hariot and *L. coulmanicum*) and *Spirorbis* sp. on hard substrate may be the deciding factor as these urchins feed on it (Bergami et al., 2019; Brey, Pearse, Basch, McClintock, & Slattery, 1995; Morley, Suckling, Clark, Cross, & Peck, 2016).

Changes in macrofaunal abundance in Terra Nova Bay has been linked to changes in fast ice conditions, which may vary seasonally (Thrush & Cummings, 2011b). During the warmer seasons when the ice is thinner, more mobile species will use freed area that was previously ice locked to feed and inhabit, potentially resulting in inaccurate values for these species over the year (Teixidó, Garrabou, Gutt, & Arntz, 2007; Thrush & Cummings, 2011b). It is possible that prolonged ice cover in Cape Armitage compared to the other sites may play a similar role in influencing species diversity. It is unknown how the variation in ice cover between the sites would have impacted the species composition for this study, as while the sites were not physically affected, ice cover at the surface could have reduced available sunlight for photosynthetic organisms (such as the seaweed), and reduced the effects of currents, wind and sedimentation (Gutt et al., 2013b; Teixidó et al., 2007; Thrush & Cummings, 2011b).

The seaweed *P. antarctica* was not present in Cape Armitage based on my study; a study by Miller and Pearse (1991) only observed very small clusters of this species at depths no greater than 18 m. A cited reason for this phenomenon is the prolonged ice cover and increased snow which obstructs sunlight, as well as a lack of suitable substrate in Cape Armitage, which influences the growth of the seaweed (Miller & Pearse, 1991; Schwarz et al., 2003). In Cape Evans, *P. antarctica* occurred at the depth at which the transects were taken, which matches the data retrieved from the study by Miller and Pearse (1991). On the other hand, the *I. cordata* was only found to occur at a depth of less than 3.5 m for both Cape

Armitage and Cape Evans (Miller & Pearse, 1991). While this is shallower than the depth of the sites selected for my study, small pieces of *I. cordata* were observed to be stuck to the spines of urchins in my study.

Both wind and current flows can structure benthic communities, particularly *S. neumayeri* and *O. validus*, which are the overall dominant species in my study (Cummings et al., 2018). Wind can shift ice, impact wave formation and displace sediment/nutrients from land masses (Thrush & Cummings, 2011b; Yoon et al., 2020), while currents act as a vector for nutrients and aid in species recruitment/dispersal in addition to shifting sediment (Cummings et al., 2018; Yoon et al., 2020). Prevailing winds are affected by the nearby land masses for all sites; both the McMurdo sites experience a prevailing north-easterly wind from over Ross Island, while Terra Nova Bay experiences Katabatic winds from the west (Ding et al., 2020; Meteoblue, 2020; NIWA, 2016; Yoon et al., 2020). The wind direction comes from the nearest land mass for all sites except Mario Zucchelli. Despite this difference, no obvious correlation was observed between wind directions and species diversity for each of the sites.

The currents mainly flow from the south towards Ross Island, curving around Cape Armitage and flowing past Cape Evans, before continuing towards the remaining two sites. The current speed at Mario Zucchelli was the lowest out of all four sites as the site is in a sheltered spot, but was relatively consistent for the remaining three sites, with Cape Armitage on the higher end (Cummings et al., 2018; Meteoblue, 2020; Sansiviero et al., 2017). It is likely that Cape Armitage relies on these currents to supply nutrients, and would explain why this site had a higher proportion of filter and suspension feeders.

Additionally, shell hash was abundant in Cape Armitage and may have played a role as biogenic habitat determining the local species distribution (Smith, O'Brien, Stark, Johnstone, & Riddle, 2015; Thrush, Hewitt, Lohrer, & Chiaroni, 2013). Mollusc shells act as a substrate for encrusting organisms, and can provide protection to other organisms against predators and other environmental stressors (Smith et al., 2015; Thrush et al., 2013). Shell hash may also reduce erosion of underlying sediment by forming a top layer.

4.3 Species Interactions

Echinodermata was the most dominant phylum overall in my study, and these organisms fulfil a range of ecosystem functions, as benthic grazers, predators and scavengers within the Ross Sea (De Domenico et al., 2006; Kidawa, Potocka, & Janecki, 2010; McClintock, Pearse, & Bosch, 1988a). Some Echinoderms such as *A. conspicuus* and *Acodontaster hodgsoni* are known to predate upon sponges and can directly contribute to changes in their populations (Dayton et. al., 1974). A study by Dayton et al. (1974) observed *A. conspicuus* and *A. hodgsoni* occurring at densities of 5.6 and 0.3 individuals per 100 m^2 respectively in Cape Armitage, whereas my study found none in this site, although the possibility of sampling errors cannot be ruled out. These discrepancies in density could be linked to the differences in sponge composition between the study by Dayton et al. (1974) and mine. On the other hand, filter-feeding sponges create habitat structures and are impacted via top down control by Echinoderm predators (Dayton et al., 2016).This was evidenced in my study by a decrease in the abundance of sponges at all sites where these Echinodermata species were dominant.

Distinct species within the Echinodermata taxon can also have complex interactions with each other, such as in the case of *A. conspicuus* and *O. validus*. *A. conspicuus* primarily feed on sponges, but are regulated in turn by their predator *O. validus,* resulting in a balance where the sponge population will not be depleted under normal circumstances (Gutt, 2006). However, *O validus* has a variety of food sources, and as phytodetritus is the main food source for *O. validus*, a change in the population of *A. conspicuus* would not necessarily influence the *O. validus* population in any significant manner (Gutt, 2006) . This results in a potentially precarious steady state in Cape Armitage's benthic ecosystem, as there is a lack of negative feedback links between the predator and its prey (Gutt, 2006). However, while comparing the 1990 transect to the 2018 transects in my study, the results have indicated that this area has either experienced a cyclic trend, or remained relatively stable (Gutt, 2006). The latter is more likely, as Bowden et al. (2006) and Kim et al. (2010) have both observed slower turnover in Antarctic species compared to their counterparts in warmer waters.

Another major component of species interactions were encrusting organisms, which were observed in several of the transects in my study. Encrusting species such as algae function as important food sources for many benthic species, and in some cases also offer physical protection (Amsler, McClintock, & Baker, 1999; Zenteno et al., 2019). Seaweed is the dominant benthic primary producer in the Ross Sea, though it is relatively hard to digest (Norkko et al., 2004). One species, *P. antarctica*, is chemically defended and unpalatable to large epibenthic grazers such as *S. neumayeri*, although it may play a greater role as a food source to microorganisms or other species not covered in this study (Thrush et al., 2006). Seaweed can either occur attached to urchins, on rocks, or unattached in the form of seaweed mats (Norkko et al., 2004; Thrush et al., 2006). Most of the seaweed observed during analysis were stuck on urchins (*S. neumayeri*), and it appears that the urchins use the seaweed as a protection mechanism from anemone *Isotealia antarctica* (Amsler et al., 1999). A study by Gutt (2006) observed the presence of sea urchin *S. neumayeri* in Cape Armitage at depths of 30-60m, but this species was not found in the shallower 1990 and 2018 Cape Armitage transects. Cape Evans is unique to the other sites in that most of the seaweed found there was not attached to urchins. The cause for this is unclear, though the relatively sheltered location of Cape Evans may limit physical agitation from strong currents (Norkko et al., 2004).

