ASSESSING THE DOWN-FJORD MECHANISTIC RELATIONSHIPS OF BIODIVERSITY AND ABUNDANCE OF ANTARCTIC BENTHIC MACROFAUNA OF ANDVORD BAY

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I certify that I have read this thesis and that, in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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Craig R. Smith Department of Oceanography For my family, friends, and Griffin for their support during my journey in the GES program.

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ABSTRACT

Glaciomarine fjords exhibit substantially different ecosystem forcing than adjacent continental shelves and can be highly sensitive to climate warming. Extensive research indicates that subpolar Arctic fjords are heavily influenced by glacial meltwater and sediment inputs, resulting in high turbidity and seafloor burial rates. These physical disturbances yield macrofaunal communities with low abundance and diversity. In contrast, poorly-studied sub-polar fjords along the Western Antarctic Peninsula (WAP) sustain weak meltwater influences, resulting in low turbidity and seafloor burial rates. Thus, benthic communities in WAP fjords may not currently be limited by turbidity and burial disturbance and may have the potential to harbor abundant and diverse macrobenthic communities. Here we characterize the benthic macrofaunal community of Andvord Bay, a subpolar fjord along the warming WAP. We compare down-fjord changes in macrobenthic abundance, diversity, and functional-group structure (groups of organisms with different ecosystem roles) to a variety of potential ecological drivers. These ecological drivers include sediment burial rate, sediment Chl-a concentration (an indicator of labile detritus availability), and sediment-community respiration (an indicator of seafloor detrital carbon flux). Sediment disturbance likely only limits the abundance of benthic communities of the inner fjord regions, but is too weak in the middle fjord to open shelf to limit the communities. The trend in abundance outside of the disturbed inner fjord sites is likely driven by POM flux to the seafloor. In areas of high abundance, the large food flux to the seafloor promotes richness, but the sedimentation disturbance is not enough to promote evenness. As global sea and air temperatures continue to rise,

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glacial melt and sedimentation in WAP fjords will increase, resulting in low benthic abundance and diversity, resembling present-day Arctic fjords.

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1.0 INTRODUCTION

1.1 GLACIOMARINE FJORDS

A fjord is a deep (typically 400-700 m) estuary or bay carved by glacial movement, often surrounded by steep mountains or glaciers, typically containing one or more sills and sediment-floored basins (Syvitsky et al. 1989). Sub-polar fjords foster glaciomarine environments, which are marine environments with sufficient proximity to glacial ice that a glacial signature can be detected within the sediments. Some or all of the sediment deposited on the fjord floor is released from grounded or floating glacial or sea ice (Powell and Domack 1995). Glaciomarine fjords often contain tidewater glaciers, which are glaciers that are in contact with the waters of the fjord, forming important boundary zones between the cryosphere and the ocean (Powell and Domack 1995). Glaciomarine fjord environments serve as major outlets for glacial ice to the sea, and are thus highly sensitive to cryosphere-ocean interactions and to climate warming (e.g., Syvitski et al. 1989, Pritchard & Vaughan 2007, Weslawski et al. 2011). Glaciomarine fjord environments exhibit different ecosystem dynamics than adjacent continental shelves due to their distinct geomorphology, circulation processes, and inputs of glacial ice, meltwater, and sediment (Syvitski et al. 1989, Powell and Domack 1995, Hop et al. 2002, Grange and Smith 2013).

Glacial sedimentation exerts important physical controls on fjord processes. Inorganic sediment in fjords is produced by the grinding of glaciers against the bedrock surrounding the fjord and is delivered to fjords via meltwater (Powell and Domack 1995). Glaciers surrounding the fjord meet the underlying bedrock at the grounding line, where

the bedrock is mechanically weathered into sediments. Melting occurs at the grounding line, which aids in the transport of sediment to the fjord. Surface melt of the glacier is caused by warm air temperatures, producing surface meltwater streams that can also deliver sediments to the fjord. Glacier melting and sediment transport to the fjord may be further facilitated when waters from outside the fjord comes in contact with glacier termini and grounding lines (Powell and Domack 1995).

Melting-induced sedimentation can create disturbances from turbidity and sediment loading in the water column and on the seafloor (Figure 1). Buoyant freshwater melted from the glacier laden with suspended particulate matter (SPM) carries the terrigenous sediments from the glacier terminus toward the fjord mouth via mid-water cold tongues and surface plumes. Eventually, the sediments will fall through the water column to the seafloor, potentially causing burial disturbance. In addition, fjord water





that has cooled from contact with the glacier sinks to the bottom, carrying terrigenous sediment from the grounding line to the fjord floor (Powell and Domack 1995). These areas of sediment transport are characterized by turbulent, murky waters. Icebergs, which have calved from the glacier and sometimes scour the seafloor to water depths of ~200 m, carry sediments and larger stones or boulders, which are transported farther to the outer fjord and open continental shelf. As an iceberg melts, it releases the glacial debris that it carries, which sinks to the seafloor (Powell and Domack 1995).

1.2 ARCTIC FJORDS

Ecosystem structure and function of subpolar fjords in the Arctic (e.g., Svalbard, Baffin Island, Greenland) have been extensively studied. Research has shown that subpolar Arctic fjords are heavily influenced by sediment inputs from glacial meltwater, resulting in high water-column turbidity and seafloor burial rates. These inputs result in low primary production and seafloor communities with very low abundance and species diversity in inner fjords (e.g., Syvitski et al. 1989, Hop et al. 2002, Powell and Domack 1995, Wlodarska-Kowalczuk et al. 2005, 2008, 2012).

Arctic sub-polar fjords are characterized by high rates of sedimentation of inorganic terrigenous material, which is accelerated by rapid glacial melting (e.g., Hop et al. 2002; Powell and Domack 1995, Syvitski et al. 1989, Weslawski et al. 2011). Rapid melting of Arctic tidal glaciers causes high turbidity and mixing, sediment instability near the glacier terminus, and high rates of inorganic particulate accumulation (Wlodarska-Kowalczuk et al. 2005). Elevated sedimentation rates yield unconsolidated, easily eroded sediments, which are readily and frequently resuspended and redeposited (Wlodarska-

Kowalczuk et al. 2005). Sedimentation and meltwater processes exert a physical control on biological processes in the fjord.