H. lecannellieri Hariot was only observed in the Mario Zucchelli site, which may explain why *S. neumayeri* is much more abundant in this site, as coralline algae are a food source for the urchins. This species has not been observed in the McMurdo Bay sites, indicating that conditions are less favourable within this region; the increased duration of ice cover in Mario Zuchelli impacts photosynthesis and may reduce the ability of this species to compete against other species.

There were also dense spicule mats found in Cape Armitage, which can grow to several centimetres thick (Rhodes, Carvalho, Palmer, Hyde, & Montagna, 2015). The mats obscured the visibility of species and underlying substrate, making counts and analyses less reliable. For example, *Rosella podagrosa* is often buried in the spicule mat, and many individuals possess small buds, making it exceedingly difficult to count (Dayton et al., 2019). While unfortunate, this reduced accuracy is unlikely to impact the conclusions around the overall differences between Cape Armitage and the other sites, due to the extremely high significance of those differences.

Spicule mats can influence the species diversity in the area by modifying the physical environment. The presence of spicule mats may deter urchins, as it may interfere with their feeding – the combination of dense spicule mats, a high density of anemones and sponges, and the absence of seaweed may explain the lack of urchins found in Cape Armitage. These spicules also play a role in the silicon cycle, which is essential for the formation and growth of certain Porifera species (Gutt, Böhmer, & Werner, 2013a). The presence of spicule mats driving the silicon cycle could explain why Cape Armitage has an increased density and diversity of Porifera compared to the other sites (Gutt et al., 2013a).

Limatula hodgsoni shells were found abundantly in Cape Armitage, indicating a high species density, though it was impossible to determine whether these bivalves were alive or dead from the video. As whelks such as *Trophonella longstaffi* feed on bivalves, the abundance of food may be the cause for the high densities of *T. longstaffi* present in Cape Armitage (Bruenggeman, 1998).

4.4 The Benefit of Long-term Monitoring

The understanding of spatial and temporal variations is crucial in efforts to preserve benthic communities in Antarctica, as climate change and commercial fishing subject the once-pristine community to ever increasing levels of stress (Dayton et al., 2016). Subtle changes in the community composition could indicate the start of anthropogenic impacts (such as fishing) and environmental changes (such as changes in substrate composition, ice etc.); this in turn could lead to a regime shift (Dayton et al., 2016). Within the Ross Sea, our current understanding of benthic species compositions and their cyclic trends is limited (Dayton et al., 2016). This includes the impact of environmental stressors on species compositions and trends, and how such trends in the Ross Sea differs from the warmer latitudes (Dayton et al., 2016). Aspects such as resilience or functional changes can be overlooked if predictions on changes in ecology are made based on limited information, especially if abiotic factors and the responses of the ecosystem were not considered. These changes can vary between sites and species, therefore the more data there is at hand, the more accurately these predictions can be made (Dayton et al., 2016).

The Ross Sea is a prime location to establish a long-term monitoring program for several reasons. Firstly, it is the most diverse region within the Southern Ocean, containing many endemic species (Moles et al., 2015; Smith et al., 2012). This necessarily includes a wide variety in feeding guilds, as well as a plethora of long-lived, short-lived, mobile, and sessile species, with overlaps occurring between these categories (Dayton et al., 2016; Post et al., 2017; Smith et al., 2012). Secondly, the selected sites for this study were located in the newly formed Ross Sea region Marine Protected Area (New Zealand Foreign Affairs & Trade, 2020). This newly established reserve allows for close monitoring of its impact on Ross Sea benthic species, and comparison of species variations inside and outside the reserve. The data obtained could then provide a better understanding of how such reserves can be implemented in other regions within the Southern Ocean.

4.5 Limitations

As videos were recorded prior to the beginning of this study, there were a few limitations that occurred as a result which could not be corrected. Several of the videos were rendered unusable due to an absence of a tape measure, making it impossible to determine quadrat sizes and therefore the densities of the organisms observed. Secondly, some of the transects were recorded incorrectly and covered mismatched areas across different years, making it impossible to compare the same sessile organisms for those years; however, these videos were still usable for density comparisons. Additionally, a complete dataset for all sites in all years was not obtained, with only an incongruent combination of years available for each given site. Ideally, videos of all the transects should be taken within the same years, as this would reduce the likelihood of major natural or anthropogenic occurrences impacting one set of data more than another. Iceberg C-19 is an example of such an occurrence, where a massive iceberg blocked off access to the McMurdo sites and restricted the flow of currents there (Arrigo & van Dijken, 2003; Thrush & Cummings, 2011b).

There is also a discrepancy in the analysis method between transects analysed in this study and the Cape Armitage 1990 transect count performed by divers. Whereas counts done for this study consisted of many small quadrats analysed via video, the Cape Armitage 1990 count examined four larger, $1m^2$ quadrats while on-site. This means that smaller species were more likely to be noticed and included in the Cape Armitage 1990 count compared to the ones in the current study. The data from this older transect count also does not include encrusting species or substrate analyses. It is expected that the discrepancy in methods between the 1990 transect and the 2018 transect would contribute to some variation in the results; however, it is unlikely that it would impact the overall significance for temporal variation, as the p-value was high (Table 6).

Certain burrowing species were excluded from the analysis, due to core samples not being part of the study design. While core samples would be beneficial for a more inclusive long-term monitoring program, the process of obtaining them would pose various logistical problems and is ultimately not worth implementing due to the trade-off in terms of difficulty. First and foremost is that retrieving core samples would disrupt the sediment, therefore impacting the macrozoobenthos within and immediately around the extracted area. To preserve the integrity of site transects, core samples would also have to be retrieved from a different location to the transect, which makes it impossible to make direct comparisons. Additionally, the process of collecting core samples is resource intensive, as ROVs would require specialized equipment, and a single diver cannot record videos and take core samples in the same dive.

Other limitations in this study include the lack of coverage both spatially and temporally, though as with all studies, there is no “one size fits all” method, and improvements remain an ongoing process. Having more transects within each region and a greater range of study sites across multiple regions would statistically improve the representation of the Ross Sea, and reducing the gap between selected sites could provide more information on overlaps in environmental conditions. The inclusion of a seasonal component and a range of environmental data to sampling would not be amiss either, although their implementation in a viable study method in Antarctica may be a challenge.

4.6 Implications and Future Research

The study data is still in the early stages of collection for all sites except Cape Armitage, which had data taken across multiple decades (1990s and 2010s). As the aim of this research was to determine spatial and temporal trends in biodiversity within the selected four locations of the Ross Sea, the continuation of this research will be beneficial in discovering any long-term directional or cyclic trends and what they involve.