The inner-middle portions of subpolar Arctic fjords (within 5-10 km of glacial termini) typically sustain high turbidity and sedimentation rates (e.g., 2-25 cm y^{-1}) (e.g., Syvitsky et al. 1989, Powell & Domack 1995, Hop et al. 2002, Fetzer et al. 2002, Włodarska-Kowalczuk et al. 2005, 2012, Weslawski et al. 2011) Turbid water caused by sedimentation interferes with primary production by blocking sunlight, limiting export flux to the seafloor. In Arctic fjords, the euphotic layer can decrease from a depth of 30 m in the outer fjord to 0.3 m in the inner fjord near the glacier terminus. The outer part of the fjord can also be heavily influenced, on a seasonal basis, by sediment-loaded glacial meltwater (Hop et al. 2002). Reduced phytoplankton production in turbid zones result in low food availability for zooplankton, whose fecal pellets can be a large contributor of sinking particulate organic matter (POM) in fjords. Additionally, freshwater plumes from glacial melting cause mortality of zooplankton by osmotic shock, resulting in extremely small zooplankton populations in and near the inner fjord (Hop et al. 2002). In areas of high meltwater input and chronic turbidity, the fjord experiences a low flux of POC to the seafloor. High rates of terrigenous sedimentation further dilute organic carbon content in the sediments of the inner-middle fjord (Wlodarska-Kowalczuk et al. 2005; Hop et al. 2002).

In addition to a decreased flux of particulate organic carbon to the seafloor, benthic burial disturbance caused by elevated inorganic sediment flux can limit the growth of benthic organisms on the seafloor (Wlodarska-Kowalczuk et al. 2005). The benthic organisms dwelling in Arctic fjords are exposed to chronic physical

sedimentation disturbance. Bottom-dwelling organisms may be buried, larval settlement may be hindered, filtering appendages of suspension feeders may become clogged by inorganic particles, and the tubes of tube-building organisms may be buried, impeding irrigation and leading to suffocation (e.g., Norkko et al. 2002, Włodarska Kowakczuk et al. 2005, Lohrer et al. 2006). In addition, the infauna may experience episodic catastrophic events such as iceberg scouring, sediment slides, and gravity flows (Włodarska-Kowalczuk et al. 2005). Inorganic sediment inputs and resulting low food

availability cause reduced biomass. abundance, and diversity in the benthic community in the inner fjord (Hop et al. 2002; Wlodarska-Kowalczuk et al. 2005). The inner fjord environment selects for



Figure 2. Composition of species throughout the fjord as they are affected by sedimentation and flux of phytoplankton-derived OM to the seafloor, including trends in biomass, species richness, species diversity, beta diversity, and faunal dispersion, as these factors are also affected by sedimentation. ENTR, CENTR, TRANS, and GLAC represent four sections of the fjord: entrance, center, transitional zone, and glacier zone respectively. Dominant animals include polychaetes (Chp: Chone paucibranchiata, Ch: Chaetozone group, Cl: Cossura longocirrata, Hf: Heteromastus filicornis, Ms: Maldanesarsi, Lt: Leitoscoloplos sp., Ts: Terebellides stroemi, Cp: Clymenura polaris, Go: Galathowenia oculata, Pr: Prionospio sp., St: Spiochaetopterus typicus), bivalves (Ys: Yoldiella solidula, Th: Thyasira dunbari, Yl: Yoldiella lenticula, Nt: Nuculoma tenuis), gastropods (Lc: Lepeta caeca), sipunculids (Sp: Sipunculida n. det.), and ophiuroids (Or: Ophiura robusta) (Wlodarska-Kowalczuk et al. 2005).

opportunistic mobile scavengers that feed on degraded detritus (Hop et al. 2002). Benthic biomass, diversity, and functional-group complexity (" functional groups" are a set of species performing a particular ecosystem function, such as surface-deposit feeding) increases away from the inner fjord toward the fjord mouth (Figure 2), where sedimentation rates decline, and labile organic-carbon becomes more available. The outer fjord has a comparatively higher diversity and biomass of benthic organisms than in the inner fjord. (Wlodarska-Kowalczuk et al. 2005, Syvitski et al. 1989, Holte & Gulliksen 1998). Thus, benthic organisms in inner-middle Arctic sub-polar glaciomarine fjords, which sustain high sedimentation rates, exhibit small body size, low diversity, and low abundance (Syvitsky et al. 1989, Włodarska-Kowakczuk et al. 2005, Renaud et al. 2007).

1.3 WAP FJORDS

While Arctic fjords have been extensively studied, sub-polar fjords along the Western Antarctic Peninsula (WAP) between 64-70° S are relatively well studied only from a geological perspective (e.g., Griffith & Anderson 1989, Domack & Ishman 1993, Powell & Domack 1995, Ashley & Smith 2000, Boldt et al. 2013). The WAP, including the Danco and Graham Coasts, harbors the most extensive system of glaciomarine fjords on the Antarctic continent (Grange and Smith 2013). Ecosystem structure and function of WAP fjords remain poorly evaluated, despite their potential to provide regionally important, climate-sensitive habitats along the Antarctic margin for important marine species, such as krill and humpback whales (e.g., Nowacek et al. 2011).

In contrast to Arctic fjord systems, meltwater processes appear to be weak in subpolar Antarctic fjords, resulting in low sedimentation rates (Powell and Domack 1995,

Domack and Ishman 1993, Boldt et al. 2013). Although inorganic sediments characterize the benthos near the glacier terminus of sub-polar WAP fjords, weak meltwater processes lead to a much smaller intensity and area of turbid sedimentation, allowing phytoplankton productivity to extend over a larger portion of the fjord than is the case in Arctic fjords (Powell and Domack 1995). Phytoplankton blooms in fjords along the western Antarctic Peninsula (WAP) have been observed to be sustained longer than on the open shelf, with blooms extending well into the fall season (Vernet et al, unpublished data). These sustained blooms may be a consequence of weak meltwater inflow, which adds nutrients and promotes stratification without creating high turbidity from glacial sediment loading (Grange and Smith 2013). Biogenic siliceous sediments are the dominant sediment type within the characteristically deep fjords along the WAP. WAP fjords are typically deep enough that icebergs are prevented from scouring biogenic accumulations and disturbing sea-floor sediment, allowing for diatomaceous sediments and phytodetritus to accumulate and dilute inorganic sediments (Powell and Domack 1995; Ziegler et al. in prep).

1.4 WAP FJORD BENTHIC ENVIRONMENT

Thus, contrary to observations in Arctic fjords, seafloor communities in WAP fjords may not be limited by turbidity and burial disturbance, and have the potential to foster highly abundant and diverse seafloor faunal communities (Grange and Smith 2013). Horizontal food subsidies from outside the fjord provide an additional POC flux to the seafloor in WAP fjords. Intense phytoplankton blooms attract aggregations of krill into fjords along the WAP (Nowacek et al. 2011, Espinasse et al. 2012). In turn, humpback whales follow the krill aggregations into the fjords to feed on them. In fact,

some of the largest aggregations of krill (e.g. 10-100 kg m-2 or ~104-106 individuals m-2) and feeding humpback whales in the Southern Ocean have been observed in WAP fjords (Nowacek et al. 2011, Grange and Smith 2013).

Therefore, in addition to phytoplankton-derived POC, other sources of POC to the seafloor in Antarctic fjords include sinking zooplankton carcasses and feces of zooplankton and whales (Grange and Smith 2013). The organic detritus sinking to the seafloor is a major energy source for benthic fauna, which are mainly scavengers and detritivores (Grange and Smith 2013). In turn, benthic fauna play an important role in mixing, sorting and binding sediment particles, and in determining the sedimentary geochemical environment (Powell and Domack 1995), acting as intermediaries between phytoplankton-supplied POC to the seafloor and either remineralization by sediment microbes and other benthic organsims, or burial of OC.

In low-current, fine sediment habitats similar to WAP fjord benthos, macro- and megabenthic abundance, biomass, and mean body size are frequently positively correlated with POC flux to the seafloor (e.g., Rex et al. 2006, C. Smith et al. 2006, 2008, Wei et al. 2010). Greater POC flux to the benthos means enhanced food availability and supplies a greater carrying capacity for benthic detritivores, allowing for greater community abundance and biomass (Rex et al. 2006, Wei et al. 2010). Andvord Bay (chosen as a representative WAP fjord in this study) has well oxygenated bottom waters (>4 ml/l), and inorganic sedimentation rates in the middle-outer basins appear too low (<0.2 cm y-1) to limit macrobenthic abundance, biomass, and body size through burial disturbance (cf. Wlodarska- Kowakczuk et al. 2005, Lohrer et al. 2006). Therefore, POC flux is expected to be the main driver of abundance, biomass, and body size in much of

the fjord.

Photosurveys from three fjords along the WAP have shown that the enhanced POC input to the benthos in WAP fjords is reflected in the extremely high abundance and diversity levels of benthic megafauna (animals larger than 2 cm in smallest dimension) compared to similar depths on the open Antarctic continental shelf. In addition, local species diversity and trophic complexity remains high from outer to inner fjord basins (Grange and Smith 2013). Patterns in WAP fjord megabenthic communities may be reflected in macrobenthic communities, i.e., animals between 300 µm and 2 cm in smallest dimension, but the macrobenthos of WAP fjords has not been studied.

Ecological theory suggests that biodiversity is reduced by high levels of disturbance when combined with low food availability and reduced habitat or trophic heterogeneity (e.g., Pearson and Rosenberg 1978, Huston 1979, Rosenzweig 1995, Levin et al. 2010). These predictions hold true for biodiversity patterns in Arctic sub-polar fjords. High rates of inorganic terrigenous sedimentation (>2 cm/y) cause intense burial disturbance, dilute available food, and create low habitat heterogeneity, causing low species diversity in the inner-middle regions of the fjords, increasing toward the fjord mouth (Syvitski et al. 1989, Włodarska-Kowakczuk et al. 2005, 2008, Renaud et al. 2007). On the other hand, ecological theory suggests that WAP fjords may sustain different biodiversity patterns due to different physical forcing. Sedimentation rates thus far measured in the middle basins of WAP fjords are moderate (e.g., 0.03-0.2 cm/yr in the middle of Andvord Bay) (Powell and Domack 1995, Boldt et al. 2013). However, ecological theory suggests that the elevated productivity and abundant food sources in the fjords are likely to offset the stress caused by this moderate sedimentation (Huston 1979,

Rosenzweig 1995). Furthermore, the middle-outer basins of WAP fjords contain high habitat heterogeneity due to the contrasting benthic environment of soft sediment and glacial dropstones, which enhances megafaunal species diversity (Ziegler et al. 2017). For these reasons, it is predicted in this study that benthic macrofaunal biodiversity will peak in the middle-outer fjord basins of Andvord Bay.

1.5 CLIMATE CHANGE

The WAP is one of the fastest warming regions on earth (Vaughan et al. 2003). Since 1950, winter air temperatures have risen by 6° C, sea-surface temperatures have risen by 1° C, and 87% of tidewater glaciers have retreated (Ducklow et al. 2007, Cook et al. 2005, Meredith and King 2005). As this warming continues, increased glacial meltwater input to WAP fjords is expected, increasing turbidity and burial disturbance to benthic communities of the fjord (Powell and Domack 1995, Grange and Smith 2013). Increased meltwater processes in WAP fjords, resulting in decreased detrital food availability and increased burial disturbance, is expected to shift benthic communities towards those of Arctic sub-polar fjords, characterized by low abundance and diversity. Therefore, evaluating the benthos in WAP fjords is important in understanding existing patterns of ecosystem structure, function, and biodiversity, and to be able to predict how sensitive these ecosystems will be to future climate change.



Figure 3. Map of study site Andvord Bay, Antarctica and the Graham and Danco Coasts of the Western Antarctic Peninsula. The sites sampled in this study were IBA, IBB, MBA, OBA, the Gerlache Strait (Gerl), and Station B.

1.6 CHARACTERIZATION OF MACROBENTHOS

This study characterizes the benthic macrofaunal community (animals collected on a 300 µm sieve) of Andvord Bay, a typical fjord along the WAP. Quantitative sediment core samples were taken at three sites 450-600 m deep in the fjord (the inner, middle, and outer basins), the Gerlache Strait outside of the fjord, and on the open WAP continental shelf (Figure 3). This study assesses the abundance of benthic invertebrates, polychaete family diversity, and functional diversity of benthic invertebrates in replicate samples collected along this transect from Andvord Bay and onto the adjacent shelf. By characterizing the benthic macrofauna community of along this transect, this study will address the following questions: 1. How does seafloor macrofaunal abundance and biodiversity at 450-600 m vary downfjord Andvord Bay (i.e. from inner fjord to the fjord mouth), and out onto the open continental shelf?