The eventual goal of this research is to develop a reliable long-term monitoring program for Antarctic marine invertebrates. Due to the challenging nature of performing research in Antarctica, safer, more robust, and more convenient methods for collecting data are the main focal points for future research. Robust data will become increasingly important if there is an increase in anthropogenic stressors in the future, as it would allow for analyses on the specific impact of these stressors on data trends. Improving the robustness of data can be done by expanding the range of environmental information retrieved. Information on water depth and the temperature profile could be retrieved from the dive logs generated by dive computers when the videos were being recorded. Water samples could also have been collected by scuba divers while performing data collection, to be analysed at a later stage for variables such as dissolved nutrients (nitrogen, phosphorus, calcium carbonate) and dissolved gases (oxygen and carbon dioxide). Long term records of key environmental variables such as light, temperature, salinity, chlorophyll fluorescence, dissolved oxygen, currents etc can be collected through deployment of data logging arrays, and an enhanced environmental understanding of each site would be expected to aid interpretation and attribution of temporal and spatial differences.

It would have been beneficial to have additional sites selected in between the current sites to investigate environmental gradients, which would have widened the range of viable statistical analyses. This holds true particularly for the McMurdo sites which are quite distinct from each other in terms of species diversity. Determining if there is a gradual or abrupt change between Cape Evans and Cape Armitage can then lead to discerning the cause of these differences between the sites. Having more than two fixed transects per site, ideally spread across different types of substrate where feasible, would also be beneficial to ensure better representation of each site. Maintaining the current fixed transects for continued monitoring would be useful to determine temporal trends, such as recruitment and/or mortality events for sessile organisms. A larger number of video replicates over time would also allow for greater statistical power and analysis of any potential cyclic trends.

Topographical information is relevant to this study and all its reiterations, as topography is known to have an impact on the type of species present by providing shelter and increased surface area for feeding and attachment (Cummings et al., 2006; Howard-Williams, Peterson, Lyons, Cattaneo-Vietti, & Gordon, 2006; Thrush et al., 2006). This information can be obtained using a technique known as structure from motion, whereby overlapping photos are used to generate a three-dimensional image of topographical variations (Burns, Delparte, Gates, & Takabayashi, 2015; Kalacska, Lucanus, Sousa, Vieira, & Arroyo-Mora, 2018). While images can be extracted from the videos recorded for this study, the tendency of the images to blur due to motion is problematic. Clear photos would provide greater fidelity, and if paired with accurate positional tracking cards or a sufficient overlap of the images, they would be ideal to use in structure from motion to generate an accurate picture (Piazza et al., 2019).

To increase the efficiency of data processing, positional tracking could have been done by having fixed quadrats indicated by markers, meaning that the quadrat size would not have to be calculated manually. However, the presence of foreign objects on the surface of the substrate may artificially favour or inhibit the natural occurrence of organisms in that area (Barnes & Conlan, 2007; Bowden et al., 2006; Dayton et al., 2013). An alternative method for future data collection would be to utilize two lasers parallel to one another at a fixed distance when recording the videos, such as was used by Dayton et al. (2016) and Dayton et al. (2019). The laser points can then be referenced during analysis to determine distance within the image, and a program can be generated to accurately calculate the area of the image taken, in addition to generating quadrats and determining organism size. This increases the efficiency of data processing as it would reduce the time spent scaling the quadrat to the correct size (Stierhoff, Murfin, Demer, Mau, & Pinkard-Meier, 2016). These lasers can be used by either divers or remotely operated vehicles (ROV). ROVs are preferable over divers as they can obtain precisely timed and accurate information on heading, distance, water depth and temperature, in addition to other environmental variables if outfitted with probes (Azis, Aras, Rashid, Othman, & Abdullah, 2012; García-Valdovinos et al., 2014; Stierhoff et al., 2016). Other major advantages of using an ROV include the increased duration that the ROV can remain submerged, and the greater depth it is able to achieve compared to divers (Azis et al., 2012; García-Valdovinos et al., 2014; Stierhoff et al., 2016). Using an ROV also minimizes the risk to human safety while collecting data.

5 Conclusion

The coastal regions of the Ross Sea are diverse systems which support many, if not all, the benthic taxonomical groups found within the Southern Ocean. This study can provide a useful reference for future research on the structure and biodiversity of Ross Sea macrozoobenthos, in addition to supporting the management and conservation of this region. Based on the results from this study, Cape Evans, Gondwana and Mario Zucchelli shared a similar level of species richness, while Cape Armitage had the greatest species richness out of all the sites surveyed. A significant spatial difference was observed across all the sites, as hypothesised. Cape Evans and Gondwana were found to be the most similar in terms of species composition, despite being geographically isolated. Cape Evans, Gondwana and Mario Zucchelli were dominated by Echinodermata, with two species being the most prevalent. This trend was consistent across all years surveyed. On the other hand, Cape Armitage was dominated by Porifera and Cnidaria, with these phyla remaining consistent between the old and new data, though the most dominant species did change over time.

This research appears to confirm the hypothesis of slow population change that was proposed due to little change being observed in three of the sites. The one site (Mario Zucchelli) that had a significant difference was mainly influenced by mobile species, which in turn could be influenced by food availability, thus showing a cyclic trend. As the cyclic trends occurring in Antarctica may take place over a longer timeframe, continuous long-term monitoring remains essential to discern if changes in benthic communities and trends are episodic, cyclic, or if there will be a persistent regime shift towards an unknown end point.

More work is needed to fully understand this unique region of the Southern Ocean. Due to limited data on cyclic trends and environmental factors, data from this study currently cannot be used to make reliable predictions regarding the larger McMurdo Sound and Terra Nova

Bay regions. Through cost effective and accurate monitoring programs, we can better determine human impacts and its associated risks on Antarctic communities, and implement efficient measures to limit future consequences by learning from past observations. In the light of many species facing extinction in recent years, the race to preserve global biodiversity is more important now than ever.