2. How are potentially important ecological drivers, particularly, sediment burial rate (a source of burial disturbance,) sediment organic-carbon and Chlorophyll-a concentrations (indicators of labile detritus availability), and sediment-community respiration (an indicator of detrital carbon flux to the seafloor), correlated with these macrofaunal patterns?

3. How well does the down-fjord burial-disturbance model for benthic macrofauna from subpolar Arctic fjords (Wlodarska-Kowalczuk et al. 2004, 2012) apply to Andvord Bay?

2.0 METHODS

2.1 MACROFAUNA SAMPLES

The sediment samples used for this study to obtain data on macrofauna communities were collected aboard the R/V Laurence M. Gould in November-December 2015 (austral spring). Three replicate 10-cm diameter core samples were collected during the 2015 cruise in the inner basin, middle basin, and outer basin of Andvord Bay, in the Gerlache Strait, and at Station B (Figure 3). The sediment was cored using an OSIL Megacorer, with 12 x 10-cm diameter cores (0.007854 m² in area). Locations for each lowering of the megacorer were selected at random within each study site (basin or station) and cores analyzed were taken from separate lowerings. Sediment cores for macrofauna were horizontally sectioned into 0-1 cm, 1-5 cm, and 5-10 cm layers and preserved in a 4% formaldehyde (10% formalin) solution buffered with sodium tetraborate decahydrate for storage. Samples were transferred to an 80% ethanol solution before sorting.

Standard techniques (Tagliapietra and Sigovini 2010, Smith and Kukert 1996, Bernardino et al. 2010) were used to sort through the sediment and save all macrofaunal animals retained on the 300 µm sieve. Meiofaunal taxa (e.g. copepoda, nematoda) found on the sieve were not included in this study. Polychaetes were visually identified to family level of classification and all other macrofaunal organisms to either class, order, or phylum level. Abundance counts of polychaeta and other macrofauna were taken by counting macrofaunal "heads" (e.g., prostomium for polychaetes). If the head was not included in a fragment of a macrofaunal individual, the fragment was not included in the

abundance count. Polychaetes and other macrofauna were then assigned to various functional groups to assess functional diversity based on Kukert and Smith (1992), Jumars et al. (2015), and Macdonald et al. (2010). Each functional group included motility, habitat, and trophic group.

2.2 ENVIRONMENTAL DATA

Data on potential drivers, including sediment Chl-a inventories, sedimentcommunity respiration, and sedimentation rates are available down-fjord from other investigators from a NSF-funded research project called FjordEco. Sediment Chl-a inventories of the top four centimeters of the sediment sampled from a separate core from each replicate megacore drop were used in this study due to the accuracy of measurements to this depth. Sediment community respiration was also calculated using a separate core from each replicate megacore drop. Sediment accumulation rates were calculated from ²¹⁰Pb cores taken during the austral fall in April 2016 aboard the R/V Nathaniel B. Palmer. Samples for sediment organic carbon and nitrogen analyses were obtained from a separate core from each replicate megacore drop. Each core was horizontally sectioned into 1 cm intervals and the samples frozen at -80° C. Sediment levels of each core chosen for this study were 0-1 cm, 1-2 cm, 3-4 cm, 5-6 cm, 7-8 cm, and 9-10 cm. The sediment samples were dried and acidified to remove carbonates prior to C and N analysis, which were completed at the University of Hawaii at Manoa's SOEST Laboratory for Analytical Biochemistry (S-LAB).

2.3 DATA ANALYSIS

Macrofauna abundances were divided by the area of each megacore tube (0.007854 m²) to obtain abundance per m²; however, statistical analyses conducted with abundances used the original abundance per tube. Polychaete families were used for biodiversity analyses. Richness was measured by counting the number of different polychaete families present in a sample. Pielou's evenness, Shannon diversity, and rarefaction analyses were conducted using the statistical program Primer-E v. 6. MultiDeimensional Scaling (MDS) of Bray-Curtis similarity through Primer-E was conducted to group sites by 50% similarity before conducting family accumulation analyses within site groups. Family accumulation analyses included polychaete families observed and richness estimators Chao1, Jacknife 1, and Bootstrap in Primer-E.

Analyses of variance (ANOVA) were conducted via Minitab for total abundance, polychaete richness, polychaete evenness, polychaete Shannon diversity, polychaete family rarefaction, percent deposit feeders, percent mobile taxa, percent omnivores, percent sessile taxa, percent suspension feeders, carbon content of the top 1 cm of sediments, and C:N ratios of the top 1 cm of sediments. Spearman correlation analyses were conducted via Minitab between total abundance, polychaete richness, polychaete evenness, and trophic groups with the data on environmental drivers: sediment carbon content. An alpha level of p=0.05 was used as the criterion for statistical significance for the ANOVA and correlation analyses.

3.1 ABUNDANCE

We found that the abundance of animals was low in IBA and IBB, but peaked at MBA, gradually decreasing again toward the open shelf (Figure 4). We found a significant difference in the average abundance between sites (ANOVA, F(5,17)=10.06, p=0.0006. The average abundance at sites MBA and OBA differed significantly from that of IBA (Tukey post-hoc test, p=0.0013, p=0.0268 respectively), and that of Station B (Tukey post-hoc test, p=0.0008, p=0.0157 respectively). Class Polychaeta was the dominant taxon at all the locations sampled, constituting an average of 76% of the total macrofaunal found at each site.



Figure 4. Average abundance (number of animals per m^2) at each site (n=3). Averages that do not share a letter are statistically different. Error bars are \pm S.E.

3.2 DIVERSITY

The average polychaete family richness (number of polychaete families) was highest at site OBA, and lowest at site IBA. Sites IBB, MBA, the Gerlache Strait, and Station B had similar values for polychaete family richness (Figure 5). Average richness differed significantly between the sites (ANOVA, F(5,17)=3.39, p=0.0386). Average polychaete family richness at site OBA was significantly higher than at site IBA (Tukey post-hoc test, p=0.0221); all other averages did not differ significantly. The average polychaete family Pielou evenness (J') was high at IBA, IBB and Station B, but was relatively lower at MBA, OBA, and the Gerlache Strait (Figure 5). An ANOVA showed that there was no significant difference between average polychaete family evenness across sites, F(5,17)=2.46. The average Shannon diversity (H') for polychaete families was high at IBB and Station B, and relatively lower at IBA, MBA, OBA, and the Gerlache Strait (Figure 6). There was no significant difference in Shannon diversity between the sites (ANOVA, F(5,17)=1.97).