References

Ambroso, S., Salazar, J., Zapata-Guardiola, R., Federwisch, L., Richter, C., Gili, J.-M., & Teixido, N. (2017). Pristine populations of habitat-forming gorgonian species on the Antarctic continental shelf. *Scientific Reports, 7*, 12251. https://doi.org/10.1038/s41598-017-12427-y

Amsler, C. D., McClintock, J. B., & Baker, B. J. (1999). An antarctic feeding triangle: Defensive interactions between macroalgae, sea urchins, and sea anemones *Marine Ecology Progress Series, 183*, 105-114. https://doi.org/10.3354/meps183105

Angulo-Preckler, C., Leiva, C., Avila, C., & Taboada, S. (2017). Macroinvertebrate communities from the shallow soft-bottoms of Deception Island (Southern Ocean): A paradise for opportunists. *Marine Environmental Research, 127*, 62-74. https://doi.org/10.1016/j.marenvres.2017.03.008

Arrigo, K. R., & van Dijken, G. L. (2003). Impact of iceberg C-19 on Ross Sea primary production. *Geophysical Research Letters, 30*, 1836-1839. https://doi.org/10.1029/2003GL017721

Arrigo, K. R., & van Dijken, G. L. (2008). Primary production in the Souther Ocean, 1997-2006. *Journal of Geophysical Research - Oceans, 113*, C08004. https://doi.org/10.1029/2007JC004551

Azis, F. A., Aras, M. S. M., Rashid, M. Z. A., Othman, M. N., & Abdullah, S. S. (2012). Problem identification for underwater remotely operated vehicle (ROV): A case study *Procedia Engineering, 41*, 554-560. https://doi.org/10.1016/j.proeng.2012.07.211

Barnes, D. K. A., & Conlan, K. E. (2007). Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society B Biological Sciences, 362*, 11-38. https://doi.org/10.1098/rstb.2006.1951

Bergami, E., Krupinski Emerenciano, A., González-Aravena, M., Cárdenas, C. A., Hernández, P., Silva, J. R. M. C., & Corsi, I. (2019). Polystyrene nanoparticles affect the innate immune system of the Antarctic sea urchin *Sterechinus neumayeri*. *Polar Biology, 42*, 743-757. https://doi.org/10.1007/s00300-019-02468-6

Blair, T. C., & McPherson, J. G. (1999). Grain-size and textural classification of coarse sedimentary particles. *Journal of Sedimentary Research, 69*, 6-19. https://doi.org/10.2110/jsr.69.6

Blott, S. J., & Pye, K. (2012). Particle size scales and classification of sediment types based on particle size distributions: Review and recommended procedures. *Sedimentology, 59*, 2071-2096. https://doi.org/10.1111/j.1365-3091.2012.01335.x

Boström, C., Pittman, S. J., Simenstad, C., & Kneib, R. T. (2011). Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. *Marine Ecology Progress Series, 427*, 191-217. https://doi.org/10.3354/meps09051

Bowden, D. A., Clarke, A., Peck, L. S., & Barnes, D. K. A. (2006). Antarctic sessile marine benthos: Colonisation and growth on artificial substrata over three years. *Marine Ecology Progress Series, 316*, 1-16. https://doi.org/10.3354/meps316001

Brey, T., Pearse, J. S., Basch, L., McClintock, J. B., & Slattery, M. (1995). Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica *Marine Biology, 124*, 279-292. https://doi.org/10.1007/bf00347132

Bruenggeman, P. (1998). *Underwater Field Guide to Ross Island & McMurdo Sound, Antarctica.* www.peterbrueggeman.com/nsf/fguide/

Burns, J. H. R., Delparte, D., Gates, R. D., & Takabayashi, M. (2015). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ, 3*, e1077. https://doi.org/10.7717/peerj.1077

Campana, G. L., Zacher, K., Deregibus, D., Mono, F. R., Wiencke, C., & Quartino, M. L. (2018). Succession of Antarctic benthic algae (Potter Cove, South Shetland Islands): Structural patterns and glacial impact over a four-year period. *Polar Biology, 41*, 377-396. https://doi.org/10.1007/s00300-017-2197-x

Carrea, C., Burridge, C. P., King, C. K., & Miller, K. J. (2016). Population structure and long-term decline in three species of heart urchins *Abatus* spp. near-shore in the Vestfold Hills region, East Antarctica. *Marine Ecology Progress Series, 545*, 227-238. https://doi.org/10.3354/meps11573

Cattaneo-Vietti, R., Chiantore, M., Gambi, M. C., Albertelli, G., Cormaci, M., & Di Geronimo, I. (2000a). Spatial and vertical distribution of benthic littoral communities In F. M. Faranda, L. Guglielmo, & A. Ionora (Eds.), *Ross Sea Ecology* (pp. 503-514). Springer.

Cattaneo-Vietti, R., Chiantore, M., Schiaparelli, S., & Albertelli, G. (2000b). Shallow- and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology, 23*, 173-182. https://doi.org/10.1007/s003000050024

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics, 11*, 265-270. https://www.jstor.org/stable/4615964

Clark, G. F., Stark, J. S., Palmer, A. S., Riddle, M. J., & Johnston, E. L. (2017). The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. *PLoS One, 12*, e0168391. https://doi.org/10.1371/journal.pone.0168391

Conlan, K. E., Kim, S. L., Lenihan, H. S., & Oliver, J. S. (2004). Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. *Marine Pollution Bulletin, 49*, 43-60. https://doi.org/10.1016/j.marpolbul.2004.01.007

Convey, P., Chown, S. L., Clarke, A., Barnes, D. K. A., Bokhorst, S., Cummings, V. J., . . . Wall, D. H. (2014). The spatial structure of Antarctic biodiversity. *Ecological Monographs, 84*, 203-244. https://doi.org/10.1890/12-2216.1

Cummings, V. J., Hewitt, J. E., Thrush, S. F., Marriott, P. M., Halliday, N. J., & Norkko, A. M. (2018). Linking Ross Sea coastal benthic communities to environmental conditions: Documenting baselines in a spatially variable and changing world. *Fronteirs in Marine Science, 5*, 232. https://doi.org/10.3389/fmars.2018.00232

Cummings, V. J., Thrush, S. F., Chiantore, M., Hewitt, J. E., & Cattaneo-Vietti, R. (2010). Macrobenthic communities of the north-western Ross Sea shelf: Links to depth, sediment characteristics and latitude. *Antarctic Science, 22*, 793-804. https://doi.org/10.1017/S0954102010000489

Cummings, V. J., Thrush, S. F., Norkko, A. M., Andrew, N. L., Hewitt, J. E., Funnell, G. A., & Schwarz, A.-M. (2006). Accounting for local scale variability in benthos: Implications for future assessments of latitudinal trends in the coastal Ross Sea. *Antarctic Science, 18*, 633-644. https://doi.org/10.1017/S0954102006000666

Dayton, P. K., Jarrell, S. C., Kim, S. L., Parnell, P., Thrush, S. F., Hammerstom, K. K., & Leichter, J. J. (2019). Benthic responses to an Antarctic regime shift: Food particle size and recruitment biology. *Ecological Applications, 29*, e01823. https://doi.org/10.1002/eap.1823

Dayton, P. K., Jarrell, S., Kim, S. L., Thrush, S. F., Hammerstom, K. K., Slattery, M., & Parnell, E. (2016). Surprising episodic recruitment and growth of Antarctic sponges: Implications for ecological resilience. *Journal of Experimental Marine Biology and Ecology, 482*, 38-55. https://doi.org/10.1016/j.jembe.2016.05.001

Dayton, P. K., Kim, S. L., Jarrell, S. C., Oliver, J. S., Hammerstrom, K. K., Fisher, J. L., . . . Roberts, J. M. (2013). Recruitment, growth and mortality of an Antarctic Hexactinellid Sponge, *Anoxycalyx joubini*. *PLoS One, 8*, e56939. https://doi.org/10.1371/journal.pone.0056939

Dayton, P. K., Robilliard, G. A., & DeVries, A. L. (1969). Anchor ice formation in McMurdo Sound, Antarctica, and its biological effects. *Science, 163*, 273-274. https://doi.org/10.1126/science.163.3864.273

Dayton, P. K., Robilliard, G. A., Paine, R. T., & Dayton, L. B. (1974). Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs, 44*, 105-128. https://doi.org/10.2307/1942321

De Domenico, F., Chiantore, M., Buongiovanni, S., Ferranti, M. P., Ghione, S., Thrush, S. F., . . . Cattaneo-Vietti, R. (2006). Latitude versus local effects on echinoderm assemblages along the Victoria Land coast, Ross Sea, Antarctica. *Antarctic Science, 18*, 655-662. https://doi.org/10.1017/S095410200600068X

Ding, Y., Cheng, X., Li, X., Shokr, M., Yuan, J., Yang, Q., & Hui, F. (2020). Specific relationship between the surface air temperature and the area of the Terra Nova Bay polynya, Antarctica. *Advances in Atmosperic Sciences, 37*, 532-544. https://doi.org/10.1007/s00376-020-9146-2

Emslie, S. D., Polito, M. J., Brasso, R., P., P. W., & Sun, L. (2014). Ornithogenic soils and the paleoecology of pygoscelid penguins in Antarctica. *Quaternary International, 352*, 4-15. https://doi.org/10.1016/j.quaint.2014.07.031

Gambi, M. C., Castelli, A., & Guizzardi, M. (1997). Polychaete populations of the shallow soft bottoms off Terra Nova Bay (Ross Sea, Antarctica): Distribution, diversity and biomass. *Polar Biology, 17,* 199-210. https://doi.org/10.1007/s003000050123

Gambi, M. C., Lorenti, M., Russo, G. F., & Scipione, M. B. (1994). Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: Zonation, biomass and population structure. *Antarctic Science, 6*, 449-462. https://doi.org/10.1017/S0954102094000696

García-Valdovinos, L. G., Salgado-Jiménez, T., Bandala-Sánchez, M., Nava-Balanzar, L., Hernández-Alvarado, R., & Cruz-Ledesma, J. A. (2014). Modelling, design and robust control of a remotely operated underwater vehicle *International Journal of Advanced Robotic systems, 11*, 1-16. https://doi.org/10.5772/56810

Gutt, J. (2006). Coexistence of macro-zoobenthic species on the Antarctic shelf: An attempt to link ecological theory and results. *Deep-Sea Research Part II, 53,* 1009-1028. https://doi.org/10.1016/j.dsr2.2006.02.012

Gutt, J. (2007). Antarctic macro-zoobenthic communities: A review and an ecological classification. *Antarctic Science, 19,* 165-182. https://doi.org/10.1017/S0954102007000247

Gutt, J., Alvaro, M., Barco, A., Böhmer, A., Bracher, A., David, B., . . . Teixidó, N. (2016). Macroepibenthic communities at the tip of the Antarctic Peninsula, an ecological survey at different spatial scales. *Polar Biology, 39,* 829-849. https://doi.org/10.1007/s00300-015-1797-6

Gutt, J., Arndt, J., Kraan, C., Dorschel, B., Schröder, M., Bracher, A., & Piepenburg, D. (2019). Benthic communities and their drivers: A spatial analysis off the Antarctic Peninsula. *Limnology and Oceanography, 64*, 2341-2357. https://doi.org/10.1002/lno.11187

Gutt, J., Böhmer, A., & Werner, D. (2013a). Antarctic sponge spicule mats shape macrobenthic diversity and act as a silicon trap. *Marine Ecology Progress Series, 480,* 57-71. https://doi.org/10.3354/meps10226

Gutt, J., Cape, M., Dimmler, W., Fillinger, L., Isla, E., Lieb, V., . . . Pulcher, C. (2013b). Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic Peninsula. *Polar Biology, 36*, 895-906. https://doi.org/10.1007/s00300-013-1315-7

Howard-Williams, C., Peterson, D., Lyons, W. B., Cattaneo-Vietti, R., & Gordon, S. (2006). Measuring ecosystem response in a rapidly changing environment: The Latitudinal Gradient Project. *Antarctic Science, 18,* 465-471. https://doi.org/10.1017/S0954102006000514

Ingall, E. D., Diaz, J. M., Longo, A. F., Oakes, M., Finney, L., Vogt, S., . . . Brandes, J. A. (2013). Role of biogenic silica in the removal of iron from the Antarctic seas. *Nature Communications, 4,* 1981. https://doi.org/10.1038/ncomms2981

Iriarte, J. L., Gómez, I., González, H. E., Nahuelhual, L., & Navarro, J. M. (2019). Subantarctic and Antarctic Marine Ecosystems: Outlining patterns and processes in a changing ocean. *Progress in Oceanography, 174*, 1-6. https://doi.org/10.1016/j.pocean.2019.05.002

Janosik, A. M., & Halanych, K. M. (2010). Unrecognized Antarctic biodiversity: A case study of the genus *Odontaster* (*Odontasteridae; Asteroidea*). *Integrative and Comparative Biology, 50*, 981-992. https://doi.org/10.1093/icb/icq119

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystems engineers. *Oikos, 69*, 373-386.

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*, 1946-1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO2

Kalacska, M., Lucanus, O., Sousa, L., Vieira, T., & Arroyo-Mora, J. (2018). Freshwater fish habitat complexity mapping using above and underwater structure-from-motion photogrammetry. *Remote Sensing, 10,* 1912. https://doi.org/10.3390/rs10121912

Kang, Y. H., Kim, S. L., Choi, S. K., Moon, K., Hang-Gu, C., Ko, Y. W., . . . Kim, J. H. (2019). Composition and structure of the marine benthic community in Terra Nova Bay, Antarctica: Responses of the benthic assemblage to disturbances. *PLoS One, 14*, e0225551. https://doi.org/10.1371/journal.pone.0225551

Kern, Y., Rodrigues, A. R., & Absher, T. M. (2014). Colonization of soft sediments by benthic communities: An experimental approach in Admiralty Bay, King George Island. *Journal of Experimental Marine Biology and Ecology, 453,* 1-12. https://doi.org/10.1016/j.jembe.2013.12.019

Kidawa, A., & Janecki, T. (2011). Antarctic benthic fauna in the global climate change. *Papers on Global Change, 18,* 71-86. https://doi.org/10.2478/v10190-010-0006-5

Kidawa, A., Potocka, M., & Janecki, T. (2010). The effects of temperature on the behaviour of the Antarctic sea star *Odontaster validus*. *Polish Polar Biology, 31*, 273-284. https://doi.org/10.2478/v10183−010−0003−3

Kiest, K. A. (1993). A relationship of diet to prey abundance and the foraging behavior of *Trematomus bernacchii Polar Biology, 13,* 291-296. https://doi.org/10.1007/BF00238355