Figure 5. Average Polychaete family richness (number of families) and average Polychaete family Pielou evenness (J', scaled by 20) at each site (n=3). Averages that share an asterisk (*) are statistically different. Error bars are \pm S.E.



Figure 6. Average Shannon diversity (H') at each site (n=3). Error bars are \pm S.E.

Polychaete family richness was strongly positively correlated with the total macrofauna higher taxa richness (rho(18)=0.84, p<0.001), which included polychaete families and all other taxa identified to class, order, or phylum level. Pielou evenness (J') and Shannon diversity (H') for polychaete families were also strongly positively correlated with evenness and Shannon diversity for the total macrofaunal higher taxa (rho(18)=0.96, p<0.001, and rho(18)=0.90, p<0.001 respectively). As previously mentioned, polychaetes dominated at each site. In addition, polychaete family identification was the lowest level of taxa classification of the macrofaunal sampled, providing the best resolution of taxa identification. For these reasons, rarefaction analysis, similarity analysis, species accumulation, and correlation analysis with environmental data (carbon respired, sediment accumulation, Chl-a inventories, sediment carbon and nitrogen content) will be performed using polychaete abundances and diversity measures.



Figure 7. Rarefaction, or the average expected number of polychaete families/core for an abundance of 53, at each site (n=3). Error bars are \pm S.E.

Rarefaction of polychaete families (estimated number of families per core) was conducted using the lowest abundance of polychaetes found in a sample, which was 53 polychaetes/core from Station B (Figure 7). The average estimated number of polychaete families was highest at OBA and lowest at IBA. Sites IBB, MBA, Gerlache Strait, and Station B had similar values for rarefaction. There was no significant difference in the expected number of families between sites (ANOVA, F(5,17)=2.29).

Cluster analysis of MultiDimensional Scaling (MDS) of Bray-Curtis similarity of samples using polychaete families indicated that samples from IBB, MBA, OBA, and the Gerlache Strait grouped at a 50% similarity, while IBA and Station B formed separate groups at this level (Figure 8). These 50% similarity groupings were used to combine stations in the species accumulation analysis (Figure 9). Because of the differences in sample size between these groupings, families observed, and richness estimators Chao 2, Jacknife 1, and Bootstrap are compared among groups at a sample size of 3. At n=3 samples for the IBB, MBA, OBA, and Gerlache Strait grouping, the families observed and the richness estimated by Bootstrap were less than the richness estimated by Chao 2 and Jacknife. The families observed, the richness estimated by Jacknife, and the richness estimated by Bootstrap for the IBA group were all much lower than the richness estimated by Chao 2, and were all generally lower than the richness estimators for the IBB, MBA, OBA, and Gerlache Strait grouping at n=3. For the Station B group, the families observed and the richness estimated by Bootstrap were slightly lower than the richness estimated by Chao 2 and Jacknife, and were all generally similar to the richness estimators for the first group (IBB to Gerlache Strait) at n=3. Because the Chao 2

estimates for all groups fell well within 2 S.E. of another, there appeared to be no significant differences in estimated family richness across the groups.



Figure 8. Cluster analysis of MultiDeimensional Scaling (MDS) of Bray-Curtis similarity between polychaete assemblages at each site, grouped by 20, 40, 50, and 60% similarity.



Figure 9. Family accumulation analyses results (polychaete family count vs number of samples) by groupings of 50% similarity (n=3). Error bars are \pm S.D.

3.3 FUNCTIONAL GROUPS

Eight functional groups were found among all animals collected: mobile epifaunal omnivores (mob/epi/omni), mobile infaunal omnivores (mob/inf/omni), mobile infaunal surface deposit feeders (mob/inf/sdf), mobile infaunal subsurface deposit feeders (mob/inf/ssdf), sessile epifaunal omnivores (sess/epi/omni), sessile infaunal omnivores (sess/inf/omni), sessile infaunal omnivores (sess/inf/sdf), and sessile infaunal suspension feeders (sess/inf/susp) (Figure 10). The top three dominant taxa at each site, with their corresponding functional group and average percent abundance are presented in Table 1. Average functional group "richness," i.e. the number of functional groups present, was lowest at IBA and increased gradually to the Gerlache Strait, where it peaked, then decreased slightly at Station B (Figure 11). The experiment-wise differences in functional group richness at IBA was significantly lower than at the Gerlache Strait (Tukey post-hoc test, p=0.004).



Figure 10. Average percent of each functional group at each site (n=3). Mob/epi/omni= mobile epifaunal omnivores, mob/inf/omni= mobile infaunal omnivores, mob/inf/sdf= mobile infaunal surface deposit feeders, mob/inf/ssdf= mobile infaunal subsurface deposit feeders, sess/epi/omni= sessile epifaunal omnivores, sess/inf/omni= sessile infaunal omnivores, sess/inf/sdf= sessile infaunal surface deposit feeders, and sess/inf/susp= sessile infaunal suspension feeders. **Table 1.** The average top three most abundant taxa by percent at each site and the corresponding functional group. Mob/epi/omni= mobile epifaunal omnivores, mob/inf/omni= mobile infaunal omnivores, mob/inf/ssdf= mobile infaunal subsurface deposit feeders, and sess/inf/sdf= sessile infaunal surface deposit feeders.