Kim, S. L., Hammerstom, K. K., Conlan, K. E., & Thurber, A. R. (2010). Polar ecosystem dynamics: Recovery of communities from organic enrichment in McMurdo Sound, Antarctica. *Integrative and Comparative Biology, 50,* 1031-1040. https://doi.org/10.1093/icb/icq058

Kim, S. L., Hammerstom, K. K., & Dayton, P. K. (2019). Epifaunal community response to iceberg-mediated environmental change in McMurdo Sound, Antarctica. *Marine Ecology Progress Series, 613,* 1-14. https://doi.org/10.3354/meps12899

Kröger, K., & Rowden, A. A. (2008). Polychaete assemblages of the northwestern Ross Sea shelf: Worming out the environmental drivers of Antarctic macrobenthic assemblage composition. *Polar Biology, 31*, 971-989. https://doi.org/10.1007/s00300-008-0437-9

Krzeminska, M., & Kuklinski, P. (2018). Biodiversity patterns of rock encrusting fauna from the shallow sublittoral of the Admiralty Bay. *Marine Environmental Research, 139*, 169-181. https://doi.org/10.1016/j.marenvres.2018.03.016

Lagger, C., Servetto, N., Torre, L., & Sahade, R. (2017). Benthic colonization in newly ice-free soft-bottom areas in an Antarctic fjord. *PLoS One, 12*, e0186756. doi:10.1371/journal.pone.0186756

Lecours, V., Devillers, R., Schneider, D. C., Lucieer, V. L., Brown, C. J., & Edinger, E. N. (2015). Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Marine Ecology Progress Series, 535*, 259-284. https://doi.org/10.3354/meps11378

Lee, Y. J., Lim, W. K., & Ewe, H. T. (2011). A study of an inversion model for sea ice thickness retrieval in Ross Island, Antarctica. *Progress in Electromagnetics Research, 111*, 381-406. http://www.jpier.org/PIER/pier.php?paper=10100411

Lohrer, A. M., Hewitt, J. E., & Thrush, S. F. (2006). Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series, 315*, 13-18. https://doi.org/10.3354/MEPS315013

Mager, S. M., Smith, I. J., Kempema, E. W., Thomson, B. J., & Leonard, G. H. (2011). Anchor ice in polar oceans. *Progress in Physical Geography, 37*, 468-483. https://doi.org/10.1177/0309133313479815

McClintock, J. B. (1994). Trophic biology of antarctic shallow-water echinoderms. *Marine Ecology Progress Series, 111*, 191-202. https://www.int-res.com/articles/meps/111/m111p191.pdf

McClintock, J. B., Pearse, J. S., & Bosch, I. (1988a). Population structure and energetics of the shallow-water antarctic sea star *Odontaster validus* in contrasting habitats *Marine Biology, 99*. https://doi.org/10.1007/BF00391986

McClintock, J. B., Pearse, J. S., & Bosch, I. (1988b). Population structure and energetics of the shallow-water antarctic sea star *Odontaster validus* in contrasting habitats *Marine Biology, 99*, 235-246. https://doi.org/10.1007/BF00391986

Meadows, P. S., Meadows, A., & Murray, J. M. H. (2012). Biological modifiers of marine benthic seascapes: Their role as ecosystem engineers. *Geomorphology, 157-158*, 31-48. https://doi.org/10.1016/j.geomorph.2011.07.007

Meteoblue. (2020). *Weather Princeton.* https://www.meteoblue.com/

Micallef, A., Le Bas, T. P., Huvenne, V. A. I., Blondel, P., Hühnerbach, V., & Deidun, A. (2012). A multi-method approach for benthic habitat mapping of shallow coastal areas with high-resolution multibeam data. *Continetal Shelf Research, 39-40*, 14-26. https://doi.org/10.1016/j.csr.2012.03.008

Miller, K. J., & Pearse, J. S. (1991). Ecological studies of seaweeds in McMurdo Sound, Antarctica. *American Zoologist, 31*, 35-48. https://doi.org/10.1093/icb/31.1.35

Moles, J., Figuerola, B., Campanyà-Llovet, N., Monleón-Getino, T., Taboada, S., & Avila, C. (2015). Distribution patterns in Antarctic and Subantarctic echinoderms. *Polar Biology, 38*, 799-813. https://doi.org/10.1007/s00300-014-1640-5

Morley, S. A., Suckling, C. C., Clark, M. S., Cross, E. L., & Peck, L. S. (2016). Long-term effects of altered pH and temperature on the feeding energetics of the Antarctic seaurchin, *Sterechinus neumayeri*. *Biodiversity (Nepean), 17*, 34-45. https://doi.org/10.1080/14888386.2016.1174956

New Zealand Foreign Affairs & Trade (2020). *Ross Sea region Marine Protected Area.* https://www.mfat.govt.nz/en/environment/antarctica/ross-sea-region-marine-protected-area/

NIWA. (2016). Plots of wind direction vs wind velocity - Cape Hallett & Scott Base.jpg. https://niwa.co.nz/file/27212

Norkko, A. M., Andrew, N. L., Thrush, S. F., Cummings, V. J., Schwarz, A.-M., Hawes, I., . . . Goring, D. (2002). *Ecology and biodiversity of coastal benthic communities in McMurdo Sound, Ross Sea: Development of sampling protocols and initial results.* https://www.researchgate.net/publication/265348371_Ecology_and_Biodiversity_of_Coastal_Benthic_Communities_in_McMurdo_Sound_Ross_Sea_Development_of_Sampling_Protocols_and_Initial_Results

Norkko, A. M., Thrush, S. F., Cummings, V. J., Funnell, G. A., Schwarz, A.-M., Andrew, N. L., & Hawes, I. (2004). Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities of McMurdo Sound, Antarctica. *Polar Biology, 27*, 482-494. https://doi.org/10.1007/s00300-004-0610-8

Obermüller, B. E., Morley, S. A., Barnes, D. K. A., & Peck, L. S. (2010). Seasonal physiology and ecology of Antarctic marine benthic predators and scavengers. *Marine Ecology Progress Series, 415*, 109-126. https://doi.org/10.3354/meps08735

Orsi, A. H., Whitworth, T., & Nowlin, W. D. (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research. Part I,* 42, 641-673. https://doi.org/10.1016/0967-0637(95)00021-w

Passaelli, C., Oliver, F., Paterson, D. M., & Hubas, C. (2012). Impacts of biogenic structures on benthic assemblages: Microbes, meiofauna, macrofauna and related ecosystem functions. *Marine Ecology Progress Series, 465*, 85-97. https://doi.org/10.3354/meps09915

Peck, L. S., Webb, K. E., Miller, A. J., Clark, M. S., & Hill, T. (2008). Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*. *Marine Ecology Progress Series, 358*, 181-189. https://doi.org/10.3354/meps07336

Peña Cantero, Á. L., Boero, F., & Piraino, S. (2013). Shallow-water benthic hydroids from Tethys Bay (Terra Nova Bay, Ross Sea, Antarctica). *Polar Biology, 36*, 731-753. https://doi.org/10.1007/s00300-013-1299-3

Piazza, P., Cummings, V. J., Guzzi, A., Hawes, I., Lohrer, A. M., Marini, S., . . . Schiaparelli, S. (2019). Underwater photogrammetry in Antarctica: Long-term observations in benthic ecosystems and legacy data rescue. *Polar Biology, 42*, 1061-1079. https://doi.org/10.1007/s00300-019-02480-w

Post, A. L., Lavoie, C., Domack, E. W., Leventer, A., Shevenell, A., & Fraser, A. D. (2017). Environmental drivers of benthic communities and habitat heterogeneity on an East Antarctic Shelf. *Antarctic Science, 29*, 17-32. https://doi.org/10.1017/S0954102016000468

Rhodes, A. C., Carvalho, N. F., Palmer, T. A., Hyde, L. J., & Montagna, P. A. (2015). Distribution of two species of the genus *Nototanais* spp. (Tanaidacea) in Winter Quarters Bay and waters adjoining McMurdo Station, McMurdo Sound, Antarctica. *Polar Biology, 38*, 1623-1629. https://doi.org/10.1007/s00300-015-1727-7

Rimondino, C., Torre, L., Sahade, R., & Tatián, M. (2015). Sessile macro-epibiotic community of solitary ascidians, ecosystem engineers in soft substrates of Potter Cove, Antarctica. *Polar Research, 34*, 1-9. https://doi.org/10.3402/polar.v34.24338

Rowden, A. A., Kröger, K., & Clark, M. R. (2015). Compositional patterns of benthic assemblages on the northwestern Ross Sea shelf, Antarctica: Interacting environmental drivers operating at multiple spatial scales. *Hydrobiologia, 761*, 211-233. https://doi.org/10.1007/s10750-015-2305-2

Sansiviero, M., Morales Maqueda, M. Á., Fusco, G., Aulicino, G., Flocco, D., & Budillon, G. (2017). Modelling sea ice formation in the Terra Nova Bay polynya. *Journal of Marine Systems, 166*, 4-25. https://doi.org/10.1016/j.jmarsys.2016.06.013

Scher, H. D., Whittaker, J. M., Williams, S. E., Latimer, J. C., Kordesch, W. E. C., & Delaney, M. L. (2015). Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies. *Nature, 523*, 580-583. https://doi.org/10.1038/nature14598

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods, 9*, 671-675. https://doi.org/10.1038/nmeth.2089

Schwarz, A.-M., Hawes, I., Andrew, N. L., Norkko, A. M., Cummings, V. J., & Thrush, S. F. (2003). Macroalgal photosynthesis near the southern global limit for growth; Cape Evans, Ross Sea, Antarctica. *Polar Biology, 26*, 789-799. https://doi.org/10.1007/s00300-003-0556-2

Shields, M. A., Woolf, D. K., Grist, E. P. M., Kerr, S. A., Jackson, A. C., Harris, R. E., . . . Side, J. (2011). Marine renewable energy: The ecological implications of altering the hydrodynamics of the marine environment. *Ocean & Coastal Management, 54*, 2-9. https://doi.org/10.1016/j.ocecoaman.2010.10.036

Silva, D. R. O., Ligeiro, R., Hughes, R. M., & Callisto, M. (2016). The role of physical habitat and sampling effort on estimates of benthic macroinvertebrate taxonomic richness at basin and site scales. *Environmental Monitoring and Assessment, 188*, 1-12. https://doi.org/10.1007/s10661-016-5326-z

Smale, D. (2008). Continuous benthic community change along a depth gradient in Antarctic shallows: Evidence of patchiness but not zonation. *Polar Biology, 31*, 189-198. https://doi.org/10.1007/s00300-007-0346-3

Smith, W. O., Ainley, D. G., Arrigo, K. R., & Dinniman, M. S. (2014). The oceanography and ecology of the Ross Sea. *Annual Review of Marine Science, 6,* 469-487. https://doi.org/10.1146/annurev-marine-010213-135114

Smith, J., O'Brien, P. E., Stark, J. S., Johnstone, G. J., & Riddle, M. J. (2015). Integrating multibeam sonar and underwater video data to map benthic habitats in an East Antarctic nearshore environment. *Estuarine, Coastal and Shelf Science, 164,* 520-536. https://doi.org/10.1016/j.ecss.2015.07.036

Smith, W. O., Sedwick, P. N., Arrigo, K. R., Ainley, D. G., & Orsi, A. H. (2012). The Ross Sea in a sea of change. *Oceanography, 25,* 90-103. https://doi.org/10.5670/oceanog.2012.80.

Stierhoff, K. L., Murfin, D. W., Demer, D. A., Mau, S. A., & Pinkard-Meier, D. R. (2016). Improving the estimations of transect length and width for underwater visual surveys of targets on or near the seabed. *ICES Journal of Marine Science, 73,* 2729-2736. https://doi.org/10.1093/icesjms/fsw110

Teixidó, N., Garrabou, J., Gutt, J., & Arntz, W. E. (2007). Iceberg disturbance and successional spatial patterns: The case of the shelf Antarctic benthic communities. *Ecosystems, 10,* 143-158. https://doi.org/10.1007/s10021-006-9012-9

Thatje, S., Hillenbrand, C.-D., & Larter, R. (2005). On the origin of Antarctic marine benthic community structure. *Trends in Ecology & Evolution (Amsterdam), 20,* 534-540. https://doi.org/10.1016/j.tree.2005.07.010

Thrush, S. F., & Cummings, V. J. (2011a). Capturing scales of spatial heterogeneity of Antarctic sea ice algae communities. *Marine Ecology, 32,* 289-299. https://doi.org/10.1111/j.1439-0485.2011.00462.x

Thrush, S. F., & Cummings, V. J. (2011b). Massive icebergs, alteration in primary food resources and change in benthic communities at Cape Evans, Antarctica. *Marine Ecology, 32*, 289-299. https://doi.org/10.1111/j.1439-0485.2011.00462.x

Thrush, S. F., Dayton, P. K., Cattaneo-Vietti, R., Chiantore, M., Cummings, V. J., Andrew, N. L., . . . Schwarz, A.-M. (2006). Broad-scale factors influencing the biodiversity of coastal benthic communities of the Ross Sea. *Deep-Sea Research Part II, 53,* 959-971. https://doi.org/10.1016/j.dsr2.2006.02.006

Thrush, S. F., Hewitt, J. E., Lohrer, A. M., & Chiaroni, L. D. (2013). When small changes matter: The role of cross-scale interactions between habitat and ecological connectivity in recovery. *United States: Ecological Society of America, 23.* https://doi.org/10.1890/12-0793.1

Torre, L., Tabares, P. C. C., Mono, F. R., Meyer, J., & Sahade, R. (2017). Climate change effects on Antarctic benthos: A spatially explicit model approach. *Climate Change, 141*, 733-746. https://doi.org/10.1007/s10584-017-1915-2