Site	Taxa	Functional group	% of total abundance
IBA	Cirratulidae	mob/inf/sdf	38.30
	Terebellidae	sess/inf/sdf	8.87
	Capitellidae	mob/inf/ssdf	7.11
IBB	Paraonidae	mob/inf/ssdf	23.49
	Cirratulidae	mob/inf/sdf	14.11
	Tanaidacea	mob/inf/omni	13.93
MBA	Cirratulidae	mob/inf/sdf	32.60
	Paraonidae	mob/inf/ssdf	19.22
	Tanaidacea	mob/inf/omni	1.63
OBA	Paraonidae	mob/inf/ssdf	44.27
	Cirratulidae	mob/inf/sdf	17.18
	Bivalvia	mob/inf/ssdf	7.06
Gerlache	Paraonidae	mob/inf/ssdf	33.94
	Cirratulidae	mob/inf/sdf	24.35
	Oligochaeta	mob/inf/ssdf	10.52
Station B	Spionidae	sess/inf/sdf	29.84
	Oligochaeta	mob/inf/ssdf	13.71
	Syllidae	mob/epi/omni	8.60

Figure 11. The average functional group richness (number of functional groups present per core) at each site (n=3), with S.E. bars. Sites with an asterisk (*) have averages that are significantly different.



The average proportion of mobile taxa peaked at MBA, corresponding with the lowest percent abundance of sessile taxa. MBA was followed by IBB, OBA, IBA, and the

Gerlache Strait. Station B had the lowest proportion of mobile taxa, corresponding with the highest proportion of sessile taxa. (Figure 12). There was a significant difference in the average proportion mobile taxa between sites (ANOVA, F(5,17)=10.17, p=0.0005). A post hoc Tukey test showed that the following differences in proportion of mobile taxa were significant: IBA greater than OBA (p=0.0442), IBA greater than Station B (p=0.0069), IBB greater than Station B (p=0.0083), MBA greater than OBA (p=0.0113), MBA greater than Gerlache Strait (p=0.0133), and MBA greater than Station B (p=0.0019). There was a significant difference in the proportion of sessile taxa between sites (ANOVA, F(5,17)=29.89, p<0.0001). The following differences in the proportion of sessile taxa were significant: IBA greater than IBB, MBA, and OBA (Tukey post-hoc test, p=0.0336, p=0.0135, p=0.0208 respectively); Station B greater than IBA, IBB, MBA, OBA, and Gerlache Strait (Tukey post-hoc test, p=0.0008, p<0.0001, p<0.0001, p<0.0001, p<0.0001 respectively).



Figure 12. Average percent of each type of motility (mobile or sessile) at each site (n=3).

Deposit feeders were abundant at IBA, with few omnivores, while deposit feeders and omnivores were similar in abundance at IBB. The proportion of deposit feeders remain high through the fjord from MBA to Station B, corresponding with a low proportion of omnivores. There were very few to no suspension feeders in the fjord, increasing from the Gerlache Strait to Station B (Figure 13). There was a significant difference in the proportion of deposit feeders between sites (ANOVA, F(5,17)=3.98, p=0.023). IBB had a significantly lower proportion of deposit feeders than OBA and the Gerlache Strait (Tukey post-hoc test, p=0.025, p=0.033 respectively). In addition, there was a significant difference in the proportion of omnivores between sites (ANOVA, F(5,17)=5.49, p=0.007). There was found to be a significantly greater proportion of omnivores at IBB than OBA, Gerlache, and Station B (Tukey post-hoc test, p=0.015, p=0.008, p=0.044 respectively). Lastly, there was no statistical significance in the proportion of suspension feeders at each site (ANOVA, F(5,17)=2.77).



Figure 13. Average percent of each trophic group (deposit feeders, omnivores, suspension feeders) at each site (n=3).

3.4 ECOLOGICAL DRIVERS

Data on carbon respired (g-C m⁻²y⁻¹) was received as averages from each site sampled. IBA was not sampled due difficulty in coring at this site. This is also the case for sediment accumulation, Chl-a inventories, and sediment carbon and nitrogen content. Therefore, IBA was not included in these analyses. At IBB the carbon respired was $17.3\pm2.0 \text{ g-C m}^{-2}\text{y}^{-1}$, at MBA it was $16.8\pm2.0 \text{ g-C m}^{-2}\text{y}^{-1}$, at OBA it was $13.4\pm1.2 \text{ g-C m}^{-2}\text{y}^{-1}$, at the Gerlache Strait it was $16.0\pm2.5 \text{ g-C m}^{-2}\text{y}^{-1}$, and at Station B it was $6.7\pm0.5 \text{ g-C}$ $\text{m}^{-2}\text{y}^{-1}$. Spearman correlations conducted between average carbon respired and average total macrofaunal abundance (rho(5)=0.3, p=0.6238), average carbon respired and average polychaete evenness (rho(5)=0, p=1), carbon respired and average polychaete richness (rho(5)=0.3, p=0.6238) were not significant.

Sediment accumulation rates were calculated from ²¹⁰Pb cores, which included two cores from IBB, and one core from MBA and OBA each. The sediment accumulation rate for Station B was obtained from Minks et al. 2005, and the Gerlache Strait was not sampled. The sediment accumulation rate at IBB was 2.65 ± 1.55 mm y⁻¹, 6.1 mm y⁻¹ at MBA, 2.4 mm y⁻¹ at OBA, and 0.3 mm y⁻¹ at Station B. Spearman correlations between sediment accumulation rate and total abundance (rho(4)=0.8, p=0.2), sediment accumulation rate and average polychaete family evenness (rho(4)=-0.4, p=0.6), and sediment accumulation rate and average polychaete family richness (rho(4)=0.4, p=0.6) were not significant. In addition, a Spearman correlation between sediment accumulation and average percent deposit feeders (rho(4)=-0.6, p=0.4) was also not significant.

However, a positive Spearman correlation between sediment accumulation rate and average percent mobile taxa was significant (rho(4)=1, p<0.0001) (Figure 14).



Figure 14. The average percent mobile taxa vs sediment accumulation rate $(mm y^{-1})$, plotted with line of best fit.

Average sediment chl-a inventory of the top 4 cm of sediment sampled was $9.34\pm0.82 \ \mu g \ cm^{-2}$ at IBB, $9.98\pm0.44 \ \mu g \ cm^{-2}$ at MBA, $14.75\pm2.72 \ \mu g \ cm^{-2}$ at OBA, $7.95\pm3.13 \ \mu g \ cm^{-2}$ at Gerlache Strait, and $1.24 \ \mu g \ cm^{-2}$ at Station B. Spearman correlations between average chl-a inventories and average total macrofauna abundance (rho(5)=0.8, p=0.2), average chl-a inventories and average polychaete family evenness (rho(5)=-0.7, p=0.1881), and average chl-a inventories and carbon respired (rho(5)=0.3, p=0.6238) were found not significant. However, a positive Spearman correlation between the average chl-a inventories and average polychaete family richness was found to be significant (rho(5)=1, p<0.0001, Figure 15).



Figure 15. Average polychaete family richness (number of families per core) vs average chl-a inventory of the top 4 cm of sediment sampled (μ g cm⁻²), plotted with line of best fit.

Average sediment organic carbon content of the top 1 cm of sediment sampled was lowest at IBB, followed by MBA. Average sediment organic carbon content peaked at OBA, and declined slightly at the Gerlache Strait and Station B (Figure 16). The difference in average carbon content between sites was significant (ANOVA, F(4,14)=81.81, p<0.0001). IBB was significantly lower than MBA, OBA, Gerlache Strait, and Station B (Tukey post-hoc test, p=0.009, p<0.0001, p<0.0001, p<0.0001 respectively), and MBA was significantly lower than OBA, Gerlache Strait, and Station B (p<0.0001, p<0.0001, p=0.0001 respectively). Spearman correlations conducted between carbon content of the top 1 cm of sediment and total macrofaunal abundance (rho(5)=0.006, p=0.8199), and carbon content and polychaete richness (rho(5)=0.27, p=0.323) were not found statistically significant. However, there was a significant negative Spearman correlation between carbon content and polychaete evenness (rho(5)=-0.514, p=0.0498, Figure 17).



Figure 16. Average sediment carbon content (% weight) of the top 1 cm of sediment sampled at each site. Averages that do not share a letter are significantly different (n=3). Error bars are \pm S.E.



Figure 17. Pielou evenness for polychaete families (J') vs sediment organic carbon content (% weight), plotted with line of best fit.

The average C:N ratio of the top 1 cm of sediment sampled was 6.98±0.28 at site IBB, 6.92±0.16 at site MBA, 7.01±0.09 at OBA, 6.94±0.04 at the Gerlache Strait, and

 6.96 ± 0.24 at Station B. There was no significant statistical difference in these values (ANOVA, F(4,14)=0.03). Carbon profiles of the top 10 cm of sediment (Figure 18) showed that carbon content (% weight) of sediments at IBB, MBA, and Gerlache Strait generally increased with depth, while carbon content of sediments at OBA and Station B generally decreased with depth.



Figure 18. Carbon content (% weight) of the top 10 cm of sediment sampled at each site (n=3). Error bars are \pm S.E.

4.0 DISCUSSION

4.1 ABUNDANCE

The clear trend in total abundance of macrofauna, low in the inner fjords, peaking at the middle basin and decreasing toward the open shelf, is what would be expected for the degree of glacial melting experienced around the fjord and for the potentially high flux of POM to the seafloor in the fjord. Low abundance of macrofauna in the two inner fjord basins could be explained by limitation due to sediment burial disturbance, which is typical of fjords surrounded that are rapidly melting glaciers (Wlodarska-Kowalczuk et al. 2005). In addition, if sediment accumulation is high, as in some sub-polar Arctic fjords, and decreases with increased distance from the glacier, macrofauna abundance would be predicted to increase with the decrease in sediment disturbance (Wlodarska-Kowalczuk et al. 2005). At moderate to low disturbance rates, however, other factors, such as food availability are likely to be more important drivers of abundance.

In Andvord Bay it was found that abundance peaked in the middle of the fjord and decreased substantially toward the open shelf. Additionally, the sediment accumulation rate at MBA (6.1 mm y^{-1}) was higher than the average sediment

accumulation rate at IBB (2.65±1.55 mm y⁻¹). It should be noted that although the sediment accumulation rate in IBB was relatively less than at MBA, IBB experiences episodic sedimentation events due to its proximity to tidewater glaciers. These catastrophic events may have a greater impact on the growth of the benthic community at IBB than steady sediment accumulation likely experienced at MBA.

Mobile taxa dominated the fjord and Gerlache Strait, peaking at the MBA site, which is a pattern that indicates that the macrofaunal communities of fjord, and possibly even the Gerlache Strait, are affected, in some degree, by sediment disturbance. Areas of sediment disturbance are often dominated by mobile taxa, which can avoid or recover from burial disturbances. The positive correlation that was found between percent mobile taxa and sediment accumulation rate throughout the fjord provides further evidence of that the fjord benthos are responding to sediment disturbance. Site IBB has the lowest average percent of deposit feeders of all sites sampled. Because areas of high sediment accumulation rates often dilute sinking POM with inorganic sediments, deposit feeders are less common in these areas of fjords. The lack of significant correlation between sediment accumulation and percent deposit feeders indicates that this dilution effect is not strong enough throughout the entire fjord to influence the abundance of these types of animals. Although not statistically significant, the increase in suspension feeders from the fjord to open shelf at Station B is notable because it is indicative of a reduced disturbance from burial or turbidity.

It is possible that large horizontal food subsidies from outside the fjord promote the large abundances observed in the benthos. Large populations of krill aggregate into WAP fjords seasonally, which are pursued by humpback whales into the fjord. Sinking

detritus from phytoplankton blooms, macroalgae, krill carcasses, and whale feces have the potential to provide copious amounts of food to the seafloor (Nowacek et al. 2011, Espinasse et al. 2012, Grange and Smith 2013). After the productive summer season in Andvord Bay, flux of phytodetritus in the inner and middle fjord areas is the greatest (Vernet et al. unpub. data).

We predict that sediment disturbance and episodic burial events in the inner bay is strong enough to reduce the abundance of macrofauna, which is why there would be low benthic abundance in an area with a potentially high flux of POM. We predict that sediment disturbance from the middle basin to the shelf is not strong enough to reduce the abundance of macrofauna. Outside of the inner fjord region, food availability likely drives the pattern in abundance down-fjord. The large abundance of macrofauna at MBA is supported by large food inputs. As the flux of food inputs decreases from the middle fjord to the open shelf, the abundance of macrofauna at each site also decreases. Station B, which is on the open shelf, had the lowest average abundance of macrofauna. If food availability is one of the main drivers of abundance on the benthos, this observation would be expected because the open shelf is likely food limited, as primary production and export flux do not appear to be as high as in the fjord.