Vacchi, M., DeVries, A. L., & Evans, C. W. (2012). A nursery area for the Antarctic silverfish Pleuragramma antarcticum at Terra Nova Bay (Ross Sea): First estimate of distribution and abundance of eggs and larvae under the seasonal sea-ice. *Polar Biology, 35,* 1573-1585. https://doi.org/10.1007/s00300-012-1199-y

Vause, B. J., Morley, S. A., Fonseca, V. G., Jażdżewska, A., Ashton, G. V., Barnes, D. K. A., . . . Peck, L. S. (2019). Spatial and temporal dynamics of Antarctic shallow soft-bottom benthic communities: Ecological drivers under climate change. *BMC Ecology, 19*, 27. https://doi.org/10.1186/s12898-019-0244-x

Wing, S. R., McLeod, R. J., Leichter, J. J., Frew, R. D., & Lamare, M. D. (2012). Sea ice microbial production supports Ross Sea benthic communities: Influence of a small but stable subsidy. *Ecology, 93*, 314-323. https://doi.org/10.1890/11-0996.1

Xu, S., Böttcher, L., & Chou, T. (2020). Diversity in Biology: Definitions, quantification and models. *Physical Biology, 17*, 031001. https://doi.org/10.1088/1478-3975/ab6754

Yoon, S.-T., Lee, W. S., Stevens, C. L., Jendersie, S., Nam, S., Yun, S., . . . Lee, J. (2020). Variability in high-salinity shelf water production in the Terra Nova Bay polynya, Antarctica. *Ocean Science, 16*, 373-388. https://doi.org/10.5194/os-16-373-2020

Zenteno, L., Cárdenas, L., Valdivia, N., Gómez, I., Höfer, J., Garrido, I., & Pardo, L. M. (2019). Unraveling the multiple bottom-up supplies of an Antarctic nearshore benthic community. *Progress in Oceanography, 174*, 55-63. https://doi.org/10.1016/j.pocean.2018.10.016

APPENDIX A

Table A1. Summarized density (#/m^2) data for each of the sites, showing the mean, min and max for a given species based on video transect analysis. Species are divided into groups based on phylum, with certain phylum divided further based on class. Classes within each phylum are ordered from most to least diverse, and species within each class are ordered from highest to lowest density based on group. Bold values indicate the three species which occurred in the highest density for the given site. *Number of quadrats in which the species was found per transect, averaged for each site.

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Porifera - Demospongiae												
Sphaerotylus antarcticus	**3.93**	**1.60**	**8.27**	0.00	0.00	0.00	0.18	0.00	0.27	0.00	0.00	0.00
Cinachyra antarctica	1.27	0.00	3.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polymastia invaginata	0.61	0.00	1.33	0.00	0.00	0.00	0.04	0.00	0.27	0.04	0.00	0.27
Kirkpatrickia variolosa	0.20	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.80
Isodictya setifera	0.43	0.00	1.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Inflatella belli	0.27	0.00	0.80	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27
Haliclona scotti	0.35	0.00	0.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Homaxinella balfouri	0.30	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemigellius fimibratus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.53

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Serites topsentii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.53
Antarctotetilla leptoderma	0.17	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Latrunculia biformis	0.14	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dendrilla antarctica	0.13	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mycale (Oxymycale) acerata	0.06	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Suberites caminatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27
Anoxycalis joubini	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Porifera - Hexactinellida												
Rosella podagrosa	0.05	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria - Anthozoa												
Alcyonium antarcticum	**1.71**	**0.27**	**5.33**	0.00	0.00	0.00	0.04	0.00	0.27	**7.42**	**3.20**	**13.07**
Artemidactis victrix	**9.36**	**4.96**	**13.07**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stomphia selaginella	0.21	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Urticinopsis antarctica	0.04	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Isotealia antarctica	0.09	0.00	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hormathia lacunifera	0.01	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria - Hydrozoa												
Zyzzyzus parvula	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata - Asteroidea												
Odantaster validus	0.64	0.27	0.84	**21.20**	**15.47**	**26.67**	**14.80**	**1.87**	**35.73**	**9.91**	**2.67**	**17.33**
Diplasterias brucei	0.07	0.00	0.27	0.60	0.27	0.80	**0.27**	**0.00**	**1.33**	1.64	0.00	4.53
Perknaster fuscus antarcticus	0.12	0.00	0.53	0.00	0.00	0.00	0.04	0.00	0.27	0.00	0.00	0.00
Odantaster meridionalis	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27
Echinodermata - Ophiuroidea												
Ophioplinthus gelida	0.81	0.00	2.67	0.33	0.00	0.53	0.00	0.00	0.00	0.04	0.00	0.27
Ophionotus victoriae	0.16	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.03	0.58	0.27	1.07
Ophiosparte gigas	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.27	0.00	0.00	0.00
Echinodermata - Echinoidea												

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Sterechinus neumayeri	0.00	0.00	0.00	**11.53**	**4.27**	**17.87**	**5.89**	**0.67**	**10.40**	**113.20**	**49.33**	**152.80**
Ctenocidaris perrieri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27
Echinodermata - Holothuroidea												
Staurocucumis turqueti	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	1.60
Annelida												
Perkinsiana littoralis	0.11	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
terebellid polychaete	0.00	0.00	0.00	0.13	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Nemertea												
Parborlasia corrugata	0.45	0.00	1.07	0.07	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca - Gastropoda												
Trophonella longstaffi	0.32	0.00	0.81	0.07	0.00	0.27	0.00	0.00	0.00	0.04	0.00	0.27
Neobuccinum eatoni	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27	0.09	0.00	0.53
Amauropsis rossiana	0.00	0.00	0.00	0.07	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Marseniopsis mollis	0.05	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Tritonia challengeriana	0.05	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca - Bivalvia												
Laternula elliptica	0.43	0.00	1.60	**1.47**	**0.00**	**2.67**	0.00	0.00	0.00	0.04	0.00	0.27
Adamussium colbecki	0.00	0.00	0.00	0.07	0.00	0.27	0.00	0.00	0.00	0.18	0.00	0.53
Yoldia (Aequiyoldia) eightsi	0.00	0.00	0.00	0.20	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00
Limatula hodgsoni	0.00	0.00	0.00	0.07	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda												
Chelicerata	0.11	0.00	0.53	0.00	0.00	0.00	0.04	0.00	0.27	0.13	0.00	0.27
Chordata: Tunicata												
Cnemidocarpa verrucosa	0.18	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.27
Synoicum adareanum	0.21	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mean presence in quadrats per transect*												
Cinachyra barbata	15.00	15.00	15.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	Cape Armitage			Cape Evans			Gondwana			Mario Zucchelli		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Spirorbis sp. (likely *Spirorbis antarctica*)	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.00	15.00	4.83	0.00	12.00
Clavularia frankliniana	2.25	0.00	5.00	0.00	0.00	0.00	3.33	0.00	8.00	0.00	0.00	0.00