Despite these predictions, indicators of food availability, respiration, chl-a inventories, and sediment organic carbon content of the top 1 cm of sediments, did not correlate significantly with total abundance. Data for this study was retrieved during the austral spring (November-December), after the austral winter when much of the fjord can be covered in sea ice (Powell and Domack 1995) and the benthos are mostly supported by detritus that accumulated during the productive summer season, when sea ice is at a

minimum. Thus, the benthos may be more food limited as they enter the austral spring, which may provide an explanation for lack of food availability-abundance relationship. The greatest discord between food availability and abundance is observed at MBA, which has the largest abundance of animals in the fjord, yet had one of the lowest measured sediment carbon contents of the fjord, after IBB. It is possible that POM might also be diluted by inorganic sediments, as is likely at IBB, but this area would not be able to support such a large abundance of organisms if available food was substantially diluted. Therefore, it is possible that much of the sediment organic carbon in MBA has been consumed by the abundant benthic community during the austral winter. Furthermore, the flux to food to the seafloor may be represented in the carbon profiles at each site (Figure 18). Sediment carbon content at IBB, MBA, and the Gerlache Strait generally increase with depth. This implies that carbon is buried before it can be completely utilized by the benthos, and with large benthic abundances at these sites, food is likely to be in excess. On the other hand, sediment carbon content of OBA and Station B generally decrease with depth, implying that carbon is mostly consumed before it can be buried. This is especially notable for Station B, which is likely food-limited, indicated by the lowest abundance of macrofauna of all sites sampled. Future studies of benthic macrofaunal communities in WAP fjords should also study indicators of food availability during the fall, after the productive season in the water column above, to better understand how the macrobenthos respond to food availability.

4.2 DIVERSITY

This study found that polychaete family richness was the greatest where evenness was the lowest, such as at MBA and OBA. In addition, sites with the greatest abundance (MBA, OBA, and Gerlache Strait), had the lowest Shannon diversity. In contrast, at IBB, evenness and Shannon diversity were relatively high. Because IBB is likely more influenced by sediment accumulation, greater diversity observed at IBB might be promoted by intermediate levels of sediment disturbance. The abundant MBA, OBA, and Gerlache Strait sites may not experience enough sediment disturbance to promote a greater frequency of opportunistic taxa, resulting in relatively low diversity values.

The lack of significant correlations found between sedimentation rate and polychaete richness or evenness provides further evidence that most sites in the fjord and on the shelf do not experience intermediate sediment disturbance to stress the benthic community. Relatively high richness and low evenness from the middle basin to the Gerlache Strait may indicate a large flux of food to the benthos in this region. A large flux of food can support many different taxa, especially those differing in feeding strategies, thereby supporting a larger richness. This is supported by the strong correlation between average chl-a inventories, an indicator of food availability, and average polychaete richness. However, without a great enough disturbance to keep dominant competitors at bay, robust taxa dominate and outcompete others, reducing evenness. This can be observed in Table 1, which shows several of the same dominant taxa throughout the fjord, including polychaete families Cirratulidae and Paraonidae.

Site IBA seems not to be influenced by the same sediment disturbance regime as site IBB. The polychaete communities at IBA and IBB were separated at 50% similarity

(Figure 8). IBA was found to have much lower polychaete family richness than IBB, while evenness was similar between the two, resulting in a lower Shannon diversity at IBA. In addition, IBA had the lowest amount of functional groups, or functional group richness. Unfortunately, much of the data on the ecological drivers studied could not be obtained, but the reason was that coring was not possible in this area because the inorganic sedimentation made the sediment not soft enough to core. Thus, IBA might experience more sediment disturbance than IBB, signified by a lower abundance. This sediment disturbance may be strong enough to have a significant effect on diversity, as IBA had the lowest polychaete familiy richness and lowest functional group richness. Future studies of Andvord Bay should try to obtain data on ecological drivers for elucidation of environmental drivers of the benthic community of IBA.

Relationships between measures of diversity and environmental drivers should be further investigated using species identifications for polychaetes instead of family identifications. Polychaete families are cosmopolitan and may provide too low resolution to observe significant patterns in diversity and community similarity. In addition, as this study is one of the first conducted in Andvord Bay, data on environmental drivers is modest, resulting in low statistical power to determine relationships and significant trends. Future in-depth studies of environmental drivers, such as indicators of food availability to the benthos and sediment accumulation, should be utilized in addition to assessing polychaete species diversity.

4.3 CLIMATE CHANGE

As global temperatures are predicted to rise in the coming years, glaciers surrounding WAP fjords will experience greater melting. With increased meltwater

inputs, and consequently greater sediment accumulation rates in the fjord, it is expected that benthic communities will experience greater stress from sediment burial than they are currently. At first, this may be expressed by decreased abundance and diversity in the inner fjord region, which likely experiences stress from intermediate sediment disturbance currently. Benthic diversity of MBA and OBA may begin to increase, now subject to intermediate sediment disturbance. As glacial melt continues, the benthic environment of WAP fjords will start to resemble that of present-day Arctic fjords. Heavy sedimentation will reduce abundance and diversity of the inner-middle fjord regions. Primary production of the inner-middle fjord regions may be reduced by turbidity and POM flux to the seafloor may be further reduced by dilution from inorganic sediments. Abundance and diversity will increase toward the outer fjord and onto the adjacent continental shelf (Wlodarka-Kowalczuk et al. 2005).

5.0 CONCLUSION

At this time, sediment accumulation rates in Andvord Bay, Antarctica are likely too low to substantially stress benthic communities in the fjord, except for site IBB, which shows signs of intermediate sediment disturbance. Greater abundances and high polychaete familiy richness was recorded near the middle and outer fjord; however, polychaete family evenness was low. The benthos in these regions likely receive large fluxes of food, supporting the abundant and rich communities. Without stress from sediment disturbance in these areas, strong competitors may dominate, reducing evenness. Station B on the open shelf is likely food-limited due to low concentrations of sinking POM that can only support a small benthic community. As warming of global temperatures continue, middle fjord communities of WAP fjords may experience an increase in diversity briefly as they are stressed by intermediate sediment disturbance, similar to IBB currently. However, further glacial melt and sedimentation will shift these fjords to resemble present-day Arctic sub-polar fjords, characterized by low abundance and diversity, increasing away from the sediment disturbance toward the outer fjord and onto the adjacent continental shelf. Future studies should analyze polychaete species diversity rather than polychaete family diversity, and should obtain a more robust dataset

on environmental drivers to better understand the relationship between these drivers and benthic communities in the fjord.

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